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Revision and Phylogenetic Affinities of the Lobeattid Species *bronsoni* Dana, 1864 and *silvatica* Laurentiaux & Laurentiaux-Vieira, 1980 (Pennsylvanian; *Archaeorthoptera*)

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> Abstract

The case of the taxonomy of the insect species *bronsoni* Dana, 1864, yielded from the deposit of Mazon Creek (IL, USA; Westphalian, Pennsylvanian), is investigated. The species *contusa* Scudder, 1885, *infernus* Scudder, 1885, *clarinervis* Melander, 1903, *extensa* Melander, 1903, *indistinctus* Melander, 1903, *ambulans* Handlirsch, 1906, *analis* Handlirsch, 1906: 700, *longicollis* Handlirsch, 1911, *lata* Handlirsch, 1911, *elatior* Handlirsch, 1911, *schucherti* Handlirsch, 1911, *acutipennis* Handlirsch, 1911, *parvula* Handlirsch, 1911, and *angusta* Handlirsch, 1911 are considered as junior synonyms of *bronsoni*. A neotype is designated for this species. The species *bronsoni* and *silvatica* Laurentiaux & Laurentiaux-Vieira, 1980 (yielded from the North Coal Basin, France; Westphalian, Pennsylvanian) share the character state 'in forewings, CuPa fuses with M + CuA'. This character state is used for defining the taxon *Miamia nom.* Dana 1864, *nov. dis.-typ.* under cladotypic taxonomy. It is demonstrated that *bronsoni* and *silvatica* belong to the taxon *Archaeorthoptera nom.* Béthoux & Nel, 2002a, *dis.-typ.* Béthoux 2007e. In particular, these species are closely related to lobeattid insects such as *schneideri* Béthoux, 2005, a new specimen of which is illustrated. The species *bronsoni* appears to be one of the most frequent insect species of the Mazon Creek entomofauna.

> Key words

Protorthoptera, Eoblatta, Spanioderidae, *Miamia*, *Spaniodera*, *Propteticus*, *Anthraconeura,* cladotypic nomenclature.

1. Introduction

The fossil record of Paleozoic and Early Mesozoic insects is characterized by the dominance of a few deposits that yielded most of the record. The deposit of Mazon Creek (IL, USA) yielded about a third of known Pennsylvanian insect species. Paradoxically, the taxonomic data for this important deposit is not homogenous. Most species were described mainly between 1885 and 1911 (*e.g.* Scudder 1885; Handlirsch 1906, 1911), when the prevalent species concept was the typological one. Only some of these species were sporadically reviewed (*e.g.* Carpenter & Richardson 1976; Burnham 1986). New species were later described (*e.g.* Richardson 1956; Béthoux 2005c). Because this entomofauna is among the earliest well-sampled ones, an up-to-date taxonomic frame would allow insect biodiversity dynamics, at the earliest stage of the evolution of the group, to be better appreciated.

However a number of difficulties prevented extensive revisions to be carried out. First, the type-material of the nearly 150 described species (Carpenter 1997) is scattered in various institutions, making comparison uneasy. With "Handlirsch's propensity to split taxa, and his failure to examine the actual specimens" (Burnham 1986), such comparison is of utmost importance. In addition, a number of species have been described on the basis of material in hands of private collectors. Once in a while these specimens are identified in material donated to (or acquired by) institutions. Furthermore, it has been demonstrated that some specimens have been subject to intensive preparation

resulting into significant artefacts (BÉTHOUX & BRIGGS 2008). Lastly, even some recent contributions failed to provide accurate morphological data, preventing identification of synonymous species and correct taxonomic placement. At the present state, an exhaustive taxonomic revision of the Mazon Creek entomofauna is still wanting.

The present contribution is dedicated to the revision of the species *bronsoni* Dana, 1864. A junior synonym of *bronsoni* is *infernus* Scudder, 1885 (see below), considered by CARPENTER (1992; following BURNHAM 1986) as the type-species of the Linnaean genus *Propteticus* Scudder, 1885, itself type-genus of the Linnaean family Spanioderidae Handlirsch, 1906 (CARPENTER 1992). The most recent contribution on the taxonomy of this species in the unpublished second part of the thesis of BURNHAM (1986; followed by CARPENTER 1992), which has been a valuable source of information for this contribution. However, a number of illustrations and interpretations are, to a significant extent, erroneous. A revision was necessary.

2. Material and method

I use the cladotypic nomenclatural procedure elaborated by BÉTHOUX (2007c, d) for taxa other than species, and follow suggestions of DAYRAT (et al. 2004; and references therein) for species names. Throughout this contribution, Linnaean taxon names are indicated by the mention of their rank. Unranked Linnaean taxa names can be differentiated from cladotypic names as the latter are italicized. For example, Archaeorthoptera is a Linnaean name while *Archaeorthoptera* is a valid cladotypic name. In addition, vernacular versions of Linnaean names will be preferred (for example, panorthopterans rather than Panorthoptera). Synonymy lists complying with the Linnaean nomenclatural procedure are provided in Appendix.

Investigated specimens of *bronsoni* are held by the Yale Peabody Museum (YPM; New Haven, CT), the Field Museum of Natural History (FMNH; Chicago, IL), and the Smithsonian Institution, National Museum of Natural History (USNM; Washington, DC, USA; the specimen USNM 440084 belongs to the John M. & Lucy McLuckie collection). I carried out no significant preparation of the specimen. Notably, preparation of the ovipositor of the specimen FMNH PE 30369 was carried out by an unknown preparator.

Specimens held by the YPM and FMNH were photographed with a Nikon Coolpix 5400 with in-built lenses. Specimens held by the USNM were photographed with a Canon EOS 400D coupled with a 50 mm macro lens and a an elongation tube, or a MP-E 65 mm Canon macro lens, as appropriate. The holotype of *silvatica* is held by the Natural History, Geology, and Ethnography Museum (MGL; Lille, France). Various binoculars and drawing tubes were used, as available in the visited institutions. Original photographs were processed using Adobe Photoshop 7.0. Some of the images are reproduced using the light-mirror technique (BÉTHOUX et al. 2004). In some cases more detail can be shown by combining photographs of a specimen dry and immersed in ethanol; such illustrations are referred to as composites. Restoration of missing parts was based on the information available from parts more completely preserved of the same individual. These restorations are indicated by black dashed lines. In addition, restoration was performed based on forewing outlines of the specimens FMNH UC 9240, FMNH PE 31967, FMNH PE UC 6391, and FMNH PE 31955. These restorations are indicated by grey dashed lines. The morphology of the specimen FMNH UC 9243 was investigated based on photographs only.

I use the wing venation nomenclature elaborated by BÉTHOUX & NEL (2002a) for *Archaeorthoptera*, itself based on that of orthopterans (BÉTHOUX & NEL 2001). Corresponding abbreviations are repeated herein for convenience:

ScP	posterior Subcosta
R	Radius
RA	anterior Radius
RP	posterior Radius
M	Media
CuA	anterior Cubitus
CuP	posterior Cubitus
CuPa	anterior branch of CuP
CuPb	posterior branch of CuP
AA	anterior Analis
AA1	first anterior Analis.

The reader who is not familiar with orthopteran and other insect wing venation nomenclature could refer to the discussion in BÉTHOUX (2005b; and references therein) and to BÉTHOUX & NEL (2002a: fig. 1b). Critics expressed by GOROKHOV (2005) regarding this homologization hypothesis are addressed in BÉTHOUX (2007a). Subsequent comments by RASNITSYN (2007) are addressed in BÉTHOUX (in press). Branches of the median vein are conservatively not distinguished as MA and MP. On figures, RFW, LFW, RHW, and LHW account for left forewing, right forewing, and right hind wing, respectively.

3. Systematic Palaeontology

Taxon *Archaeorthoptera nom.* Béthoux & Nel, 2002a, *dis.-typ.* Béthoux, 2007e

Taxon *Miamia nom.* Dana, 1864, *nov. dis.-typ.*

Taxon *Miamia nom*. Dana, 1864: 35;
Scudder 1866: 17; Handlirsch 1906: 698;
Carpenter 1992: 133.

Definition. Species that evolved from the metapopulation lineage in which the character state 'in forewings, CuPa fuses with M + CuA', as exhibited by *bronsoni* Dana, 1864 and *silvatica* Laurentiaux & Laurentiaux-Vieira, 1980, has been acquired (venation designations as in Béthoux & Nel 2001, 2002a; and see Figs. 1–9, 11–12).
Cladotypes. Specimen FMNH PE 31967 (neotype of *bronsoni* Dana, 1864; Fig. 8) and specimen MGL 4234 (holotype of *silvatica* Laurentiaux & Laurentiaux-Vieira, 1980; Fig. 11).
Paracladotypes. Specimens FMNH UC 9240 (Fig. 3), YPM 25 (Figs. 4.2, 5), YPM 26 (Fig. 4.3), YPM 28 (Fig. 6.2), FMNH PE 31955 (Fig. 9), FMNH PE 29399 (negative imprint, right forewing), all belonging to *bronsoni* and exhibiting the defining character state.
Composition. *Miamia nom*. Dana, 1864, *nov. dis.-typ.* is provisionally composed of its cladotypic species only. The species *carpentieri* Pruvost, 1919 shares the defining character state of *Miamia nom*. Dana, 1864, *nov. dis.-typ*. (see Béthoux 2007b), but the forewing morphology of this species strongly differs from that of *bronsoni* and *silvatica* in several aspects. A phylogenetic analysis might solve this question. The species *rigida* Scudder, 1885, if considered as valid (but see below), should be included in *Miamia*.
Diagnosis. Forewings: ScA distinct from the anterior wing margin at wing base (known in *bronsoni* only); area between anterior wing margin and ScP narrow; ScP with oblique and strong veinlets; ScP reaching RA; area between RA and RP narrow for some distance; RA and RP diverge abruptly opposite the end of ScP on RA; CuPa fuses with M + CuA; M branched; free stem of M (diverging from M + CuA + CuPa) and posterior branch of M markedly concave; posterior branch of M simple; CuA + CuPa posteriorly pectinate, branched near the point of divergence of M and CuA + CuPa, with at least 3 branches; CuPb concave, AA1 convex, both simple; cross-veins rarely reticulated, except in the area between AA1 and other AA veins.
Occurrence. Laurentia; Westphalian (Pennsylvanian).
Remarks. New information on the wing venation of *bronsoni* suggests that this species is closely related to *silvatica*. Both species share (in forewing) a narrow area between the anterior wing margin and ScP; an area between RA and RP narrow for some distance, abruptly broadened opposite the end of ScP on RA; a fusion of CuPa with M + CuA. The later character state can be polarized by comparison with the condition exhibited by *dumasii* Brongniart, 1879, which does not exhibit a complete fusion of CuA with CuP in hind wings (see Béthoux 2003), qualifying it as a relevant outgroup. In this species, CuPa fuses with CuA once this vein already diverged from M + CuA. This is then the presumed ancestral state of *Miamia nom*. Dana 1864, *nov. dis.-typ*.

Regarding the choice of the taxon name, I preferred to adapt the name *Miamia* because it is not pre-occupied, and because it allows the combination '*Miamia bronsoni* Dana, 1864' to be preserved and valid under all nomenclatural procedures.

Species *bronsoni* Dana, 1864

(Figs. 1–10)

Species *bronsoni* Dana, 1864: 35, fig. 1
(erected as type-species of the genus *Miamia* Dana, 1864); Scudder 1866: 18, figs. 2, 4; Handlirsch 1906: 698; Carpenter 1992: 133; location of the holotype unknown.

Species *contusa* Scudder, 1885: 330, pl. 20, fig. 6 (erected as typespecies of the genus *Didymophlebs* Scudder, 1885); Handlirsch 1906: 808; Carpenter 1992: 132; new synonymy;
holotype: FMNH UC 6392 (Fig. 1.1).

Species *infernus* Scudder, 1885: 334, pl. 31, figs. 3, 4; Handlirsch 1906: 698; Carpenter 1992: 122, fig. 1; new synonymy; holotype: FMNH UC 6391 (Fig. 1.2).

Species *clarinervis* Melander, 1903: 185, pl. VI, fig. 1, pl. VII fig. 8; Handlirsch 1906: 698 (erected as type-species of the genus *Camptophlebia* Handlirsch, 1906); Carpenter 1992: 122 (synonymy with *infernus* Scudder, 1885); new synonymy;
holotype: FMNH UC 9240 (Fig. 1.3).

Species *extensa* Melander, 1903: 186, pl. VI, fig. 2, pl. VII, fig. 9; Handlirsch 1906: 698 (erected as type-species of the genus *Parachaliphlebia* Handlirsch, 1906); Carpenter 1992: 122 (synonymy with *infernus* Scudder, 1885);

new synonymy;
holotype: FMNH UC 9241 (Fig. 2).

Species *indistinctus* Melander, 1903: 191, pl. VI, fig. 6, pl. VII, figs. 12–13 (erected as type-species of the genus *Petromartus* Melander, 1903); HANDLIRSCH 1906: 699; CARPENTER 1992: 122 (synonymy with *infernus* Scudder, 1885); new synonymy; holotype: FMNH UC 9243.

Species *ambulans* Handlirsch, 1906: 697, figs. 23–25 (erected as type-species of the genus *Spaniodera* Handlirsch, 1906); CARPENTER 1992: 122 (synonymy with *infernus* Scudder, 1885); new synonymy; holotype: USNM 38817 (Fig. 3.1).

Species *analis* Handlirsch, 1906: 700: fig. 27 (erected as type-species of the genus *Metryia* Handlirsch, 1906); CARPENTER 1992: 122 (synonymy with *infernus* Scudder, 1885); new synonymy; holotype: USNM 38834 (Fig. 3.2).

Species *longicollis* Handlirsch, 1911: 305, fig. 8; new synonymy; holotype: YPM 24 (Fig. 4.1).

Species *lata* Handlirsch, 1911: 306, fig. 9; new synonymy; holotype: YPM 25 (Figs. 4.2, 5).

Species *elatior* Handlirsch, 1911: 307, fig. 10; new synonymy; holotype: YPM 26 (Fig. 4.3).

Species *schucherti* Handlirsch, 1911: 308, fig. 11; new synonymy; holotype: YPM 27 (Fig. 6.1).

Species *acutipennis* Handlirsch, 1911: 308, fig. 12; new synonymy; holotype: YPM 28 (Fig. 6.2).

Species *parvula* Handlirsch, 1911: 309, fig. 13; new synonymy; holotype: YPM 29 (Fig. 7.1).

Species *angusta* Handlirsch, 1911: 309, fig. 14; new synonymy; holotype: YPM 30 (Fig. 7.2).

Diagnosis. Antennae narrow, at least as long as the head; head circular; foreleg femora and tibia of similar length; foreleg tarsus with 4 or 5 tarsomeres; prothorax twice long as broad; f o r e w i n g : mean length 32.5 mm (standard deviation 3.8 mm), mean width (at wing mid-length) 9.6 mm (standard deviation: 1.4 mm); point of divergence of RA and RP opposite the first quarter of wing length; long narrow area between RA and RP; RP branched distally, with 3-5 branches; M (diverging from M + CuA + CuPa) simple for a short distance; anterior branch of M branched distally, with 2-4 branches; CuA + CuPa with 5-8 branches reaching posterior wing margin; coloration homogeneous, with R, RA, RP, CuA and AA veins darker; h i n d w i n g : area between RA and RP very narrow for a short distance, then gradually broadened; RP with about 4 branches; M branched; CuPa fuses with CuA; CuA + CuPa posteriorly pectinate, with about 5 branches.

Occurrence. Francis Creek Shale Member of the Carbondale Formation, Illinois, USA; Westphalian D (Pennsylvanian).

Descriptions. Specimen FMNH UC 6392 (holotype of *contusa* Scudder, 1885; Fig. 1.1): poorly preserved negative imprint, fragment of right forewing, incomplete left forewing, and unidentifiable other body remains; r i g h t f o r e w i n g : area between RA and RP with sigmoid cross-veins; l e f t f o r e w i n g : width about 11.2 mm; area between anterior wing margin and ScP narrow (1.2 mm at the approximate first third of the wing length); R forked near wing base; as preserved, RP simple; M poorly preserved; CuA + CuPa posteriorly pectinate, with at least 7 branches reaching posterior wing margin.

Specimen FMNH UC 6391 (holotype of *infernus* Scudder, 1885; Fig. 1.2): moderately well-preserved positive imprint, with head and thoracic remains, incomplete left and right forewings, and very incomplete left hind wing; f o r e w i n g s : ScA distinct from anterior wing margin, parallel to it for a long distance; ScP reaching RA; area between RA and RP narrow for a long distance; RA and RP diverging abruptly; distal to this divergence, area between RA and RP with strong sigmoid cross-veins, reticulated in the broadest part of the area; l e f t f o r e w i n g : estimated length about 33 mm, estimated width (at wing mid-length) about 9 mm; RP simple for 14.8 mm, with at least 4 branches reaching posterior wing margin; anterior branch of M forked distally, posterior branch of M simple; CuA + CuPa posteriorly pectinate, with 5 or 6 branches reaching posteriorly wing margin; r i g h t f o r e w i n g : ScP with strong and oblique veinlets; l e f t h i n d w i n g : CuPa fuses with CuA; CuA + CuPa strongly bent, posterior pectinate, with 4 preserved branches.

Specimen FMNH UC 9240 (holotype of *clarinervis* Melander, 1903; Fig. 1.3): well preserved isolated right forewing, positive imprint; apex and anal area missing; estimated wing length about 31 mm, width (at wing mid-length) 9.8 mm; ScP with strong and oblique veinlets; RA and RP diverge near wing base; area between RA and RP narrow for a long distance; RP simple for 15.9 mm, with at least 4 distal branches;

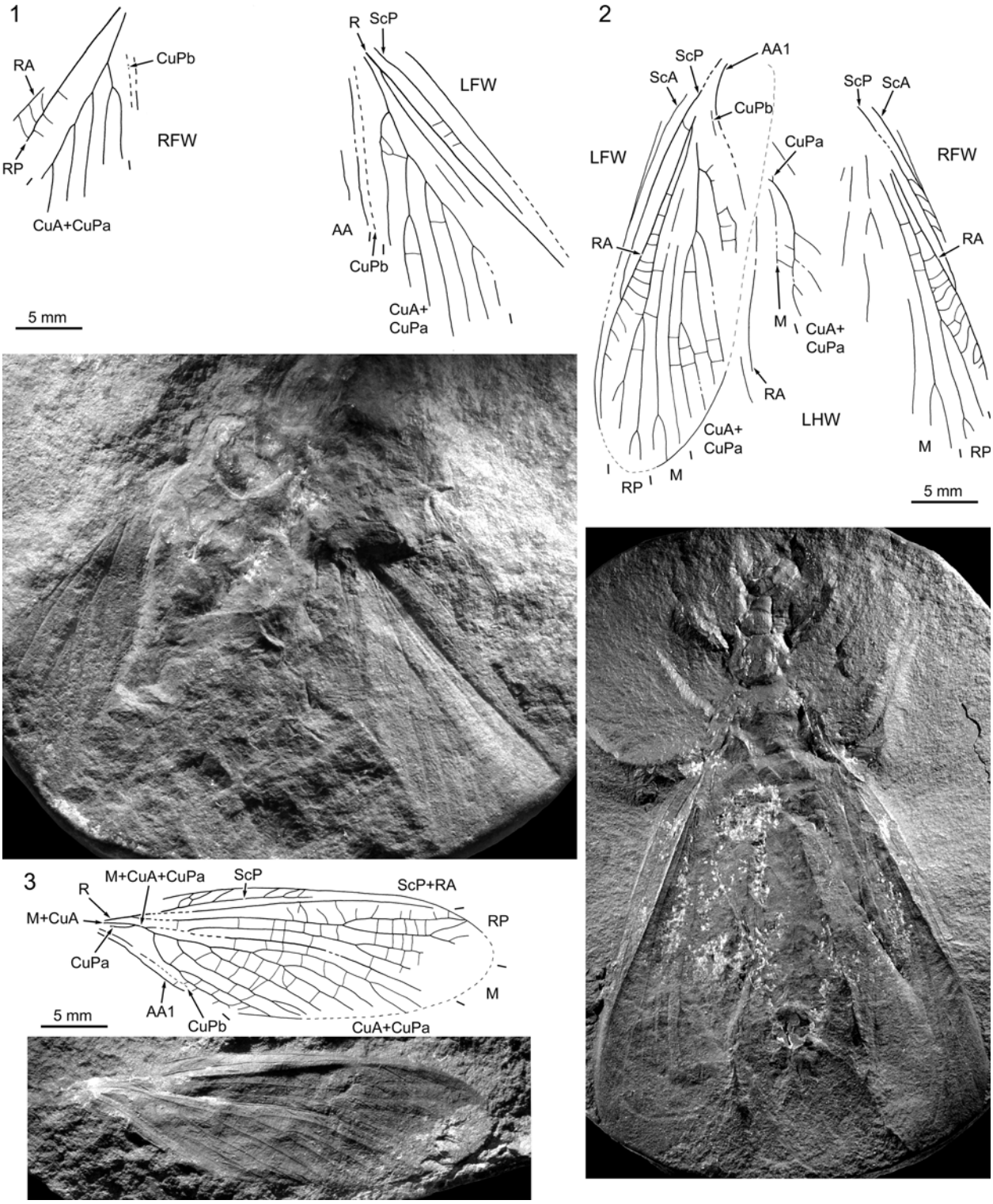

Fig. 1. Species *bronsoni* Dana, 1864 (Pennsylvanian; Mazon Creek, IL, USA; see text for abbreviations). **1**: Specimen FMNH UC 6392 (holotype of *contusa* Scudder, 1885): reconstruction of the wing venation and photograph (negative imprint). **2**: Specimen FMNH UC 6391 (holotype of *infernus* Scudder, 1885): reconstruction of the wing venation and photograph (positive imprint, dry). **3**: Specimen FMNH UC 9240 (holotype of *clarinervis* Melander, 1903), reconstruction of the venation and photograph (positive imprint, composite).

CuPa fuses with M + CuA; M + CuA + CuPa 0.9 mm long, separating into M and CuA + CuPa; stem of M and posterior branch of M strongly concave; anterior branch of M simple for a long distance; as preserved, posterior branch of M simple; CuA + CuPa posteriorly pectinate, with 8 branches reaching the posterior wing margin; cross-veins spaced apart, mostly not reticulated.

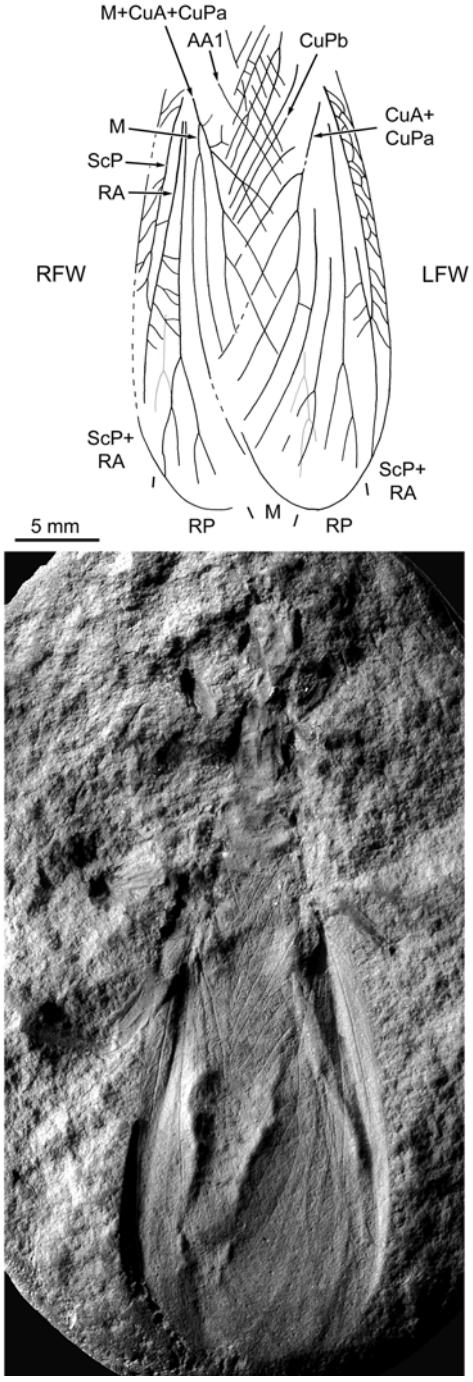

Fig. 2. Species *bronsoni* Dana, 1864 (Pennsylvanian; Mazon Creek, IL, USA), specimen FMNH UC 9241 (holotype of *extensa* Melander, 1903), reconstruction of the wing venation (hind wings in gray) and photograph (negative imprint, composite).

Specimen FMNH UC 9241 (holotype of *extensa* Melander, 1903; Fig. 2): moderately well-preserved specimen, with well visible head and thoracic remains, wings in resting position, negative imprint; hind wing remains not interpretable; head and prothorax about 5 mm and 7 mm long, respectively; forewings: length about 31 mm; ScP with strong and oblique veinlets, with cross-veins between them; RP branched distally; right forewing: M branched 1.8 mm distal to its divergence from M + CuA + CuPa; CuA + CuPa branched 1.8 mm distal to its divergence from M + CuA + CuPa; left forewing: ScP + RA simple; anterior branch of M branched, posterior branch of M simple; CuA + CuPa posteriorly pectinate, with 5 branches reaching posterior wing margin; CuPb concave, AA1 convex, both simple; numerous AA veins.

Specimen FMNH UC 9243 (holotype of *indistinctus* Melander, 1903): poorly preserved specimen, thorax, abdomen, and forewings in resting position, positive and negative imprint; forewings: length about 35 mm, ScP reaching RA; strong sigmoid cross-veins between RA and RP; CuA + CuPa strongly convex, posteriorly pectinate.

Specimen USNM 38817 (holotype of *ambulans* Handlirsch, 1906; Fig. 3.1): well-preserved specimen, with head and thoracic remains, negative and positive imprint; head and prothorax about 4.5 mm and 6.7 mm long, respectively; forewings: length about 33 mm, width about 9.3 mm; ScP with strong and oblique veinlets; ScP reaching RA; R branched opposite the first quarter of wing length; ScP + RA simple; area between RA and RP narrow, abruptly broadened opposite the end of ScP (on RA); M branched about 4.1 mm / 5.9 mm distal to its divergence from M + CuA + CuPa (left / right forewing, respectively); anterior branch of M forked distally; CuA + CuPa posteriorly pectinate, with 5 / 6 branches reaching the posterior wing margin; left forewing: RP simple for 13.2 mm, with 3 preserved branches; area between the posterior branch of CuA + CuPa and CuPb filled with strong, reticulated cross-veins; right forewing: RP with 5 branches reaching wing apex; posterior branch of M forked distally; right hind wing: length about 27 mm; area between RA and RP very narrow, but for a short distance; RP simple for 11.7 mm; M branched; CuPa fuses with CuA; anterior stem of CuA + CuPa sigmoid; CuA + CuPa posteriorly pectinate, with 5 branches.

Specimen USNM 38834 (holotype of *analis* Handlirsch, 1906: 700; Fig. 3.2): poorly preserved specimen, with nearly complete right forewing, very incomplete left forewing, and unidentifiable other body remains, positive imprint; right forewing: length about 37 mm long, width (at mid-length) 11.8 mm; area between anterior wing margin and ScP narrow. ScP with strong and oblique veinlets; area between RA and RP narrow for a long distance; left forewing: stem of M and posterior branch of M strongly concave.

Specimen YPM 24 (holotype of *longicollis* Handlirsch, 1911; Fig. 4.1): well-preserved specimen, with

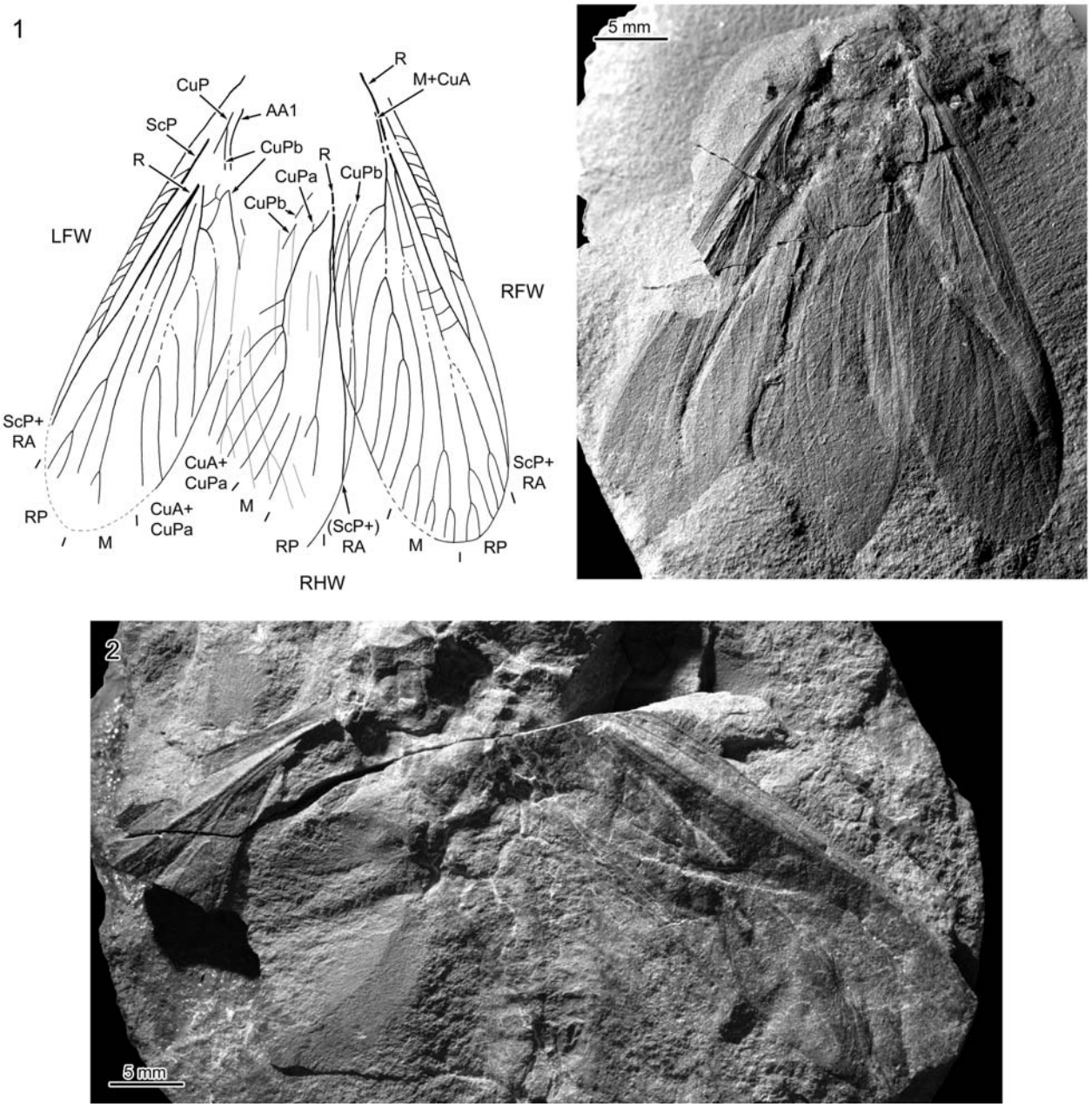

Fig. 3. Species *bronsoni* Dana, 1864 (Pennsylvanian; Mazon Creek, IL, USA). **1**: Specimen USNM 38817 (holotype of *ambulans* Handlirsch, 1906): reconstruction of the wing venation (left hind wing in light gray) and photograph (positive imprint, dry). **2**: Specimen USNM 38834 (holotype of *analis* Handlirsch, 1906: 700), photograph (positive imprint, dry).

head and thoracic remains, positive and negative imprint; forewings: length about 36 mm, width (at wing mid-length) 10.7 mm; ScP reaching RA; ScP with strong and oblique veinlets, with cross-veins between them; RA and RP diverging near the first quarter of wing length; area between RA and RP abruptly broadened opposite the end of ScP on RA, with strong cross-veins; stem of M and posterior branch of M strongly concave; CuA + CuPa posteriorly pectinate; area between the posterior branch of CuA + CuPa broad with a reticulated (aborted) CuA + CuPa branch; area between CuPb and AA1 narrow; CuPb concave, AA1 convex, both simple; cross-veins spaced apart, rarely reticulated; left forewing: anterior branch of M branched distally; CuA + CuPa with 8 branches reaching posterior wing margin; right forewing: ScP + RA simple; RP with at least 4 distal branches; M branched 2.7 mm distal of its origin from M + CuA + CuPa; anterior branch of M branched at its mid-length, with 4 preserved branches; posterior branch of M simple; CuA + CuPa branched near its point of divergence from M + CuA + CuPa, with 7 branches.

Specimen YPM 25 (holotype of *lata* Handlirsch, 1911; Figs. 4.2, 5): well-preserved specimen, mostly forewing remains, positive and negative imprint; forewings: length about 28.5 mm, width 7.9 mm;

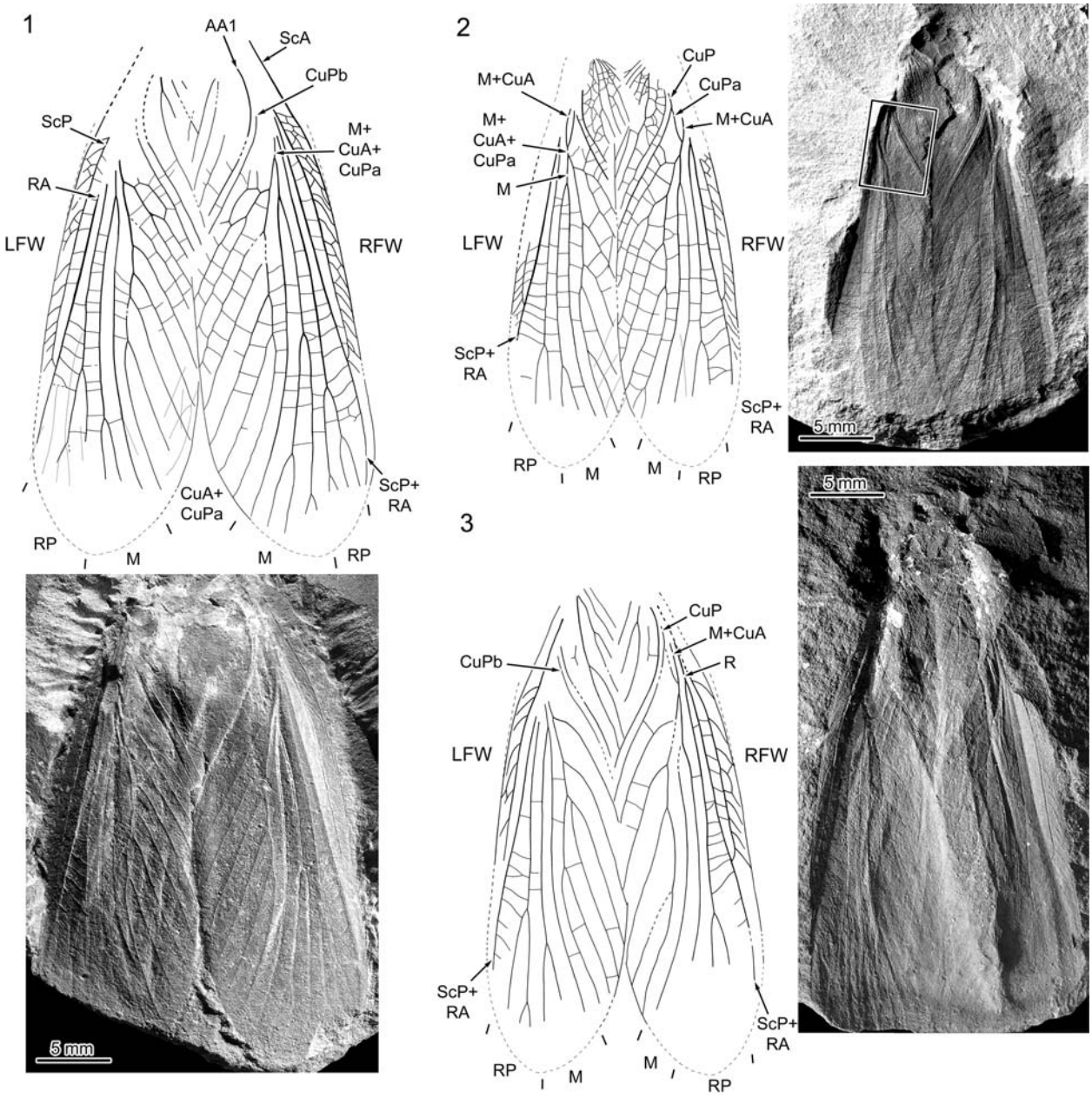

Fig. 4. Species *bronsoni* Dana, 1864 (Pennsylvanian; Mazon Creek, IL, USA). **1**: Specimen YPM 24 (holotype of *longicollis* Handlirsch, 1911): reconstruction of the wing venation (hind wings in gray) and photograph (positive imprint, dry). **2**: Specimen YPM 25 (holotype of *lata* Handlirsch, 1911): reconstruction of the wing venation (hind wings in gray) and photograph (negative imprint, composite, flipped horizontally). **3**: Specimen YPM 26 (holotype of *elatior* Handlirsch, 1911): reconstruction (hind wing venation omitted) and photograph (negative imprint, dry, flipped horizontally, light-mirrored).

ScP reaching RA; RP branched 13.7 mm / 13.5 mm distal to its origin (left / right forewing, respectively); CuPa fuses with M + CuA; M + CuA + CuPa short (0.5 mm / 0.9 mm); M + CuA, M + CuA + CuPa, and CuA + CuPa convex and dark; M branched 1.9 mm distal of its origin from M + CuA + CuPa; as preserved, posterior branch of M simple; CuA + CuPa with 7 branches; area between the most proximal branch of CuA + CuPa and CuPb narrow; as preserved, CuPb concave, AA1 convex, both simple; numerous AA veins; cross-veins mostly not reticulated, except in the area between AA1 and other anal veins; coloration homogenous but for radial, CuA, and anal veins, indicated by darker coloration.

Specimen YPM 26 (holotype of *elatior* Handlirsch, 1911; Fig. 4.3): moderately well-preserved specimen, fore- and hind wing remains overlapping, positive and negative imprint; hind wing remains hardly interpretable; forewings: length about 33.6 mm, width about 9.4 mm; ScP with strong and oblique veinlets; ScP reaching RA; as preserved, ScP + RA simple; area between RA and RP narrow for a long distance, broader opposite the end of ScP, with

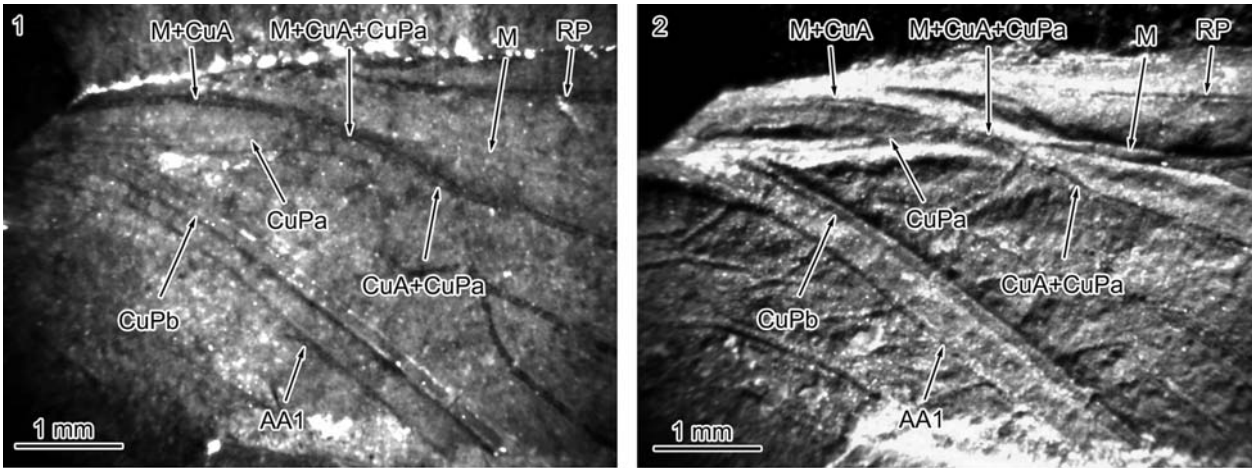

Fig. 5. Species *bronsoni* Dana, 1864 (Pennsylvanian; Mazon Creek, IL, USA), specimen YPM 25, photographs of the wing base as indicated on Fig. 4.2 [negative imprint; (**1**) ethanol, and (**2**) dry and light-mirrored].

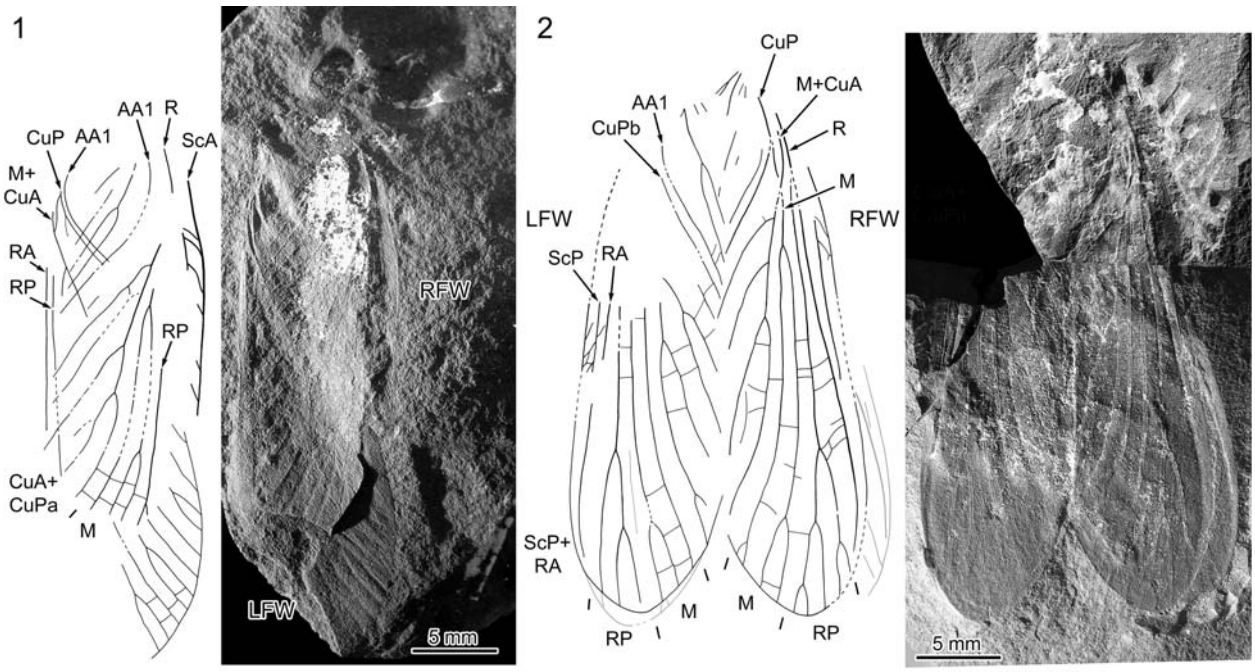

Fig. 6. Species *bronsoni* Dana, 1864 (Pennsylvanian; Mazon Creek, IL, USA). **1**: Specimen YPM 27 (holotype of *schucherti* Handlirsch, 1911): reconstruction of the wing venation and photograph (positive imprint, dry). **2**: Specimen YPM 28 (holotype of *acutipennis* Handlirsch, 1911): reconstruction of the wing venation (hind wings in gray) and photograph (positive and negative imprint, negative imprint flipped horizontally, dry).

strong cross-veins; RP branched distally; as preserved, posterior branch of M simple; CuA + CuPa posteriorly pectinate with 6 / 5 branches (left / right forewing, respectively); as preserved, CuPb concave, AA1 convex, both simple; left forewing: anterior branch of M branched distally; right forewing: CuPa fuses with M + CuA; M + CuA + CuPa short (0.7 mm).

Specimen YPM 27 (holotype of *schucherti* Handlirsch, 1911; Fig. 6.1): well-preserved but very incomplete specimen, forewing pair, positive imprint; forewings: length about 31 mm; left forewing: area between RA and RP narrow for a long distance; CuP branched; right forewing: ScP with strong and oblique veinlets; RP and M branched; CuA + CuPa with 6 or 7 branches.

Specimen YPM 28 (holotype of *acutipennis* Handlirsch, 1911; Fig. 6.2): moderately well-preserved specimen, mostly a pair of incomplete forewings, positive and negative imprint; forewings: length about 32.6 mm; RP with 3 / 5 branches (left / right forewing, respectively); anterior branch of M forked; posterior branch of M simple; left forewing: CuA + CuPa

with 5 or 6 branches; right forewing: long narrow area between RA and RP; right forewing: CuP branched; CuPa fuses with M + CuA; CuA + CuPa posteriorly pectinate, with at least 4 branches.

Specimen YPM 29 (holotype of *parvula* Handlirsch, 1911; Fig. 7.1): poorly preserved and very incomplete specimen, negative imprint; forewings: length about 25 mm, width about 7.4 mm; left forewing: ScP directed towards RA; RP branched distally; CuA + CuPa posteriorly pectinate, with 5 branches.

Specimen YPM 30 (holotype of *angusta* Handlirsch, 1911; Fig. 7.2): poorly preserved specimen, head and thoracic remains; left forewing: ScP with strong and oblique anterior veinlets; ScP reaching RA; RP branched; right forewing: area between RA and RP narrow for a long distance; M branched proximally.

Specimen FMNH PE 31967 (neotype; Fig. 8): well preserved specimen, thoracic remains, mostly forewings and apex of hind wings, negative and positive imprint; forewings: length about 39 mm, width 11.0 mm; area between RA and RP narrow for a long distance, abruptly broader opposite the end of ScP on RA; strong cross-veins in the area between RA and RP; RP branched distally, with 5 branches; RA + ScP reaching the anterior branch of RP; CuPa fusing with M + CuA; M + CuA + CuPa short (0.5 mm / 1.0 mm, right and left forewing, respectively); M branched 3.1 mm / 2.8 mm distal to its origin from M + CuA + CuPa; anterior branch of M branched proximally with respect to RP; CuA + CuPa posteriorly pectinate, with 6 / 7 branches; area between the posterior branch of CuA + CuPa and CuPb with strong cross-veins; CuPb concave, AA1 convex, both simple; right forewing: CuP concave, branched; left forewing: anterior branch of M posteriorly pectinate, with 4 branches; posterior branch of M simple.

Specimen FMNH PE 31955 (Fig. 9): moderately well preserved and very incomplete specimen, forewing bases and incomplete hind wings; forewings: area between AA1 and other anal veins broad, with reticulated cross-veins; left forewing: CuP, CuPa and CuPb concave; CuPa fuses with M + CuA; M + CuA + CuPa convex, short; hind wings: area between RA and RP very narrow for a short distance; in wing distal half, area between RA and RP very broad; RP with 4 or more branches.

Specimen FMNH PE 30369 (Fig. 10): well-preserved female specimen, dorsal view, positive imprint; head, thorax, forelegs, base of mid- and hind legs, forewings and abdomen visible; body length (apex of head to end of abdomen) 38.3 mm; head globular, 3.8 mm long, 3.2 wide; prothorax 6.0 mm long, about 3 mm wide; forelegs: femur 4.7 mm long, tibia 4.4 mm long; tarsus with 4 distinguishable tarsomeres, apex incomplete; at least some tarsomeres with lateral expansions; forewings: 30.4 mm long; ScP reaching RA; area between RA and RP broadened opposite the end of ScP on RA, with strong sigmoid cross-veins;

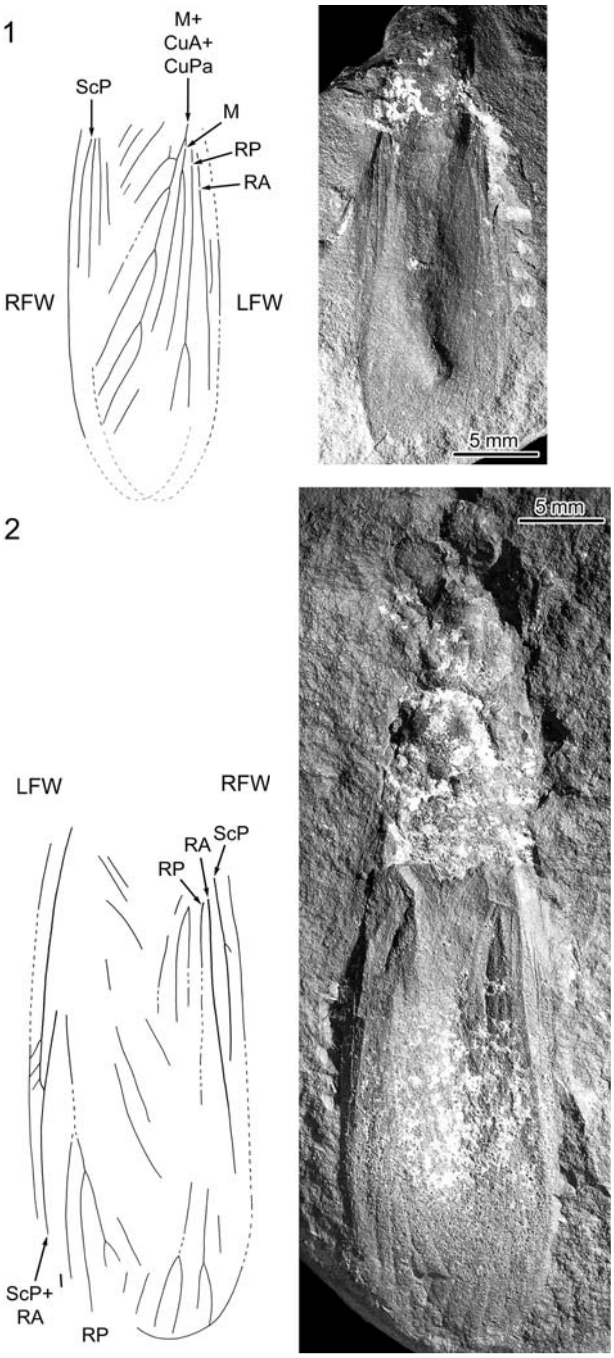

Fig. 7. Species *bronsoni* Dana, 1864 (Pennsylvanian; Mazon Creek, IL, USA). **1**: Specimen YPM 29 (holotype of *parvula* Handlirsch, 1911): reconstruction of the wing venation and photograph (negative imprint, dry, light-mirrored). **2**: Specimen YPM 30 (holotype of *angusta* Handlirsch, 1911): reconstruction of the wing venation and photograph (positive imprint, dry).

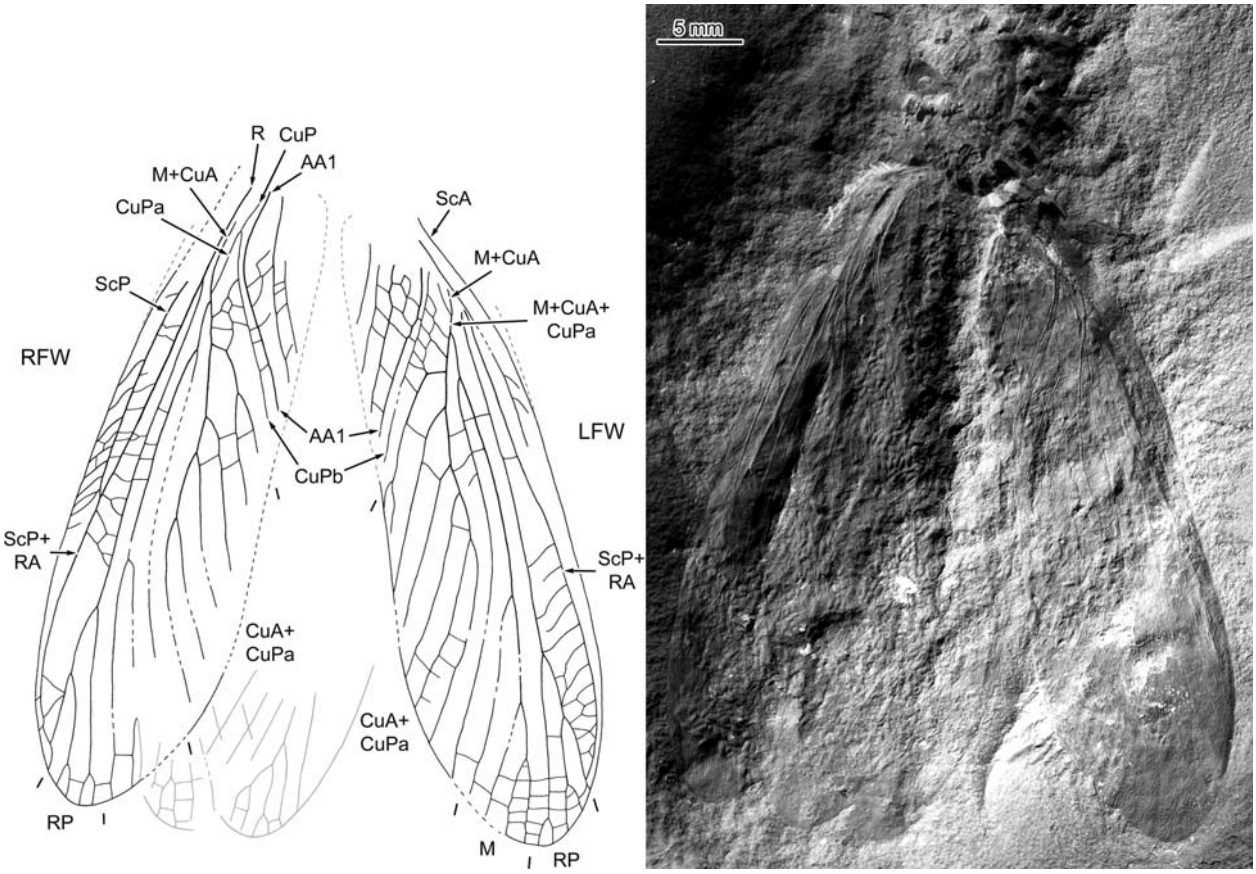

Fig. 8. Species *bronsoni* Dana, 1864 (Pennsylvanian; Mazon Creek, IL, USA), specimen FMNH PE 31967 (neotype): reconstruction of the wing venation (hind wings in gray) and photograph (negative imprint, composite, light mirrored).

RP branched distally, with 5 branches reaching apex; o v i p o s i t o r : as preserved, gonapophyses VIII 2.1 mm long; coxae VIII and subgentital plate might be preserved.

Type material. FMNH PE 31967 (neotype).
Other material. FMNH UC 6391, FMNH UC 6392, FMNH UC 9240, FMNH UC 9241, FMNH UC 9243, FMNH PE 29399, FMNH PE 30369, FMNH PE 31955, FMNH PE 31967, FMNH PE 32044, USNM 38156, USNM 38817, USNM 38834, YPM 24, YPM 25, YPM 26, YPM 27, YPM 28, YPM 29, YPM 30; additional specimens listed by Burnham (1986) but not documented in the current revision: FMNH PE 28731; FMNH PE 29368; FMNH 29376; FMNH 29402; USNM 38805; in addition Burnham (1986) lists the following material from the private collection of S. LeMay, SLM 1417, which is currently held by the Museum of Comparative Zoology (MA, USA).

Remarks. The specific identity of the specimens listed above will to be discussed first. The case of the holotype of *bronsoni* will be discussed later on.

The two incomplete forewings of the specimen FMNH UC 6392 (holotype of *contusa*) exhibit a proximal point of divergence of RA and RP, a long narrow area between RA and RP, RA and RP diverging abruptly, and a posteriorly pectinate CuA (+ CuPa), with at least seven branches reaching the posterior wing margin. As far as it can be observed, most cross-veins are not reticulated. The well-preserved specimens YPM 24 (Fig. 4.1), YPM 25 (Figs. 4.2, 5), and USNM 31967 (Fig. 8) can be assigned to same species on the basis of these character states. These specimens allow the following forewing character states to be added to the diagnosis of *bronsoni*: ScP with oblique anterior veinlets, with cross-veins between them; ScP reaching RA; in its distal half, area between RA and RP broad, with reticulated cross-veins; RP branched distally; CuP branched; CuPa fused with M + CuA (hence the 'CuA' of previous authors is CuA + CuPa); M branched proximally; posterior branch of M simple. In the left and right forewings of the specimen YPM 24, CuA + CuPa is provided with 8 and 7 branches, respectively. In the right and left forewings of the specimen FMNH PE 31967, CuA + CuPa is provided with 6 and 7 branches, respectively. The diagnostic range of variation of the number of branches of CuA + CuPa is then 6-8.

In the specimen USNM 38817 (Fig. 3.1), which conforms to the current diagnosis, CuA + CuPa exhibit 6 branches in the right forewing, and 5 in the left one. The range of variation of the number of branches of CuA + CuPa should then be extended to 5–8. Based

on information gathered from this specimen, the diagnosis of *bronsoni* is: (forewing with) CuA + CuPa with 5–8 branches; (hind wing with) RP branched; M branched; CuP branched; CuPa fused with CuA; CuA + CuPa posteriorly pectinate, with at least five branches reaching the posterior wing margin.

The specimen FMNH PE UC 6391 (Fig. 1.2) complies with this diagnosis, except for its ScA distinct from the anterior forewing margin. Incomplete preservation of this area, known in genuine orthopterans (BÉTHOUX & NEL 2002b: fig. 2), can be accounted for the apparent lack of this structure in other specimens of *bronsoni*. Indeed, the inflexion of the 'apparent anterior wing margin' (*i.e.* actual ScA) in the specimen YPM 24, among others, is typical of a ScA distinct from the anterior wing margin. All other specimens listed in the Material sub-section comply with this diagnosis.

BURNHAM (1986) maintains the species *infernus* (holotype on Fig. 1.2), *ambulans* (holotype on Fig. 3.1), and *schucherti* (holotype on Fig. 6.1) as valid different species. The species *infernus* is said to have forewings narrower than *ambulans*, with less numerous and more distant branches of CuA; and the prothorax of *infernus* is said to be quadrate. However, in both holotypes of *infernus* and *ambulans*, forewing width approximates 9 mm, and the holotype of *schucherti* is so incomplete that forewing width cannot be reliably estimated; the range of the number of branches of CuA + CuPa is consistent with a specific identity, as indicated by intra-individual variations (see above); and the prothorax of *infernus* is not quadrate but elongate (see Fig. 1.2). The species *ambulans* is said to differ from *infernus* and *schucherti* after broader forewings, held slightly apart; and CuA + CuPa with 5–6 branches spaced apart. However, as previously mentioned, all these character states fall within the range of individual variation (the position of the wings is arguably uninformative). Regarding *schucherti*, BURNHAM (1986) maintains the species on the basis of a presumed lower size, with an estimated forewing length of 25 mm. However, my observations suggest that the forewing length of the holotype of *schucherti* is about 31 mm. This figure is not significantly different from the wing length of the holotypes of *infernus* and *ambulans* (both about 33 mm). In addition, a Shapiro-Wilk test carried out on forewing length of the specimen illustrated in this contribution indicates that the hypothesis of a normal distribution is most likely (W: 0.97; p: 0.90). Therefore, the species *infernus*, *ambulans* and *schucherti* can no longer be considered as distinct. All species whose holotypes are listed in this sub-section are then putative junior synonyms.

As stated by BURNHAM (1986: 165), the location of the holotype of *bronsoni* is unknown. Information on the specimen can be found in DANA (1864) and SCUDDER (1866). According to the figures provided by these

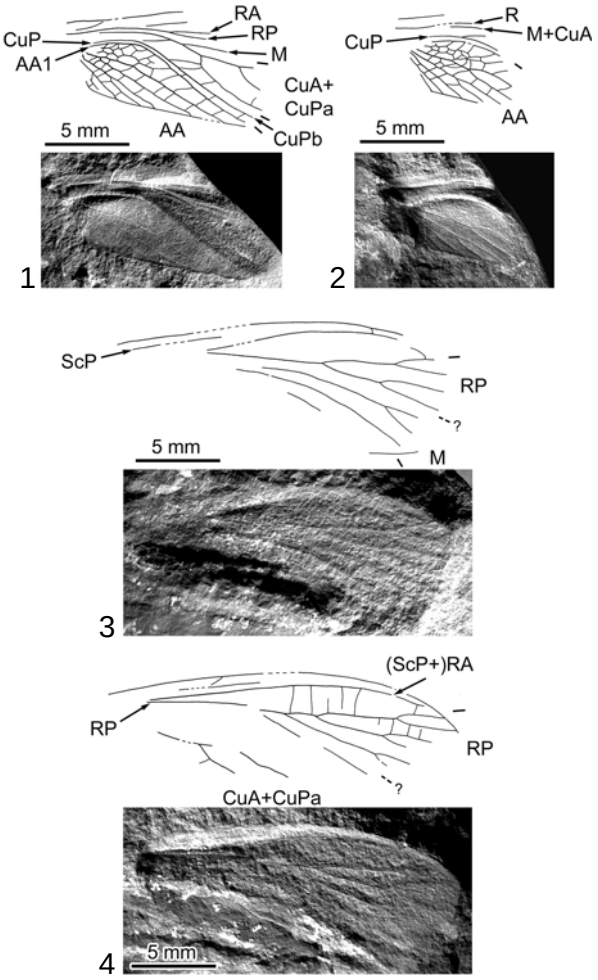

Fig. 9. Species *bronsoni* Dana, 1864 (Pennsylvanian; Mazon Creek, IL, USA), specimen FMNH PE 31955: reconstructions and photographs (negative imprint, dry, might mirrored) of **1**: the left forewing, **2**: right forewing (flipped horizontally), **3**: left hind wing, and **4**: right hind wing (flipped horizontally).

authors, the forewing length was about 30–33 mm, which is consistent with the size range of the specimens listed above. In addition, these authors figured a ScP with strong and oblique veinlets, with cross-veins between them. SCUDDER (1866) figured a broad area with sigmoid cross-veins similar to the area between RA and RP, opposite the end of ScP, as in specimens listed above. After both authors, RP is distally branched, as in specimens listed above. After DANA (1864) a posteriorly pectinate vein, similar to CuA + CuPa as in specimens listed above, can be identified. Therefore, the species the holotypes of which are listed above are likely synonymous with *bronsoni*. Since the holotype of *bronsoni* has not been recovered, and since the taxonomic status of a number of potentially synonymous species must be clarified, I propose to designate the specimen FMNH PE 31967 as neotype. It has been collected in the same locality as the holotype of *bronsoni*, it is not the holotype of another species, and it is well preserved.

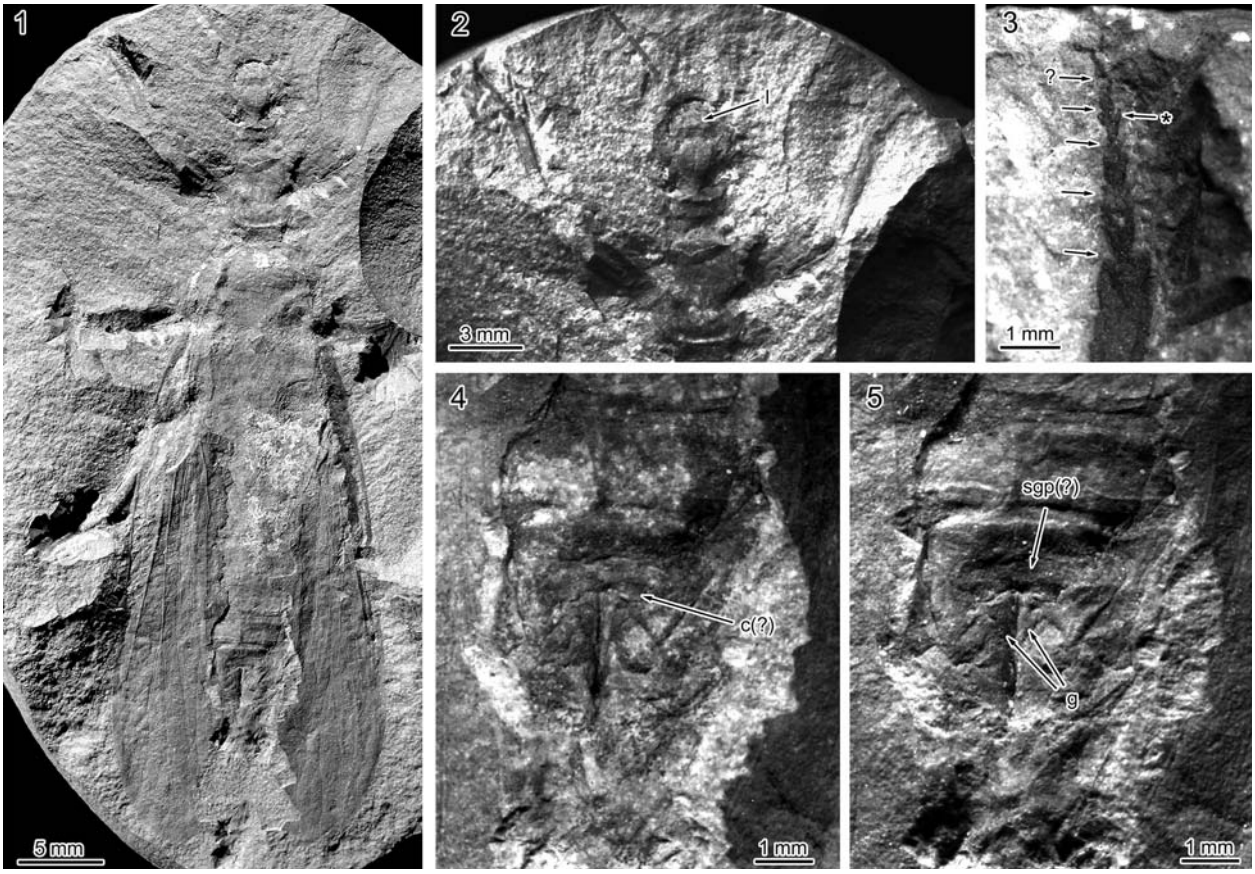

Fig. 10. Species *bronsoni* Dana, 1864 (Pennsylvanian; Mazon Creek, IL, USA), specimen FMNH PE 30369. **1**: Photograph of the complete specimen (positive imprint dry). **2**: Photograph of the head, forelegs, and thorax (composite); l: labrum. **3**: Photograph of the left foreleg tarsus (ethanol); * indicates a lateral extension of a tarsomere. **4**: Photograph of the ovipositor (ethanol); c(?): coxa VIII(?). **5**: Photograph of the ovispositor (dry); spg(?): subgenital plate (?); g: gonapophyses VIII.

The species *longicollis* Handlirsch, 1906, erected as type-species of the genus *Gyrophlebia* Handlirsch, 1906 and assigned to the Linnaean family Spanioderidae by Handlirsch (1906), is here considered as a *nomen dubium*. The positive imprint of the holotype (USNM 38150) has been subjected to intensive preparation similar to that described by Béthoux & Briggs (2008). The extent of this treatment prevents authentic fossil parts to be identified. The negative imprint provides no valuable information for the taxonomic assignment of this species.

Species *silvatica* Laurentiaux & Laurentiaux-Vieira, 1980

(Fig. 11)

Species *silvatica*
Laurentiaux & Laurentiaux-Vieira, 1980: 407, figs. 1–2, pl. II figs. 1–4 (erected as type-species of the genus *Anthraconeura* Laurentiaux & Laurentiaux-Vieira, 1980); Carpenter 1992: 103; holotype: MGL 4234.

Diagnosis. F o r e w i n g : length about 16 mm, width about 4 mm; RP with at least 7 branches; fusion of CuPa with M + CuA, divergence of M and CuA + CuPa, and first fork of CuA + CuPa occurring near or at the same point; anterior branch of M simple; CuA + CuPa with 3 branches.

Occurrence. North Coal basin, Pas-de-Calais, France; Westphalian C (Pennsylvanian).

Description. Specimen MGL 4234 (Fig. 11): positive and negative imprints of a well-preserved forewing pair; f o r e w i n g s : length 15.9 mm, width 4.3 mm; ScP reaching RA, with strong and oblique anterior veinlets; ScP + RA simple; RA and RP diverge opposite the first third of wing length; area between RA and RP narrow for some distance, and broader opposite the end of ScP on RA; RP branched 4.1 mm / 5.3 mm distal to its origin (left / right forewing, respectively); M + CuA and CuA + CuPa convex; anterior branch of M simple; fusion of CuPa with M + CuA, divergence of M and CuA + CuPa, and first fork of CuA + CuPa occurring near or at the same point; CuA + CuPa with 3 branches; CuPb and AA1 simple; area between CuPb and AA1 narrow; numerous AA veins; cross-veins spaced apart, mostly not reticulated; l e f t

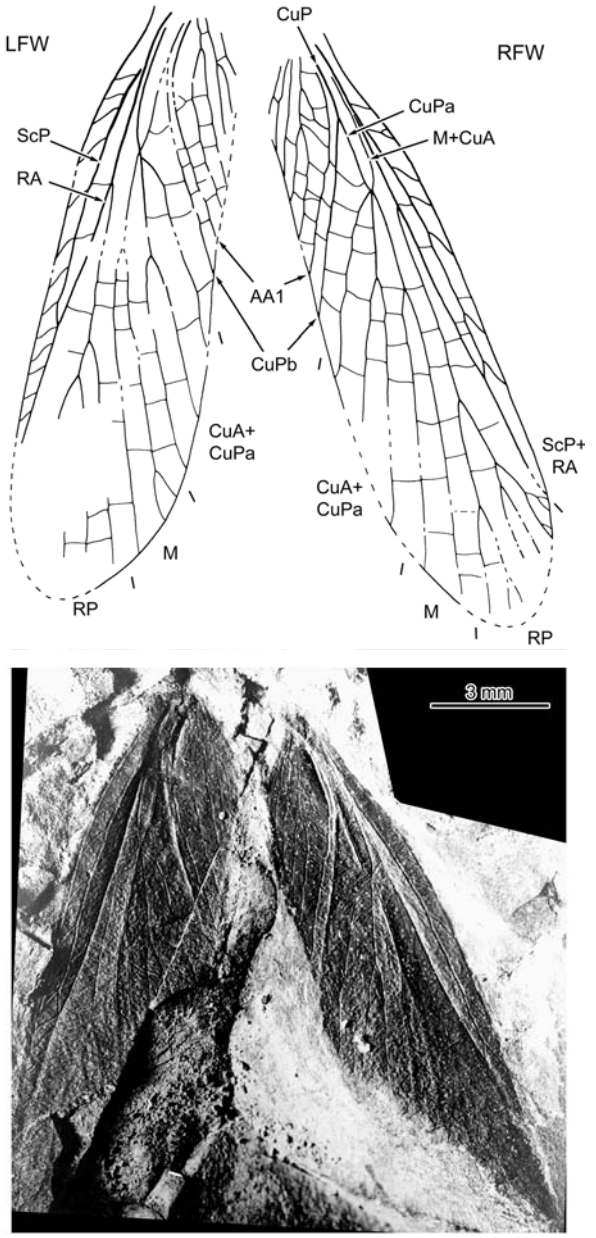

Fig. 11. Species *silvatica* Laurentiaux & Laurentiaux-Vieira, 1980 (Pennsylvanian; North Coal Basin, France), specimen MGL 4234 (holotype): reconstruction and photograph (positive imprint; reproduced from LAURENTIAUX & LAURENTIAUX-VIEIRA 1980; courtesy of the 'Société Géologique du Nord').

forewing: posterior branch of M with a distal fork; right forewing: M branched 2.7 mm distal to its divergence from M + CuA; RP with at least 7 branches reaching wing apex.

Type material. MGL 4234, housed at the Natural History, Geology, and Ethnography Museum of Lille (France; *contra* LAURENTIAUX & LAURENTIAUX-VIEIRA 1980).

Remarks. As for most specimens of *bronsoni*, the anterior wing margin is most probably not preserved near the wing base. The vein sector ScA was probably distinct from the anterior wing margin, as indicated by the strong curvature of the preserved 'margin'. The homologization of the forewing venation on *silvatica* by LAURENTIAUX & LAURENTIAUX-VIEIRA (1980) is supported by my observation: CuP is divided into two clearly concave veins, the anterior one fusing with the convex M + CuA composite vein; CuA + CuPa is provided with 3 clearly convex veins.

Species *rigida* Scudder, 1885, *nomen dubium*

(Fig. 12)

Species *rigida* Scudder,
1885: 336, pl. 29 fig. 10; HANDLIRSCH 1906: 699 (referred to as *rigidus*; erected as type-species of the genus *Dieconeurites* Handlirsch, 1906); CARPENTER 1992: 132.

Occurrence. Pittston, PA (USA); Westphalian (Pennsylvanian).

Description. Specimen USNM 38156: poorly preserved and incomplete forewing; preserved length about 18 mm, width 6.4 mm; ScP reaching RA; RA and RP diverging proximally; area between RA and RP broadened opposite the end of ScP on RA; M (diverging from M + CuA + CuPa) branched proximally; CuA + CuPa posteriorly pectinate, with 5 or 6 branches.

Type material. USNM 38156.

Discussion. All observable character states of the wing venation of the holotype of *rigida* are similar to those observed in *bronsoni* (*contra* BURNHAM 1986). The specimen differs from all *bronsoni* specimens by its narrower forewing. However, it is plausible that the specimen experienced plastic deformation, making irrelevant a distinction of a species based on size only. Therefore *rigida* is considered as a *nomen dubium*, because the holotype specimen might actually belong to *bronsoni*. As a result, according to the Linnaean procedure, the genus *Dieconeurites* Handlirsch, 1906, which type-species is *rigida*, must, at best, be considered as a junior synonym of *Miamia* Dana, 1864 (if not as a *nomen dubium*; see Appendix).

4. Discussion

4.1. Phylogenetic position of *bronsoni* and *silvatica*

An eoblattid-spanioderid assemblage, including *bronsoni*, is considered by RASNITSYN (2002 a, b) as the

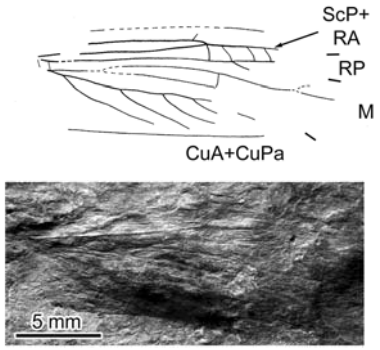

Fig. 12. Species *rigida* Scudder, 1885, *nomen dubium* (Pennsylvanian; PA, USA), specimen USNM 38156: reconstruction and photograph (positive imprint, composite).

"core" of a paraphyletic order Eoblattida, stem-group of 'Polyneoptera' (Rasnitsyn's Gryllones). It has now been suggested that, within polyneopterans, a number of species considered by Rasnitsyn (2002a) as stem-polyneopterans are more closely related to representatives of the Linnaean order Orthoptera (i.e., grasshoppers, crickets) than to any other Linnaean order (Béthoux & Nel 2004; Béthoux 2005c; Béthoux & Nel 2005; see also Prokop & Ren 2007). The taxon *Archaeorthoptera nom*. Béthoux & Nel 2002a, *dis.-typ*. Béthoux 2007e encompasses orthopterans and some of their 'eoblattidan' fossil relatives.

Several species of Rasnitsyn's eoblattid-spanioderid assemblage are now assigned to a distinct group, namely the order Cnemidolestodea Handlirsch, 1937, within *Archaeorthoptera* (Béthoux 2005a). Remaining species, such as *cubitalis* Handlirsch, 1911, *elongata* Brongniart, 1893: 433, and *robusta* Brongniart, 1893: 431, have an uncertain position within *Archaeorthoptera*. A number of new species were recently described and considered as close relatives of lobeattids [*huangheense* Prokop & Ren, 2007, *mazonus* Béthoux, 2005c, and *schneideri* Béthoux, 2005c (a new specimen of which is illustrated on Fig. 13)]. Béthoux (2005c) considered these species as related, belonging to a 'lobeattid' group. The point is to determine whether *bronsoni* and *silvatica* are related to this subset, partly supporting Rasnitsyn's (2002a,b) proposition. In first instance this revision demonstrates that *bronsoni* exhibits the defining character state of *Archaeorthoptera*, that is 'in forewings, CuA (fused with M or diverging from it) connected to CuP or one of its branches' (Béthoux 2007e). The occurrence of a CuPa branch in *bronsoni* has been overlooked by all previous researchers. It is distinctly preserved in specimens FMNH UC 9240 (Fig. 1.3), YPM 25 (Figs. 4.2, 5), YPM 26 (Fig. 4.3), YPM 28 (Fig. 6.2), FMNH PE 31967 (Fig. 8), and FMNH PE 31955 (Fig. 9). Laurentiaux & Laurentiaux-Vieira's (1980) homologization of the forewing venation of *silvatica*, supported by our re-investigation, implies that *silvatica* also exhibit the defining character state of *Archaeorthoptera*.

Within *Archaeorthoptera*, *bronsoni* and *silvatica* do not exhibit the diagnostic character states of the cnemidolestodeans, nor of the more derived panorthopterans (see Béthoux & Nel 2002a; Béthoux 2005a). Indeed, like lobeattids, these species have, in forewings, (1) a very short free part of CuA (after its divergence from M and before its fusion with CuPa; it is even inexistent in *Miamia*), (2) a point of divergence of RA and RP located proximally with respect to the end of AA1 on the posterior wing margin, and (3) a long narrow area between RA and RP (Béthoux 2005c; Béthoux & Nel 2004, 2005; Prokop & Ren 2007; Fig. 13). These character states can be considered as diagnostic of lobeattid insects.

Polarizing these states is difficult, because putative amitataxa and adelphotaxa are poorly known. The species *dumasii* does not exhibit a fusion of CuA with CuP in hind wings, this qualifying it as a relevant outgroup (see Béthoux 2003). This species exhibit a comparatively longer free part of CuA [as opposed to (1)], and a comparatively more distal point of divergence of RA and RP. The state for the third character is difficult to appreciate in this species, due to the incompleteness of the available material. The position of *spilopterus* Handlirsch, 1911 within *Archaeorthoptera* is uncertain (see Béthoux 2006). In this species the free part of CuA is comparatively long [as opposed to (1)], the divergence of RA and RP is located distally [as opposed to (2)], and the area between RA and RP is progressively broadened [as opposed to (3)]. The morphology of the few (and poorly known) species whose phylogenetic position within *Archaeorthoptera* is also uncertain (notably *macroptera* Van Beneden & Coemans, 1867, *palmiformis* Bolton, 1922, and *carbonis* Handlirsch, 1904; see Béthoux & Nel 2004, 2005) suggests that the states listed above for lobeattids are derived.

Most Pennsylvanian panorthopterans neither share the character states (1), (2), or (3) (Béthoux & Nel 2003; unpubl. obs.). However, caloneurodeans share the character states (1) and (2) (see Béthoux et al. 2004). Among cnemidolestodeans, some species such as *oustaleti* Brongniart, 1885 share the character states (2) and (3). Therefore, there is some conflict between the diagnostic character states of lobeattids, panorthopterans, and cnemidolestodeans. As a working hypothesis, I assume that panorthopteran and cnemidolestodan clades hold. In other words, I provisionally consider that their representatives acquired the character states (1), (2), and/or (3) convergently, hence lobeattids form a monophyletic group. At this step a numerical cladistic analysis is necessary for a more positive assessment of the lobeattids as a valid

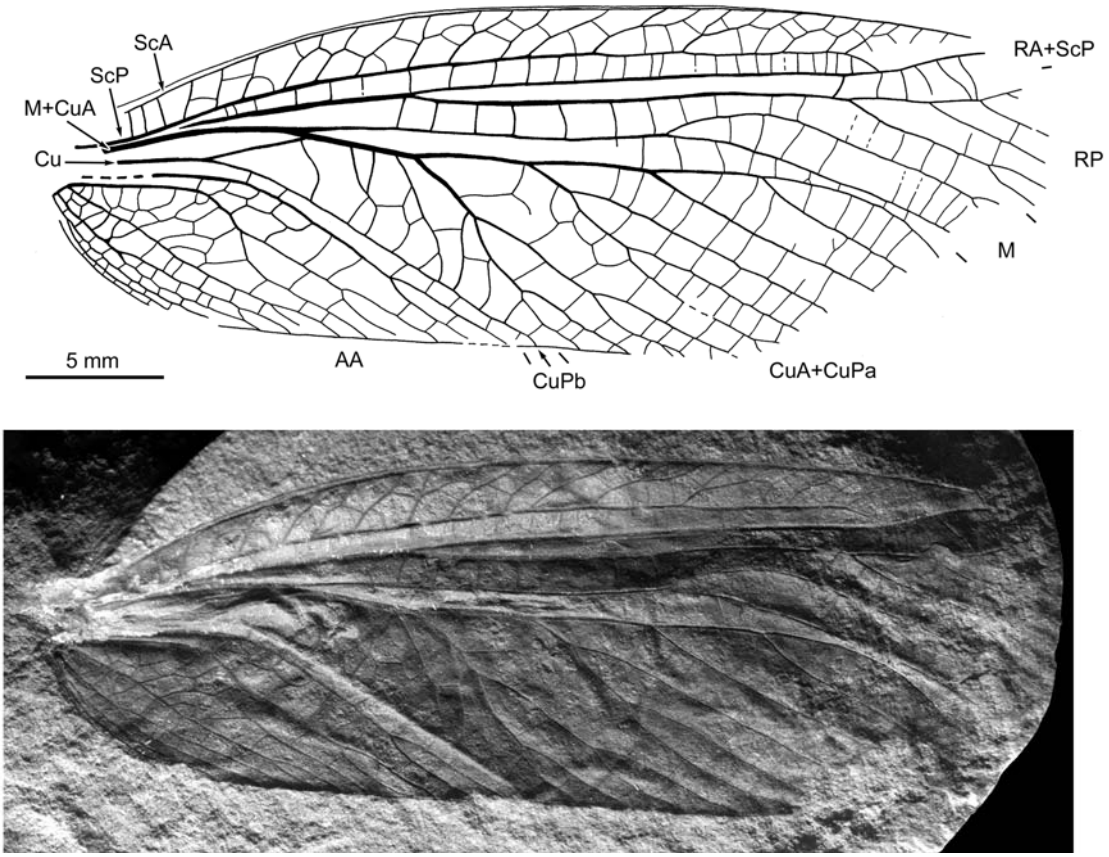

Fig. 13. Species *schneideri* Béthoux, 2005c (Pennsylvanian; Mazon Creek, IL, USA), specimen USNM 440084: reconstruction and photograph (negative imprint, reversed, light-mirrored, composite).

(*i.e.* monophyletic) taxon, eventually allowing a formal definition.

In summary, our current knowledge suggests that RASNITSYN (2002a,b) is correct at assuming that 'spanioderid' and (some of his) 'eoblattid' insects form an 'assemblage', although his argumentation was based on an erroneous homologization of the wing venation of *bronsoni* (and although he erroneously assigned *silvatica* to the order Hypoperlida in RASNITSYN 2002c: 111).

4.2. Intra-specific variability

Variability in forewing size and venation pattern is unknown for the vast majority of Pennsylvanian insects, because most species are known after few specimens, most frequently incomplete. The species *bronsoni* is the first lobeattid species known after more than five well-preserved specimens exhibiting mostly complete forewing pair. A number of conditions that could be qualified of 'unusual' could be observed. In the right forewing of the specimen USNM 38817 (Fig. 3.1) the posterior branch of M is forked, while this vein is simple in other specimens. In the right forewing of the specimen YPM 24 (Fig. 4.1) and in both forewings of the specimen FMNH PE 31967 the vein M is branched proximally with respect to RP, while the usual condition involves a more distal branching of M. There is some variability in the location of the first fork of M (Figs. 3, 4.3). The venation pattern in the area between the posterior branch of CuA + CuPa and CuPb is poorly constrained. It is filled with crossveins, or aborted or reticulated genuine branches of CuA + CuPa (see Fig. 4.1). The documentation of such variation might prevent the erection of invalid species in the future.

5. Conclusion

Fifteen insect species from Mazon Creek, the taxonomic status of which was not properly assessed, happen to be synonymous. As a result, the species *bronsoni* appears as one of the commonest insect species of this locality. New information on *bronsoni* allowed its close relationship with *silvatica*, from the Pennsylvanian of France, to be evidenced, and their assignment to the taxon *Archaeorthoptera* to be assessed. This revision suggests that substantial additional contribu-

tions on Mazon Creek insect taxa will be necessary for completing synthetic results on the early steps of winged insect evolution.

6. Acknowledgement

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Appendix

Genus *Miamia* Dana, 1864

Miamia Dana, 1864: 35; Carpenter, 1992: 133.

Didymophlebs Scudder, 1885: 330; Handlirsch 1906: 808; Carpenter 1992: 132: new synonymy.

Propteticus Scudder, 1885: 334; Handlirsch 1906: 698; Carpenter 1992: 122; new synonymy.

Petromartus Melander, 1903: 191; Handlirsch 1906: 699; Carpenter 1922: 122 (synonymy with *Propteticus*); new synonymy.

Spaniodera Handlirsch, 1906: 696; Carpenter 1992: 122 (synonymy with *Propteticus*); new synonymy.

Camptophlebia Handlirsch, 1906: 698; Carpenter 1992: 122 (synonymy with *Propteticus*); new synonymy.

Paracheliphlebia Handlirsch, 1906: 699; Carpenter 1992: 122 (synonymy with *Propteticus*); new synonymy.

Dieconeurites Handlirsch, 1906: 699; Carpenter 1992: 132; new synonymy.

Metryia Handlirsch, 1906: 700; Carpenter 1992: 122 (synonymy with *Propteticus*); new synonymy.

Anthraconeura Laurentiaux and Laurentiaux-Vieira, 1980: 407; Carpenter 1992: 103; new synonymy.

Type-species. *Miamia bronsoni* Dana, 1864.

Other species. *Miamia silvatica* (Laurentiaux-Vieira, 1980) comb. nov.

Species *Miamia bronsoni* Dana, 1864

Miamia bronsoni Dana, 1864: 35, fig. 1 (erected as type-species of the genus *Miamia* Dana, 1864); Scudder 1866: 18, figs. 2, 4; Handlirsch 1906: 698; Carpenter 1992: 133; location of the holotype unknown.

Didymophlebs contusa Scudder, 1885: 330, pl. 20, fig. 6 (erected as type-species of the genus *Didymophlebs* Scudder, 1885); Handlirsch 1906: 808; Carpenter 1992: 132; new synonymy; holotype: FMNH UC 6392 (Fig. 1.1).

Propteticus infernus Scudder, 1885: 334, pl. 31, figs. 3, 4 (erected as type-species of the genus *Propteticus* Scudder, 1885); Handlirsch 1906: 698; Carpenter 1992: 122, fig. 1; new synonymy; holotype: FMNH UC 6391 (Fig. 1.2).

Dictyoneura clarinervis Melander, 1903: 185, pl. VI fig. 1, pl. VII fig. 8; Handlirsch 1906: 698 (erected as type-species of the genus *Camptophlebia* Handlirsch, 1906); Carpenter 1992: 122 (synonymy with *infernus* Scudder, 1885); new synonymy; holotype: FMNH UC 9240 (Fig. 1.3).

Cheliphlebia extensa Melander, 1903: 186, pl. VI, fig. 2, pl. VII, fig. 9; Handlirsch 1906: 698 (erected as type-species of the genus *Paracheliphlebia* Handlirsch, 1906); Carpenter 1992: 122 (synonymy with *infernus* Scudder, 1885); new synonymy; holotype: FMNH UC 9241 (Fig. 2).

Petromartus indistinctus Melander, 1903: 191, pl. VI, fig. 6, pl. VII, figs. 12–13 (erected as type-species of the genus *Petromartus* Melander, 1903); Handlirsch 1906: 699; Carpenter 1992: 122 (synonymy with *infernus* Scudder, 1885); new synonymy; holotype: FMNH UC 9243.

Spaniodera ambulans Handlirsch, 1906: 697, figs. 23–25 (erected as type-species of the genus *Spaniodera* Handlirsch, 1906); Carpenter 1992: 122 (synonymy with *infernus* Scudder, 1885); new synonymy; holotype: USNM 38817 (Fig. 3.1).

Metryia analis Handlirsch, 1906: 700: fig. 27 (erected as type-species of the genus *Metryia* Handlirsch, 1906); Carpenter 1992: 122 (synonymy with *infernus* Scudder, 1885); new synonymy; holotype: USNM 38834 (Fig. 3.2).

Spaniodera longicollis Handlirsch, 1911: 305, fig. 8; new synonymy; holotype: YPM 24 (Fig. 4.1).

Spaniodera lata Handlirsch, 1911: 306, fig. 9; new synonymy; holotype: YPM 25 (Figs. 4.2, 5).

Spaniodera elatior Handlirsch, 1911: 307, fig. 10; new synonymy; holotype: YPM 26 (Fig. 4.3).

Spaniodera schucherti Handlirsch, 1911: 308, fig. 11; new synonymy; holotype: YPM 27 (Fig. 6.1).

Spaniodera acutipennis Handlirsch, 1911: 308, fig. 12; new synonymy; holotype: YPM 28 (Fig. 6.2).

Spaniodera parvula Handlirsch, 1911: 309, fig. 13; new synonymy; holotype: YPM 29 (Fig. 7.1).

Spaniodera angusta Handlirsch, 1911: 309, fig. 14; new synonymy; holotype: YPM 30 (Fig. 7.2).

Species *Anthraconeura silvatica* Laurentiaux & Laurentiaux-Vieira, 1980

Anthraconeura silvatica Laurentiaux & Laurentiaux-Vieira, 1980: 407, figs. 1–2, pl. II, figs. 1–4 (erected as type-species of the genus *Anthraconeura* Laurentiaux & Laurentiaux-Vieira, 1980); CARPENTER 1992: 103; holotype: MGL 4234.

Taxa considered as *nomina dubia*

Genus *Gyrophlebia* Handlirsch, 1906: 697.

Gyrophlebia longicollis Handlirsch, 1906: 697.