Paoliida, a putative stem-group of winged insects: Morphology of new taxa from the Upper Carboniferous of Poland

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New representatives of a stem group Paoliida attributed to family Paoliidae (Insecta: Protoptera) are described from the Upper Carboniferous (Langsettian) sphero-sideritic concretions of the Upper Silesian Coal Basin (USCB) in Poland. *Zdenekia silesiensis* sp. nov. is based on forewing venation and supplemented by material of isolated hindwing similar in venation pattern. *Darekia sanguinea* gen. et sp. nov. differs from all other paoliid genera by the presence of a short contact between veins MP and CuA behind the division CuA and CuP. Composition of insect fauna exhibits high abundance of paoliid insects in the early Late Carboniferous ecosystems known also from other European localities such as Hagen Vorhalle in Ruhr Basin (Germany), and South Limbourg (Belgium and the Netherlands). It is the first record of true paoliids from the Polish part of paralic USCB supplementing a single historical record of *Stygne roemeri* considered as a taxon closely related to Paoliidae. The high abundance of paoliid insects from sphero-sideritic concretions in Sosnowiec and coal deposits previously known from the Czech part of Upper Silesian Coal Basin indicates considerable similarity of both faunas supported as well by their close stratigraphical correlation. Morphology of basal wing parts with remnants of articular sclerites preserved supports neopteran relationships of paoliids. Discovery of the first paoliid immature wing is reported suggesting similar living habitat for larvae and adults.

Key words: Insecta, Neoptera, Protoptera, Paoliidae, wing articulation, Langsettian, Upper Silesian Coal Basin, Poland.

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Introduction

The oldest known pterygotes (winged insects) based on unambiguous fossils are known from the Early–Late Carboniferous (Namurian) boundary interval (Brauckmann et al. 1996; Prokop et al. 2005). One of their first fossils remnants (large wing described as *Stygne roemeri* Handlirsch, 1906; Handlirsch 1906–1908; Schwartzbach 1939) were reported from Namurian B of Upper Silesian Coal Basin (USCB), Alfred coal mine (Chorzów, Poland) (Roemer 1883). According to Kukalová (1958a), this species probably belonged to Paoliidae. Unfortunately, this cannot be confirmed as the material housed at the Wrocław University was lost during the Second World War. Krawczyński et al. (1997, 2001) provided preliminary reports on entomofauna from Sosnowiec and reported e.g., *Idoptilus onisciformis* Wootton, 1972, *Rochdalia parkeri* (Woodward, 1911), both taxa currently considered as immature stages of Palaeodictyoptera (Rolfe 1967; Wootton 1972), and *Zdenekia* sp. Kukalová, 1958 which belongs to the Paoliidae.

The majority of Carboniferous insects from USCB were found in Karviná Formation (lower and upper part of Suchá Beds Member, see Fig. 1B) of Westphalian A (Langsettian) age, described by Kukalová (1958a, b, 1959, 1960), Prokop and Nel (2007), and Pruvost (1933). The following insect groups are represented: Palaeodictyoptera, Paoliida, and “Protorthoptera”. In addition Prokop et al. (2005) discovered a single specimen from the drilling core in the basal part of the Ostrava Formation (Petřkovice Beds Member) of the early Namurian A age attributed to Archaeorthoptera that should be considered as the oldest reliable evidence of winged insects (Pterygota).

Newly excavated insect fauna consisting of more than 230 specimens was discovered from a dump of “Porąbka-Klimontów” coal mine in Sosnowiec (Silesia, Poland). A preliminary survey indicates that paoliids are the dominant group of insects recovered from this locality. The corresponding material is mostly composed of small fragments difficult to assign at the generic level. The second rather well represented group contains various immature stages of insects mostly attributable to Palaeodictyoptera followed by sparsely recorded other groups like Archaeognatha, Palaeodictyoptera, Grylloblattida and remaining “Protorthoptera”.

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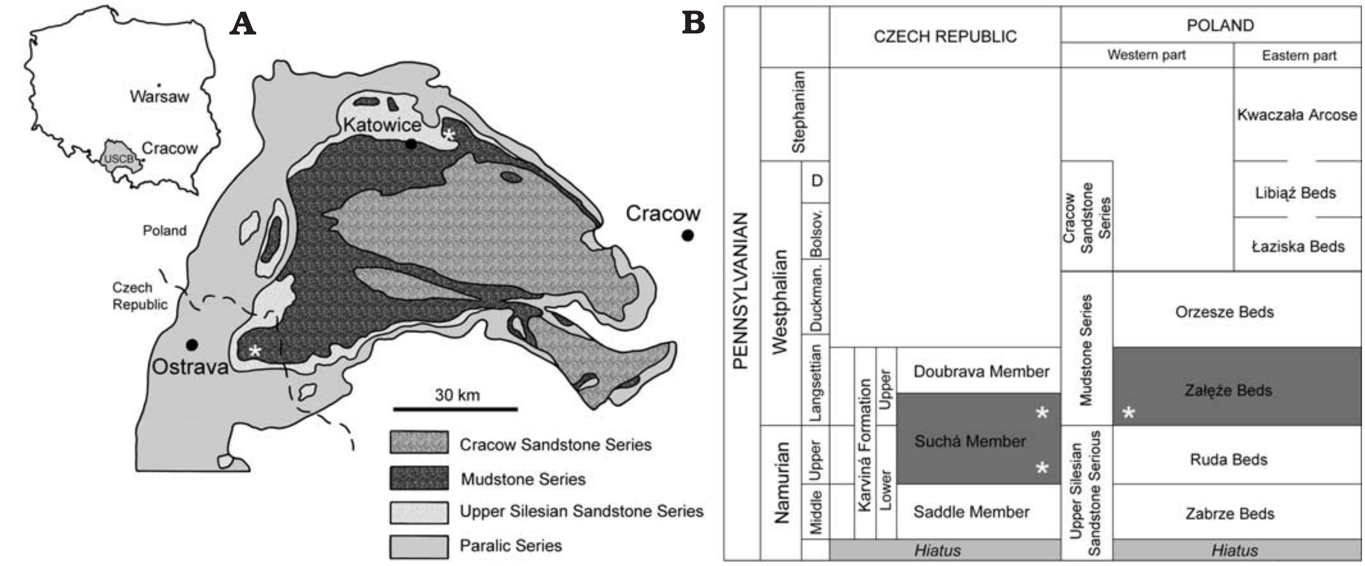


Fig. 1. **A**. Geographical situation and geological map of the Upper Silesian Coal Basin with position of insect localities: Horní Suchá (Czech Republic) and Sosnowiec (Poland) indicated by white asterisks (modified after Jureczka et al. 1995). **B**. Lithostratigraphic division of Pennsylvanian strata of Czech and Polish parts of the Upper Silesian Coal Basin after Dopita et al. (1997) with corresponding stratigraphical levels of both localities indicated by white asterisks. Abbreviations: Bolsov., Bolsovian; Duckman., Duckmantian.

Other groups of arthropods like syncarid crustaceans, malacostracans, xiphosurans, arachnids, scorpions, and myriapods as well as bivalves, gastropods and vertebrates are also recorded (Filipiak and Krawczyński 1996; Krawczyński et al. 1997; Stworzewicz et al. 2009). This composition is similar to that of faunas from the Czech part of USCB, and Hagen Vorhalle (Ruhr Basin; Germany; Brauckmann et al. 2003).

The present contribution is the first part of a series on systematic description of new entomofauna from Langsettian locality in Sosnowiec (USCB) pointing out its taxonomical significance in comparison to other particularly Euroamerican faunas, and supplementing early history of winged insect communities.

Institutional abbreviation.—MP ISEA, Natural History Museum of the Institute of Systematics and Evolution of Animals, Polish Academy of Science, Kraków, Poland.

Other abbreviations.—USCB, Upper Silesian Coal Basin. The venational symbols used here specified as follows (capitals denote the longitudinal veins): AA/AP, analis anterior/posterior; C, costa; CuA/CuP, cubitus anterior/posterior; MP, media posterior; RA/RP, radius anterior/posterior; ScP, subcosta posterior. The basal articulation of wings follows: BAA/BAP, anal anterior/posterior basivenale; BM, medial basivenale, FM, medial fulcalare.

Geological setting and taphonomy

The Upper Silesian Coal Basin (USCB) is a triangular sedimentary structure situated mainly in the Silesian part of Poland and partly in the NE of Moravia (Czech Republic) (see Dopita et al. 1997; Fig. 1A). From a palaeogeographical point of view, it is similar to the coal basins of the European Variscides, forming a belt stretching from the British Isles through Belgium to northern Germany and Poland. The USCB was formed as a top molasse stage of the polytypic foreland basin (Dopita et al. 1997). The basin is filled with the Lower and Upper Carboniferous continental and marine sediments divided into three main lithostratigraphical units (Hradecko-Kyjovické Formation, Ostrava Formation, Karviná Formation) in the Czech part and equivalents in Polish part (Malinowice Beds, Paralic Series, Upper Silesian Sandstone Series, Mudstone Series, Cracow Sandstone Series) (see a section of Pennsylvanian lithostratigraphic division on Fig. 1B). Zoopaleontological and phytopalaeontological records from Czech part were extensively reviewed by Dopita et al. (1997), Řehoř and Řehořová (1972), and Šusta (1928). Terrestrial and freshwater fauna from the Polish part of USCB were summarized by Krawczyński et al. (1997), Hannibal and Krzemiński (2005) and later supplemented by Stworzewicz et al. (2009). The palaeogeographical position of USCB and other foreland basins along the Variscan fold belt presumed hot and humid climatic equatorial conditions (see Opluštil and Cleal 2007).

The fossils studied are preserved in sphero-sideritic concretions deposited by exploitation during 1980s on spoil-heaps in Sosnowiec-Klimontów (50°17'N, 19°07'E). This material comes originally from the Porąbka-Klimontów coal mine, about one kilometer from the temporary locality (Fig. 1A). Lithostratigraphically the nodules belong to the Mudstone Series (lower part of the Załęże beds) of the Upper Carboniferous (Westphalian A/Langsettian) strata according to the data from macropalaeobotany and palynology (Krawczyński et al. 1997; Pacyna 2003) (Fig. 1B). The preservation in sideritic nodules allows morphological details and 3-D structures of animal bodies to be studied. It is a great advantage of this material especially useful for comparative morphology as certain body structures like insect wings are preserved with tiny structural details also visible on immature specimens.

Nodules include rich terrestrial and freshwater fauna such as mollusks (Stworzewicz et al. 2009), crustaceans, arachnids (Krawczyński et al. 1997), and common plant remains (e.g., *Calamites*, *Sigillaria*, and *Lepidostrobus*; Pacyna and Zdebska 2002). Taphonomy with a unique state of preservation in syngenetic sideritic concretions is best comparable to the fossils from Mazon Creek Lagerstätte (Illinois, USA) (e.g., Baird et al. 1985, 1986), the British Coal Measures (UK) (e.g., Prokop et al. 2006), and the basin of Montceau-les-Mines (France) (e.g., Vannier et al. 2003; Béthoux and Nel 2010).

Material and methods

All material included here is housed in MP ISEA. The fossil specimens were observed under a stereomicroscope Leica MZ16, MZ75 and Zeiss Cytoplast in dry state and some selected also under a film layer of ethyl alcohol. The venation patterns were drawn directly using a stereomicroscope with a camera lucida or alternatively, drawings of large specimens were redrawn from enlarged color photographs and revised by direct observation under stereomicroscope. Drawings were finally readjusted with the photographs scale using of computer graphic software (Adobe Photoshop CS). Photographs were made from dry specimens by means of digital camera Nikon D80 equipped with a macro lens Nikon AF-S VR Micro-Nikkor 105 mm in high contrast by single sided cross-light pre-exposure. Specimens were prepared by WK and DW with vibrating needle.

The wing venation nomenclature follows that of Kukalová-Peck (1991) and Kukalová-Peck and Brauckmann (1992). Systematics and divisions follow the conceptions of Carpenter (1992), partially Kukalová-Peck and Brauckmann (1992), and recently updated by Prokop and Nel (2007).

Systematic paleontology

Infraclass Neoptera Martynov, 1923

Order Paoliida Handlirsch, 1906

Family Paoliidae Handlirsch, 1906

Type genus: *Paolia* Smith, 1871.

Composition.—Genera included by Carpenter (1992) supplemented by Brauckmann (1984) and reviewed by Rasnitsyn (2002b) and Prokop and Nel (2007): *Holasicia* Kukalová, 1958; *Kemperala* Brauckmann, 1984; *Mertovia* Prokop and Nel, 2007, *Olinka* Kukalová, 1958; *Paolia* Smith, 1871; *Paoliola* Handlirsch, 1919; *Pseudofouquea* Handlirsch, 1906; *Sustaia* Kukalová, 1958; *Zdenekia* Kukalová, 1958 (a list of species is provided in the Appendix 1).

Comments.—The order Paoliida Handlirsch, 1906 (= Protoptera Sharov, 1966) is a small group of pterygote insects comprising ten genera and twelve species. Paoliids are known only from the continents belonging to former Laurussia (North America, East USA; Europe, Belgium, Czech Republic, England, Germany, the Netherlands, Wales), and from a relatively short period in the early Upper Carboniferous (Namurian B to Westphalian A [= Langsettian]).

The possible affinities of paoliid insects have been widely discussed. The family Paoliidae was created by Handlirsch (1906), who attributed this taxon to Palaedictyoptera (an extinct palaeopteran order) and proposed close relationships with spilapterids. Originally two species, *Paolia vetusta* Smith, 1871 and *Paoliola gurleyi* (Scudder, 1885) were included on the basis of rich branching of cubital and anal veins forming a network along the posterior wing margin (Handlirsch 1906). Before that the first mentioned species was placed amongst protolocustids (i.e., stem-Caelifera) by Brongniart (1883), only to be somewhat later transferred by Scudder (1885) to protophasmids (i.e., stem-Phasmatodea) together with *Paolia gurleyi*. The latter species was illustrated for the first time by Melander (1903).

Carpenter (1954) re-assigned paoliids together with the oldest pterygotes (*Ampeliptera* Pruvost, 1927 and *Stygne* Handlirsch, 1906) to the Palaeodictyoptera. At a later stage Kukalová (1958a), in her extensive work on fossil insects from the Upper Silesian Coal Basin in Czech Republic included this family in the order "Protorthoptera" (Cacurgoidea), currently considered as paraphyletic group (e.g., Béthoux and Nel 2005). Sharov (1962) first considered Paoliidae to fall into "Paraplecoptera" (currently treated as stem group of Grylloblattodea) and later transferred them in the infraclass "Archaeoptera", acknowledged by him as a basal stem group of Pterygota (Sharov 1966: 115). He noticed the position of wing in imago of Paoliidae directed backwards at certain angle to the body at the rest, a position similar to many Palaeozoic larvae and, according to him, distinguishing this group from the Neoptera. Sharov (1966) also reviewed other characters in comparison to Neoptera, such as absence of any folds along cubital and anal veins. A new order Protoptera was created by him on the basis of fore and hind wings being homonomous, the absence of an anal fan and a specific position of the wings at the rest. Furthermore, Sharov (1966) noticed in the Paoliidae also an archedictyon (= dense pattern of reticulated crossveins), widely considered as a plesiomorphic character. He believed that the group might have given rise to the whole clade of winged insects (Pterygota), including Palaeoptera and Neoptera. Carpenter (1992: 100) considered the Paoliidae, together with Homoeodictyidae and Thoronysididae, as the most basal Protorthoptera, all having reticulate venation as well as concave MP in forewings. Further rearrangement into "hemipteroid lineage" was done by Kukalová-Peck and Brauckmann (1992) on the basis of the presence of an "arculus" between veins MP and CuA and accompanied by a simple CuP (or only terminal twigging), a deeply incised claval fold with tendency to form anal loops, and a pointed anal lobe as occurs in modern hemipteroids. Kukalová-Peck and Brauckmann (1992) proposed to include into paoliid line the following families: Paoliidae, Eucaenidae, Strephocladidae, Blattinopsidae, Synomaloptilidae, Cymbopsidae, and unassigned taxa: *Limburgina antigua* Laurentiaux, 1950 (assigned to Protorthoptera incertae sedis by Béthoux and Nel, 2002) and *Heterologopsis ruhrensis* Brauckmann and Koch, 1982 (later transferred in Archaeorthoptera sensu Béthoux and Nel, 2002). Haas and Kukalová (2001) considered hindwings of Paoliidae to represent the ancestral hemipteroids. Finally Rasnitsyn (1976, 2002a: fig. 1) postulated that paoliids are a basal stem group of the Pterygote lineage as was previously proposed by Sharov (1966), but without denoting any distinct synapomorphies.

Genus *Zdenekia* Kukalová, 1958

Type species: *Zdenekia grandis* Kukalová, 1958; Karviná Formation, Suchá Beds (Member), Langsettian, Upper Carboniferous, Czech Republic.

Zdenekia silesiensis sp. nov.

Figs. 2A–C, 3A–C, 4A.

2001 *Zdenekia* sp. (Protorthoptera): Krawczyński et al. 2001: 27, fig. 3.

Etymology: Named after Silesia, a historical region of Central Europe (in the Czech Republic and Poland) where the outcrop is located.

Type material: Holotype: specimen MP ISEA I-F/MP/1488/2a/08 (imprint) and MP ISEA I-F/MP/1488/2b/08 (counter-imprint) of the medial four-fifths of a well preserved fore wing in sphero-sideritic concretion. Paratype: specimen MP ISEA I-F/MP/1540/25/09 (counter-imprint) of the medial three-fourths of a well preserved fore wing in sphero-sideritic concretion.

Type locality: Sosnowiec-Klimontów, originally Porąbka-Klimontów Mine, Upper Silesian Coal Basin, Poland. All specimens listed below come from the type locality.

Type horizon: Załęże beds, Mudstone series, Langsettian, Westphalian A, Upper Carboniferous.

Referred material.—Fore wings are fragmentary and represent medial or basal portions of wings. Medial portions: MP ISEA I-F/MP/1492/338ab/09 (imprint and counter-imprint) and MP ISEA I-F/MP/1488/7ab/08 (imprint and counter-imprint). Basal portions: MP ISEA I-F/MP/1488/16ab/08 (imprint and counter-imprint); MP ISEA I-F/MP/1488/28/08 (counter-imprint); MP ISEA I-F/MP/1492/22/09 (counter-imprint); MP ISEA I-F/MP/1488/19ab/08 (imprint and counter-imprint); MP ISEA I-F/MP/1488/13ab/08 (imprint and counter-imprint); MP ISEA I-F/MP/1488/6/08 (imprint); MP ISEA I-F/MP/1488/10/08 (imprint); MP ISEA I-F/MP/1488/29/08 (counter-imprint).

Hind wings: Two nearly complete wings MP ISEA I-F/MP/1488/3/08 (imprint) and MP ISEA I-F/MP/1488/4/08 (counter-imprint), and about a distal half of wing MP ISEA I-F/MP/1488/5ab/08 (imprint and counter-imprint). The following specimens represent basal wing portions: MP ISEA I-F/MP/1488/21ab/08 (imprint and counter-imprint), MP ISEA I-F/MP/1488/12ab/08 (imprint and counter-imprint); MP ISEA I-F/MP/1492/340ab/09 (imprint and counter-imprint), MP ISEA I-F/MP/1492/343ab/09 (imprint and counter-imprint), MP ISEA I-F/MP/1492/346ab/09 (imprint and counter-imprint), MP ISEA I-F/MP/1492/337ab/09 (imprint and counter-imprint), MP ISEA I-F/MP/1488/11/08 (counter-imprint).

Immature forewing: Specimen MP ISEA I-F/MP/1488/29/08 (counter-imprint).

Diagnosis.—Based on fore wing venation characters: costal margin deflected on level of connection with ScP; MP deeply bifurcated about midwing, anterior branch secondary bifurcated well behind bifurcation of first branch of RP, posterior branch of MP ending with 3–4 main branches on posterior wing margin; CuA convex strongly diverges towards MP from its origin; first branch of CuA terminating on CuP or vanished, CuA with five main branches ending in posterior wing margin.

Description of the type material.—Holotype (MP ISEA I-F/MP/1488/2ab/08; Figs. 2A, 3A) is a nearly complete fore wing with uniform dark coloration, dense net of crossveins (= archedictyon) and a rather thick membrane. Length of preserved part 68 mm, estimated total length about 84 mm, maximum width 30 mm. Costal margin deflected opposite the end of ScP; area between C and ScP 3.2 mm wide, with a net of two rows of cells in basal half and three rows with anterior sigmoidal crossveins (veinlets) in distal half; ScP clearly concave, ending on costal margin about 2/3 wing length; RA convex, straight and simple, ending probably close to the wing apex; RP emerging from R about 28 mm from wing base, RP anteriorly bent, ending with three main branches as preserved, first branch opposite the end of ScP, second and third 42.8 mm distal from separation of RA and RP; MP concave, bifurcated about midwing; anterior branch of MP forked distal to the end of ScP; posterior branch of MP ending with three main branches; strong, convex and oblique arculus (= crossvein mp-cua) positioned about 21 mm from wing base; CuA convex, strongly diverges towards MP at its origin, CuA with five main posterior branches and one anterior branch emerging from CuA distally, all except first reaching posterior wing margin; point of separation between CuA and CuP about 8 mm from wing base, apparently very basal; CuA and CuP are slightly divergent; CuP simple, strongly concave, and straight; three convex anal veins partly preserved.

Paratype (MP ISEA. I-F/MP/1540/25/09; Figs. 2B, 3B) represents a middle part of fore wing with probably original dark coloration; different color of proximal and distal part of wing is due to preservation, no spot or other color pattern. Membrane rather thick; dense net of crossveins present. Preserved length 67 mm, estimated total length about 85 mm, maximum width 30.5 mm. Costal margin not well preserved on the level of connection with ScP; area between Costa and ScP 4.5 mm wide, with a net of three or four rows of cells in basal half and several sigmoidal cross-veins (veinlets) in distal half; ScP concave, ending probably on costal margin about 2/3 wing length; RA convex, straight and simple, ending probably close to the wing apex (tips of ScP and RA are

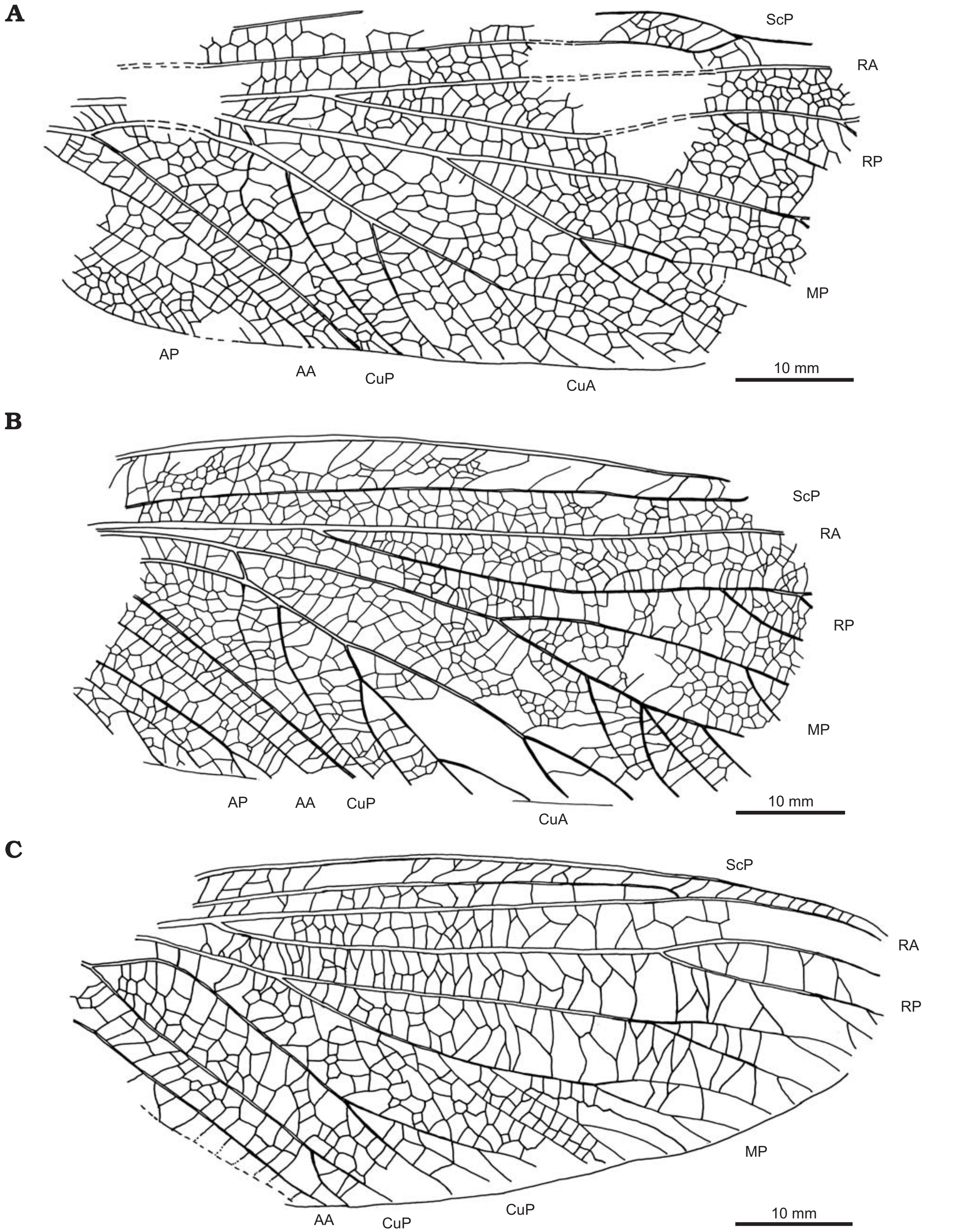


Fig. 2. Line drawings of paoliid insect *Zdenekia silesiensis* sp. nov., Załęże beds, Mudstone series (Langsettian, Upper Carboniferous), Sosnowiec-Klimontów, Upper Silesian Coal Basin, Poland (after Kukalová-Peck 1991). **A**. Fore wing holotype specimen MP ISEA I-F/MP/1488/2ab/08. **B**. Fore wing paratype specimen MP ISEA I-F/MP/1540/25/09. **C**. Hind wing specimen MP ISEA I-F/MP/1488/3/08.Vein symbols are abbreviated as follows: ScP, Subcosta posterior; RA/RP, Radius anterior/posterior; MP, Media posterior; CuA/CuP, Cubitus anterior/posterior; AA/AP, Analis anterior/posterior.

not preserved); concave RP emerging from R about 26.5 mm from wing base, RP anteriorly bended, ending with three main branches as preserved, first branch on the level of ending ScP, second 43.7 mm distal from separation of RA and RP; MP concave, deeply bifurcated about midwing; anterior branch of MP forked distal to the first fork of RP; posterior branch of MP with four main branches ending on posterior wing margin; strong, convex and oblique arculus (= mp-cua) about 20 mm distal from wing base; CuA convex, strongly diverges to MP (the most basal part not preserved); CuA and CuP are slightly divergent; CuA with five main posterior branches, first one vanishing in network close to CuP, third branch terminally bifurcated, others simple, terminating in posterior wing margin; CuP strongly concave, straight, simple; three convex anal veins simple or terminally twigged.

Description of referred material.—Hind wing (Figs. 2C, 3C). Description is based on two nearly complete specimens (MP ISEA I-F/MP/1488/3/08 and MP ISEA I-F/MP/1488/4/08). Wing with uniform dark coloration, with dense net of crossveins, and a rather thick membrane. Estimated total length of former, better preserved specimen 72.8 mm, maximum width 29.0 mm; preserved length of the second specimen 60 mm. Area between costa and ScP with a net of numerous veinlets and 2 mm wide at best; ScP strongly concave, reaching RA about 2/3 wing length; RA convex, nearly straight and simple, ending close to the wing apex; division of RA and RP about 14 mm from wing base; RP concave from the point of separation, with a numerous veinlets in area between RA and RP and RP and MP; RP with two main branches separating opposite the end of ScP; posterior branch of RP terminally twigged; MP concave, bifurcated about 1/3 wing length; anterior branch of MP dichotomously branched; posterior branch of MP with four main branches, second and third terminally twigged; convex arculus perpedicular to CuA and located at highest point of basal curve of this vein, about 10 mm from wing base; CuA convex, strongly diverges to MP from division of CuA and CuP; CuA with two main branches reaching posterior wing margin, anterior branch terminally twigged; reticulated venation with a dense network of crossveins between CuA and MP; point of separation between CuA and CuP close to base; CuP strongly concave and straight, with apical twigging; two anal veins partly visible.

Immature forewing: Specimen MP ISEA I-F/MP/1488/29/08 (Fig. 4A) with uniform dark coloration, without preserved crossveins. Length of preserved part 19.5 mm, estimated total length about 23 mm, maximum width 7.5 mm. Costal margin distally curved, posterior margin slightly deflected on the level of CuP well separating anal field; area between C and ScP basally broad about 0.6 mm wide; ScP clearly concave, ending on costal margin about 2/3 wing length; RA convex, straight and simple, reaching wing apex; RP emerging from stem of R about 7.5 mm from wing base, area between RA and RP distally rather broad; RP ending with three main branches, first branch emerges slightly behind the level of ending ScP to costa, second 11.1 mm distal from separation of RA and RP; first and second branch terminally twigged; concave vein MP deeply bifurcated before midwing, anterior branch secondarily bifurcated slightly before ending ScP and terminally twigged, posterior branch of MP terminally twigged; arculus between MP and CuA not preserved, probably not well developed; convex CuA basally diverges to MP, CuA with two main apical branches; simple CuP strongly concave and straight; anal area reduced with two convex simple anal veins reaching posterior wing margin.

Remarks on variability of adult wing venation.—Fore wings of holotype and paratype differ mainly in arrangement of main branches of posterior MP, which is double dichotomous in holotype, while in paratype one posterior branch is followed by a triple fork (compare Figs. 2AB, 3AB). Also the position of the bifurcation point of MP is variable in relation to origin of RP and first point of bifurcation of this vein. In the paratype the fork of MP is almost equally distant from both these landmarks, while in holotype it is closer to the origin of RP.

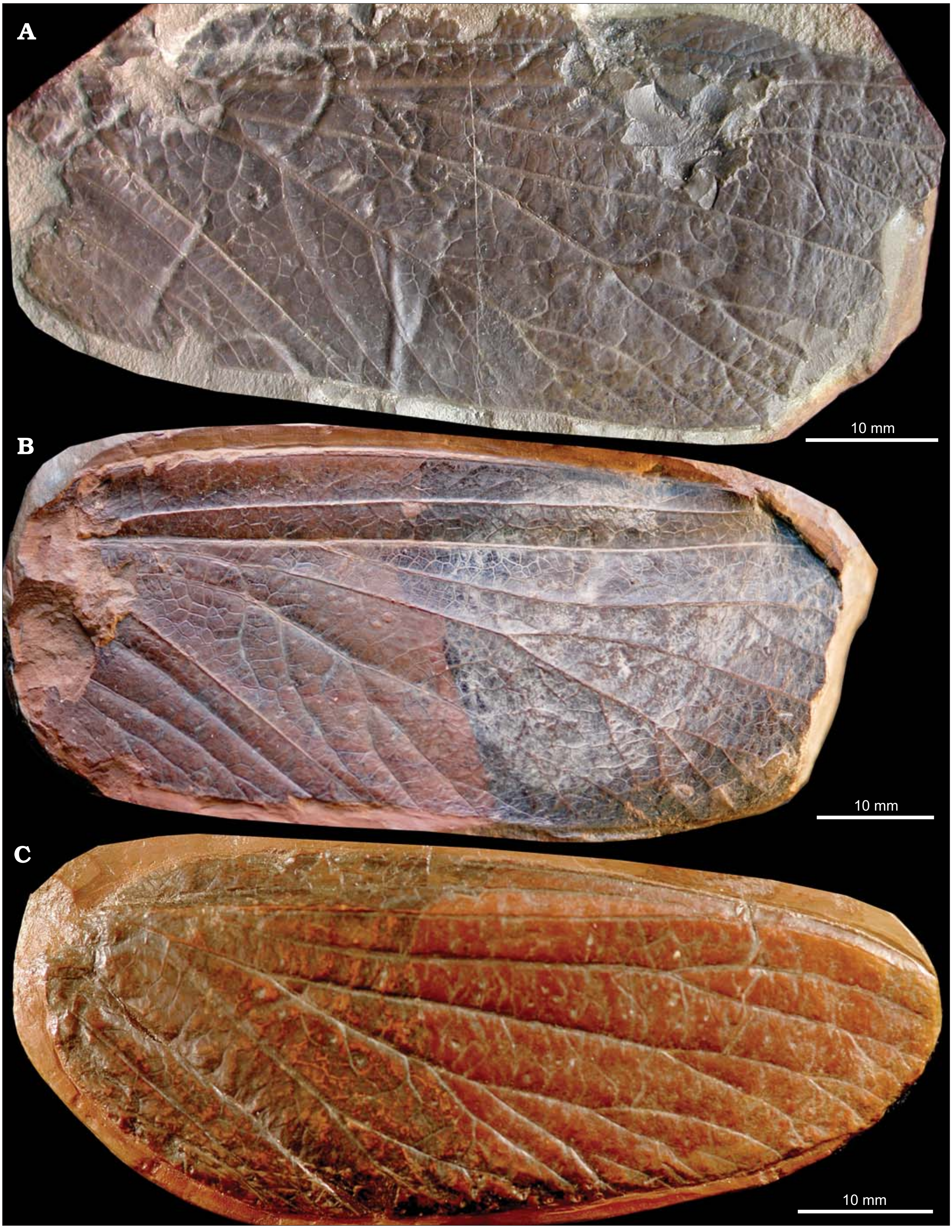
Among the supplementary material, two medial wing parts (MP ISEA I-F/MP/1488/3/08 and MP ISEA I-F/MP/1488/4/08) show branching of MP dichotomous as in the holotype. Medial position of fork of MP into anterior and posterior branch is visible, but further comparison of this position is hindered by absence of corresponding landmarks. Basal wing portions do not provide details other than those described. Strong and oblique crossvein (= arculus) between MP and CuA is visible in all these specimens. The preserved parts of veins CuA and CuP are strongly basally divergent as in the type specimens.

Hind wings of two almost complete specimens on which the description is based are very similar in wing venation. In the distal wing portion of specimen MP ISEA I-F/MP/1488/5ab/08 the first fork of anterior MP is positioned somewhat more distally, beyond first fork of RP, and not just under it. However, only such relative difference can be stated in absence of complete specimens.

Remaining fragments of hind wings included represent only fragments and are congruent with the description in having: arculus perpendicular, four main branches of MP arranged as described, CuA strongly divergent from CuP in basal section and ending with several branches terminally twigged.

Discussion.—The present fore wings (principally based on holotype and paratype specimens) are attributable with genus *Zdenekia* Kukalová, 1958 sharing ScP well separated from RA. This feature is also present in *Mertovia* Prokop and Nel, 2007, from which *Zdenekia* differs in having ScP distinctly

Fig. 3. Photographs of paoliid insect *Zdenekia silesiensis* sp. nov., Załęże beds, Mudstone series (Langsettian, Upper Carboniferous), Sosnowiec-Klimontów, Upper Silesian Coal Basin, Poland. **A**. Fore wing holotype specimen MP ISEA I-F/MP/1488/2ab/08. **B**. Fore wing paratype specimen MP ISEA I-F/MP/1540/25/09. **C**. Hind wing specimen MP ISEA No. I-F/MP/1488/3/08. →


A
B
C
10 mm
10 mm
10 mm

shorter, and not reaching wing apex, and the vein RP with three distal posterior branches. The vein ScP of *Holasicia* Kukalová, 1958, *Pseudofouquea* Handlirsch, 1906, *Paoliola* Handlirsch, 1919, *Olinka* Kukalová, 1958, and *Paolia* Smith, 1871 ends in RA, and RP has more numerous posterior branches (Melander 1903; Kukalová 1958a: text-figs. 3, 5, 9–12; Maples 1989, 1991). In *Kemperala* Brauckmann, 1984 the vein ScP terminates also in RA, but RP is deeply dichotomously bifurcated well before end of ScP (Brauckmann 1984; Brauckmann et al. 1985, Kukalová-Peck and Brauckmann 1992). Furthermore, *Zdenekia* Kukalová, 1958 has wings considerably broader in comparison to *Holasicia* Kukalová, 1958, and MP is forked at about midwing. In addition, hind wings assigned to *Zdenekia* are basally broader than in distal part, branches of MP forming a large area along posterior wing margin (see Kukalová 1958a).

The genus *Zdenekia* is currently represented by two species of Westphalian A (Langsettian) age, viz. *Z. grandis* Kukalová, 1958 (Czech part of USCB) and *Z. occidentalis* Laurentiaux-Vieira and Laurentiaux (1986) (Charbonnages de Ressaix, Belgium). *Z. silesiensis* sp. nov. differs from both species in having CuA less developed, with five main branches ending on posterior wing margin instead of seven present in *Z. grandis* and *Z. occidentalis*. MP is reduced; anterior branch of MP is nearly straight with the first bifurcation well behind the level of first branch of RP instead clearly before as in *Z. grandis* and *Z. occidentalis* (Kukalová 1958a; Laurentiaux-Vieira and Laurentiaux 1986). Also, the posterior branch of MP is shorter in *Z. silesiensis* than in both congeners. On the basis of above mentioned characters it is possible to separate *Z. silesiensis* from the other two previously described species.

Furthermore, Kukalová (1958a) assigned an isolated hind wing to *Zdenekia* cf. *grandis* basing on wing proportions and a venation pattern similar to those known in forewings of *Zdenekia grandis*. We found similar situation with *Z. silesiensis* in our locality where we discovered several nearly complete and fragmentary fore and hind wings similar in organization of the venation pattern to latter taxon. We tentatively attribute hind wings described in supplementary material to *Z. silesiensis* sp. nov. on the basis of the following characters: (i) reduced RP area with only two main branches; (ii) anterior branch of MP rather long with first division on the level or slightly behind division of RP. Nevertheless, it should be noticed that we cannot be sure until more complete specimen is discovered.

The well preserved immature wing can be assigned with confidence to Paoliidae, sharing the main diagnostic pattern of forewing organisation features of *Z. silesiensis* sp. nov.: ScP ending in C, RP with two main branches secondarily forked, MP deeply forked and CuA with few branches. Nevertheless some branches of main veins or dense pattern of cross-veins as we can observe on adult wing are probably still not well developed due to progressive tracheation.

Genus *Darekia* nov.

Type species: *Darekia sanguinea* sp. nov., see below; by monotypy.

Etymology: Named after Darek (diminutive of Polish first name Dariusz), the Greek form of Persian Darayavahush, composed of the elements daraya "to possess" and vahu "good"; feminine in gender.

Diagnosis.—As for the species.

Darekia sanguinea sp. nov.

Fig. 4B.

Etymology: Named after sanguineous color of the holotype (Latin *sanguinea*); gender feminine.

Type material: Holotype: Specimen No. MP ISEA I-F/MP/1488/14a/08 imprint and MP ISEA I-F/MP/1488/14b/08 counter-imprint, a well preserved basal part of fore wing.

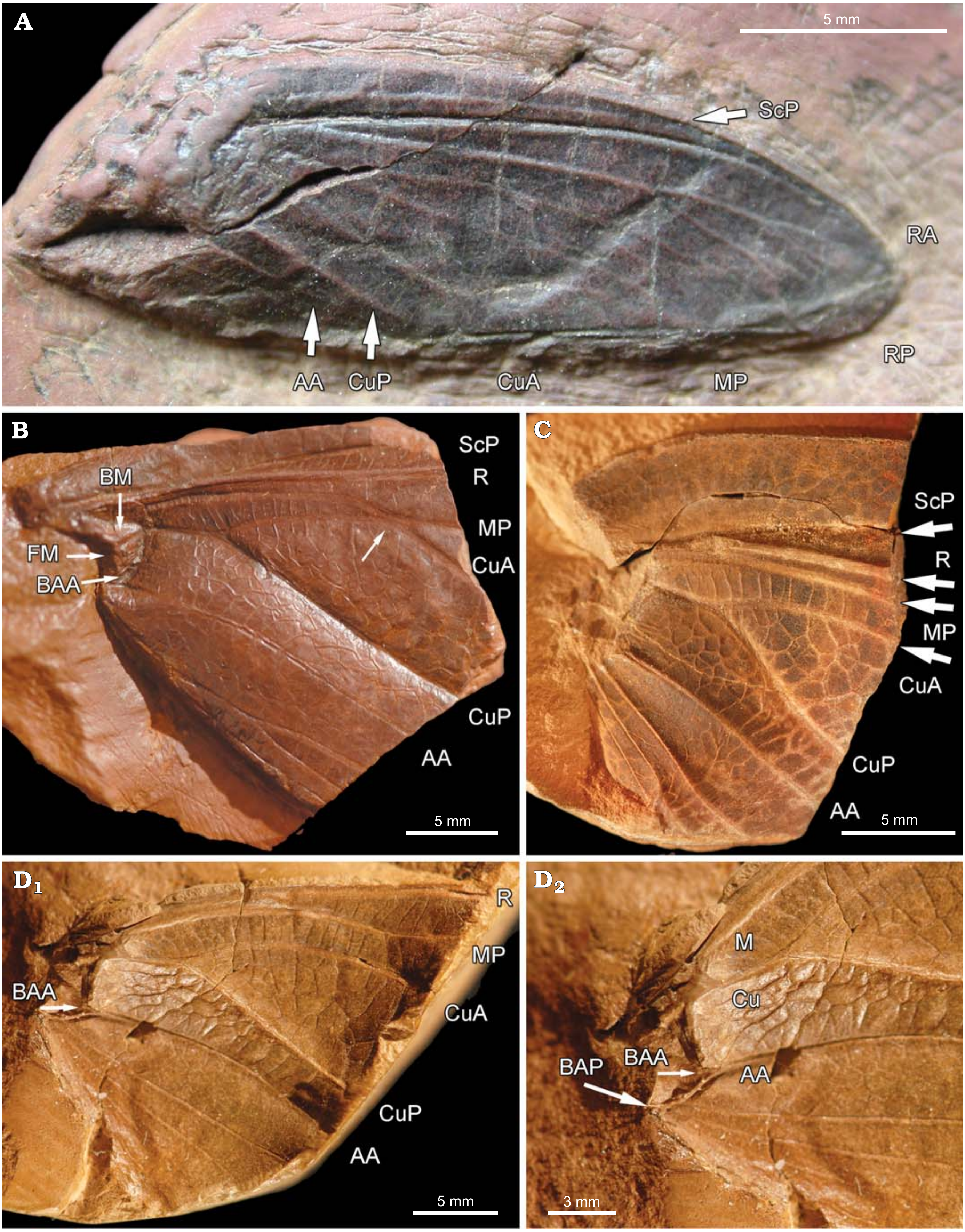
Type locality: Sosnowiec-Klimontów, originally Porąbka-Klimontów Mine, Upper Silesian Coal Basin, Poland.

Type horizon: Załęże beds, Mudstone series, Langsettian, Westphalian A, Upper Carboniferous.

Diagnosis.—Based on wing venation pattern of basal fore wing. Dense pattern of cross-veins; convex stem of R well basally separated from MP; division of RA and RP well behind the connection of MP and CuA, stem of Cu well separated and basally concave or neutral; point of separation between CuA and CuP close to wing base; CuA convex, strongly diverges to MP from division of CuA and CuP; convex CuA shortly connected to MP; concave CuP simple and straight running to posterior wing margin; broad area between CuA and CuP with four rows of cells; convex 1A (AA) basally remote from stem of Cu; anal area strongly reduced.

Description.—Holotype MP ISEA I-F/MP/1488/14ab/08 (Fig. 4B): no evidence of original coloration; dense pattern of cross-veins present; membrane rather thick. Length of wing fragment 25.9 mm, estimated wing length about 85 mm, and maximum width about 22 mm; area between C and ScP with a net of numerous veinlets; concave ScP nearly straight; convex stem of R well basally separated from MP and attached to axillary plate, nearly straight; MP concave and basally well separated; stem of Cu well separated and basally concave or neutral; point of separation between CuA and CuP 10.9 mm from wing base, apparently very basal; CuA convex, strongly diverges to MP from division of CuA and CuP;

Fig. 4. Photographs of paoliid insects from Upper Sileasian Coal Basin, Załęże beds, Mudstone series (Langsettian, Upper Carboniferous), Sosnowiec-Klimontów, Poland. **A**. *Zdenekia silesiensis* sp. nov. (Paoliidae), immature wing of specimen MP ISEA I-F/MP/ 1488/29/08. **B**. *Darekia sanguinea* gen. nov. et sp. nov. (Paoliidae), fore wing holotype specimen MP ISEA I-F/MP/1488/14a/08. **C**, **D**. Paoliidae gen. et sp. indet. **C**. Fore wing base specimen MP ISEA I-F/MP/1492/342/09. **D**. Specimen MP ISEA I-F/MP/1488/15a/08. fore wing base (D_1) and detail of basal articulation (D_2). Vein symbols are abbreviated as follows: ScP, Subcosta posterior; R, Radius; RA/RP, Radius anterior/posterior; M, Media; MP, Media posterior; Cu, Cubitus; CuA/CuP, Cubitus anterior/posterior; AA/AP, Analis anterior/posterior, after Kukalová-Peck (1991). The basal articulation of wings follows: BM, medial basivenale; FM, medial fulcalare; BAA/BAP, anal anterior/posterior basivenale (after Haas and Kukalová 2001). →


A
5 mm
ScP
RA
RP
AA
CuP
CuA
MP
B
BM
FM
BAA
ScP
R
MP
CuA
CuP
AA
5 mm
C
ScP
R
MP
CuA
CuP
AA
5 mm
D1
R
MP
BAA
CuA
CuP
AA
5 mm
D2
M
Cu
BAP
BAA
AA
3 mm

convex CuA shortly connected to MP 10.6 mm from division of CuA and CuP; numerous simple cross-veins between MP and stem of Cu and CuA; concave CuP simple and straight, running to posterior wing margin; broad area between CuA and CuP with four rows of cells; convex 1A (AA) basally remote from stem of Cu; area between stem Cu and 1A with five rows of cells; concave 2A (AP) running close to the posterior wing margin with three or four rows of cells between 1A and 2A; vein 2A distally branched; anal area strongly reduced.

Discussion.—The fore wing base described herein is attributable to Paoliidae mainly due to presence of basal division of CuA and CuP close to wing base, dense network of crossveins, and reduced anal area. *Darekia* gen. nov. clearly differs from all other paoliid genera by the presence of a short connection between veins MP and CuA. *Pseudofouquea* Handlirsch, 1906 described from Wales bears similar pattern of wing base but both these veins are just close together, and not connected. *Stygne* Handlirsch, 1906 known from Polish part of USCB, but from the older strata (Paralic Series, equivalent Ostrava Formation, Namurian) shares also rapprochement of veins MP and CuA, but these veins are also not connected, and the area between CuA and CuP is markedly narrower, with a net of crossveins less dense than in *Darekia*. Moreover, the division of RA and RP in *Stygne* is about the level of closest point between MP and CuA. Although this fork is not preserved in the available material of *Darekia*, it is at least located in a more distal position. Nevertheless, *Stygne* is considered as closely related to paoliid genera by many authors (see e.g., Carpenter [1992], Kukalová [1958a]). We support this assumption due to presence of deep branching of MP and CuA with numerous branches ending on posterior wing margin, but only with reservation when considering regular pattern of simple cross-veins unusual in paoliids.

It should be noticed that anastomosed CuA with MP occurs also in Pachytylopsidae (see e.g., *Protopachytylopsis leckwicki* Laurentiaux and Laurentiaux-Vieira, 1981; Westphalian A of Belgium), in which however CuA is basally divided into anterior branch CuA1 anastomosed with MP and a posterior branch CuA2 (Laurentiaux and Laurentiaux-Vieira 1981: fig. 2A). This situation is markedly different from pattern present in *Darekia*. Therefore, the combination of characters unique among the Paoliidae justify designation of a new genus *Darekia*.

Paoliidae gen. et sp. indet.

Fig. 4C, D.

Material.—Fore wing bases MP ISEA I-F/MP/1492/342/09 (counter-imprint); MP ISEA I-F/MP/1488/15a/08 (imprint) and MP ISEA I-F/MP/1488/15b/08 (counter-imprint).

Geographic and stratigraphic range.—Sosnowiec-Klimontów, originally Porąbka-Klimontów Mine, Upper Silesian Coal Basin, Poland. All specimens mentioned above come from the type locality. Załęże beds, Mudstone series, Langsettian, Westphalian A, Upper Carboniferous.

Description.—Specimen MP ISEA I-F/MP/1492/342/09 (Fig. 4C). Fore wing base with dense pattern of crossveins and rather thick membrane; length of wing fragment 14.3 mm, maximum width of wing fragment 18.6 mm; area between C and ScP rather broad with four or five cells in between; concave ScP partially preserved, nearly straight; convex stem of R straight, basally separated from MP; concave MP basally running parallel to stem of R; stem of Cu well separated and basally concave; point of separation between CuA and CuP 6.4 mm from wing base; CuA convex, diverges to MP from division of CuA and CuP; one row of simple crossveins between MP and stem of Cu and CuA; concave CuP simple and slightly curved, running to posterior wing margin; broad area between CuA and CuP with four rows of cells; convex first anal vein (possibly AA1+2) basally remote from stem of Cu; area between stem Cu and first anal vein with five rows of cells; three other simple anal veins basally very close each other forming strongly reduced anal area.

Specimen MP ISEA I-F/MP/1488/15ab/08 (Fig. $4D_1$, D_2). Fore wing base with dense pattern of crossveins and rather thick membrane; basal articulation partly preserved; length of wing fragment 27.6 mm, maximum width 19.7 mm, estimated width about 22 mm; costal margin not preserved; concave ScP nearly straight partially preserved; convex stem of R nearly straight, basally well separated from MP; concave MP running parallel to stem of R with simple crossveins in between; stem of Cu well separated and basally concave; point of separation between CuA and CuP 8.9 mm from wing base; convex CuA diverges to MP from stem Cu; one or two rows of crossveins between MP and stem of Cu and CuA; strong oblique arculus between MP and CuA present 11.7 mm from division of CuA and CuP; concave CuP simple running straight to posterior wing margin; area between CuA and CuP markedly broad with four or five rows of cells in widest part; convex first anal vein (AA1+2) basally remote from stem of Cu and other anal veins; area between stem Cu and first anal vein with three rows of cells; four other simple anal veins basally very close each other forming strongly reduced anal area connected by simple crossveins.

Discussion.—We provide description of these paoliid wing bases although we could not clearly attribute them within the known genera. Nevertheless, the excellent preservation state of these basal parts and their morphology is giving at least evidence of folding mechanism as occurring in neopteran insects. Generally the wing articulation consists of movable parts less sclerotized when compared to the wings and other external body structures with higher preservation potential. The presence of fragmentary preserved wing articulation provides for the first time an evidence of corresponding articular sclerites (medial basivenale [BM], medial fulcalare [FM], anal anterior basivenale [BAA], anal posterior basivenale [BAP]), or at least their distal parts connected to the main veins (see arrows in Fig. 4B, D). Basing on their arrangements and proportions we could generally infer the supposed position of axillary sclerites. The pattern of basal articulation exhibits the wing folding due to the presence of the 3rd axillary sclerite and supporting the placement into Neoptera contra Sharov (1966). Nevertheless, the precise systematical position of paoliids within the Neoptera remains unresolved until more complete specimens will be discovered.

Conclusions

Paoliids display quite high abundance in early Late Carboniferous ecosystems, but of rather low diversity in comparison to the other groups of neopteran insects well diversified from Duckmantian/Bolsovian on. This phenomenon is also observed among paoliid fauna from Hagen Vorhalle where only two taxa were described: *Holasicia rasnitsyni* Brauckmann, 1984 and *Kemperala hagenensis* Brauckmann, 1984 based on large material of more than 200 specimens (see Ilger and Brauckmann 2007). This is also the case of Sosnowiec locality where paoliids dominate in taphocoenosis, but diversity based on variability of venation pattern is considerably low. Unfortunately, it is difficult to assess an intraspecific variability of venation due to fragmentary preservation of the majority of specimens. We suspect that numbers of paoliid taxa described by Kukalová (1958a) from compressed fossils are slightly overestimated and could result from deformations and intraspecific variability. All the newly and previously described taxa support an idea about favorable living conditions for paoliids in the territory of the Upper Silesian Coal Basin, considering that 6 out of 13 world known species are from this area (see check-list of Paoliidae and related taxa in the Appendix 1). A rather short time of existence of this group known from the Late Namurian to Langsettian deposits could be probably caused by environmental change like a decrease of humidity "first drier interval" on the boundary in Langsettian/ Bolsovian, well documented in plant record and considered as a major event in Euroamerican coalswamp vegetation (Phillips and Peppers 1984; Galtier 1997).

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Appendix 1

Check-list of taxa attributed to Paoliidae.

Species name	Occurence
Darekia sanquinea gen. et sp. nov.	Upper Silesian Coal Basin (Poland)
Holasicia vetula Kukalová, 1958	Upper Silesian Coal Basin (Czech Republic)
Holasicia rasnitsyni Brauckmann, 1984	Hagen-Vorhalle (Germany)
Kemperala hagensis Brauckmann, 1984	Hagen-Vorhalle (Germany)
Mertovia sustai (Kukalová, 1958)	Upper Silesian Coal Basin (Czech Republic)
Olinka modica Kukalová, 1958	Upper Silesian Coal Basin (Czech Republic)
Paolia vetusta Smith, 1871	Indiana (USA), South Limbourg (the Netherlands)
Paoliola gurleyi (Scudder, 1885)	Indiana (USA)
Pseudofouquea sp. of Anderson et al. (1997)	Bickershaw (England)
Pseudofouquea cambrensis (Allen, 1901)	Llanbradach Colliery (Wales)
Sustaia impar Kukalová, 1958	Upper Silesian Coal Basin (Czech Republic)
Zdenekia grandis Kukalová, 1958	Upper Silesian Coal Basin (Czech Republic)
Zdenekia occidentalis Laurentinaux, 1986	Charbonnages de Ressaix (Belgium)
Zdenekia silensiensis sp. nov.	Upper Silesian Coal Basin (Poland)

Unassigned taxa probably closely related to Paoliida or inclusive (see discussion in text).

Species name	Occurence
Ampeliptera limburgica Pruvost, 1927	South Limbourg (the Netherlands)
Stygne roemeri Handlirsch, 1906	Upper Silesian Coal Basin (Poland)
Katerinka candida Prokop and Nel, 2007	Upper Silesian Coal Basin (Czech Republic)

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