

Revision of the scorpionfly family Holcorpidae (Mecoptera), with description of a new species from Early Eocene McAbee, British Columbia, Canada

S. BRUCE ARCHIBALD

Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC, V5A 1S6, Canada

Abstract. The scorpionfly family Holcorpidae (Mecoptera) has been informally discussed since the early 1960's, but a detailed treatment in accordance with the provisions of the International Code of Zoological Nomenclature for naming families was not provided until Willmann did so in 1989; he is recognized as author of the family. The Holcorpidae concept is revised here based on examination of its two specimens of *Holcorpa maculosa* from the Late Eocene of Florissant, Colorado, and a third, new specimen from the Early Eocene Okanagan Highlands locality at McAbee, British Columbia, Canada. This new specimen belongs to a second, new species, which is described here, *Holcorpa dillhoffi* n. sp.

Résumé. Révision des Mécoptères Holcorpidae, avec la description d'une nouvelle espèce de l'Eocène inférieur de la Colombie Britannique, Canada. Les Holcorpidae ont fait l'objet de discussions informelles depuis les années 1960 mais le premier traitement en accord avec les recommandations en vue la nomination des familles du Code International de Nomenclature est celui de Willmann (1989), qui est considéré comme l'auteur de cette famille. Le concept d'Holcorpidae est revu sur la base de l'examen des deux spécimens originaux d'*Holcorpa maculosa* de l'Eocène supérieur de Florissant, Colorado, et d'un troisième nouveau spécimen de l'Eocène inférieur d'Okanagan Highlands, McAbee, Colombie Britannique, Canada. Ce nouveau spécimen appartient à une nouvelle espèce qui est décrite ici : *Holcorpa dillhoffi* n. sp.

Keywords: Holcorpidae, *Holcorpa*, McAbee, Okanagan Highlands, Eocene.

The enigmatic scorpionfly genus *Holcorpa* is particularly noted for its extremely extended sixth through eight abdominal segments and details of its wing venation. It has been much discussed for more than a century, since the discovery of the two fossils of *H. maculosa* (Scudder 1878) from the Late Eocene of Florissant, Colorado, USA (Fig. 1).

The first, holotype specimen was found by Mrs. Fisher in 1877 (Scudder 1878). The body is poorly preserved, incomplete beyond the eighth abdominal segment. The second, more spectacular specimen was collected by George N. Rohwer in 1907 at station 14, but was not reported for almost 20 years, when it was figured without comment by Cockerell (1927, not 1926 as reported by Carpenter 1931). Both specimens were later treated in detail by Carpenter (1931). The abdomen of the second specimen is well preserved: the male genitalia with distinctively enlarged genital bulb (A9) and extended pincher-like dististyli are clearly visible (Figs. 1A–B, 3G). It is larger than the holotype, which Carpenter explained as sexual dimorphism, concluding that the holotype is a female, contrary

to Scudder's opinion (1878), and designated the new specimen as the allotype (a type not regulated by the ICZN: International Trust for Zoological Nomenclature 1999).

Scudder placed *Holcorpa* in the family Panorpidae, but its media with five branches in both the fore- and hind wings (both with four branches in all Panorpidae) led Carpenter (1931) to later consider it at best a basal member, and Penny (1975) to speculate that it belonged to an extinct, closely related lineage. Martynova (1962: 291, Russian edition pagination) mentioned *Holcorpa* in a footnote to her section on Panorpidae (translated from the Russian): "According to Prof. Carpenter, the genera *Holcorpa* Scudd., 1878 and *Panorpodes* McL., 1875 should be placed into separate families." Zherikhin (1970: 74) wrote (translated from the Russian): "an extinct insect family Holcorpidae (Mecoptera) is known from the Oligocene of USA—consisting of one monotypic genus, *Holcorpa* Scudd. from Florissant." Willmann (1989: 138) later discussed *Holcorpa* as in Holcorpidae and to its only species as the type. He did not explicitly propose the family, nor was an author given, but stated that this species (translated from the German): "was until now understood as within Panorpidae. It has a large number of derived character states, which influenced

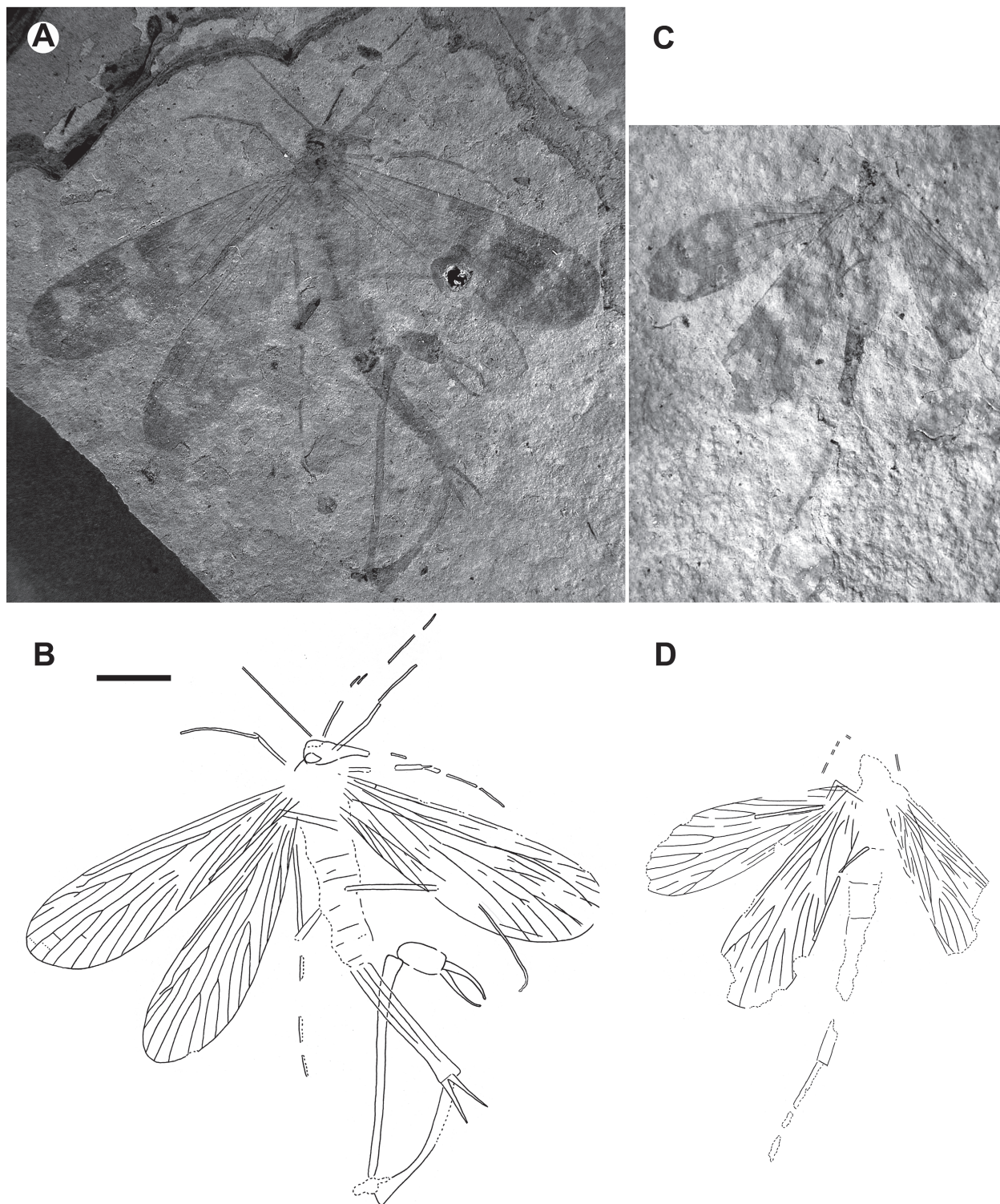


Figure 1
Holcorpa maculosa. A, photo of the allotype (male) UCM 4494, University of Colorado Museum; B, drawing from the part and counterpart (AMNH 18887 and UCM 4494) of the allotype male; C, photo of the holotype (female) MCZ; D), drawing of the holotype. A-D to scale = 5 mm.

earlier authors to reject it as a member of this group as it is constituted (for example, Zherikhin 1969: 74 spoke of an exclusive family Holcorpidae)” (the date should be 1970).

Willmann provided a functional, if not specifically labelled diagnosis, discussing character states that exclude *Holcorpa* from Panorpidae and Panorpididae. He considered it to be basal to the clade Panorpidae + Panorpididae, in a lineage perhaps descended from the paraphyletic (Willmann 1987), Mesozoic “Orthophlebiidae”. In his treatise on fossil insects, Carpenter (1992: 390) retained *Holcorpa* within Panorpidae, expanding the family concept to include it: “M usually with 4 branches, rarely with 5”. Subsequently, Willmann & Novokshonov (1998: 284) discussed reasons that *Holcorpa* should not be considered within Panorpidae, not mentioning Holcorpidae, calling it a “quasi” orthophlebiid, a remnant of this group that had survived into the Cenozoic. Novokshonov (2002) cited Zherikhin (1969 [sic]) as the author of Holcorpidae, however, he speculated that *Holcorpa* might be better placed in the “Orthophlebiidae”. Grimaldi & Engel (2005) discussed it as a panorpid, while noting that some place it in its own family; their phylogeny (their Fig. 21.1) places it as sister to Panorpidae + Panorpididae + Bittacidae, immediately descended from a paraphyletic orthophlebiid grade.

Although many of the above authors expressed dissatisfaction with *Holcorpa* as a panorpid, and in some cases mentioned the name “Holcorpidae”, no one until Willmann (1989) provided a description distinguishing and defining the family as required by article 13 of the International Code of Zoological Nomenclature (1999) for family names published after 1930. While Willmann did not indicate that he was formally erecting the family and his description and diagnosis are not labelled as such, they serve in that capacity, and so follow the ICZN requirements. That work (Willmann 1989) should, then, be considered the formal proposition of the family Holcorpidae.

Here, the two specimens of *Holcorpa maculosa* are examined, figured, and some aspects of wing venation reported by Carpenter (1931) are revised; the new species *H. dillhoffi*, from the Ypresian (Early Eocene) McAbee beds of British Columbia, Canada is described; and the Holcorpidae concept is amended based on this information.

Material and methods

The matrix within which the McAbee specimen is preserved is fine-grained, well-bedded and easily splitting medium brown lacustrine shales. The collector did the initial preparation, presumably with a pneumatic air scribe. The author did a small

amount of subsequent preparation, exposing distal portions of the abdomen with an insect pin in a pin vise. Wings are all figured in standard aspect with the apex to the right (some reversed left-right). Comparative character states are provided in brackets.

Abbreviations of institution names: American Museum of Natural History, New York, USA: AMNH; Museum of Comparative Zoology, Cambridge, MA: MCZ; Royal British Columbia Museum, Victoria, British Columbia, Canada: RBCM; University of Colorado, Boulder, Colorado, USA: UC.

Venational terminology follows Willmann (1989). Willmann’s (1987, 1989) and Willmann & Novokshonov’s (1998) Mecoptera systematics is followed, except as for Orthophlebiidae and the genus *Orthophlebia*, which they (and others) considered paraphyletic as then constituted. These were subsequently revised by Hong & Zhang (2004, 2007), which I follow here. When “Orthophlebiidae” as understood prior to this revision is meant, I refer to the name in quotation marks or as a grade. The species of *Orthophlebia* from Karatau referred to here were maintained in the genus by Hong & Zhang (2007).

Taxonomy

Holcorpidae Willmann 1989

Holcorpidae of Zherikhin 1970: 74 (unavailable, fails article 13, no description or definition)

Holcorpidae Willmann 1989: 138 (first available use of Holcorpidae)

Type genus. *Holcorpa* Scudder 1878.

Diagnosis (amended). This family separated from other mecopteran families by a combination of: (1), fore-, hind wing media both with five branches; (2), abdominal segments 6-8 elongate (both male, female), with A8 distinctly longest. It may be further separated from Panorpidae and Panorpididae by (3), male: extended, slender dististyli, lacking basal tooth; from Panorpidae by (4), female: medigynium circular, without tongue-shaped processes; from Dinopanorpidae by (5), R_1 curved around pterostigma, meeting C on anterior wing margin well before apex [extended, curving posteriad in Dinopanorpidae]; Mecoptera outside of Panorpini Willmann 1987 differ increasingly in many characters.

Description. See genus description (male and female).

Distribution (range and age). Early to Late Eocene (Ypresian to Priabonian) of western North America: McAbee, near Cache Creek British Columbia, Ypresian (~51 Ma: Ewing 1981); Florissant, Colorado, Priabonian (34.07 ± 0.10 Ma by ^{40}Ar - ^{39}Ar decay: Evanoff *et al.* 2001).

Biology. Holcorpidae inhabited mesic montane forests of higher mid-paleolatitude western North America dominated by Fagaceae, with elements of Pinaceae, Cupressaceae (including “Taxodiaceae”). These forests experienced upper microthermal to mid-mesothermal climates, yet with mild winters that had few if any freezing days, constrained to >5 °C coldest month mean temperature by the presence of cold winter-intolerant taxa such as palms (Greenwood & Wing 1995; Greenwood *et al.* 2005; Moss *et al.* 2005).

Included genera. *Holcorpa*.

Discussion. Carpenter (1931) noted striking similarities between *Holcorpa* and the panorpids then called *Leptopanorpa longicauda* Weele 1909 (now recognized as a junior synonym of *L. ritsemae* MacLachlan 1875) from Java (see Liefstinck 1936: Fig. 7 and Plate 8) and *Neopanorpa cornutua* (Esben-Petersen 1915) from India, thereby suggesting that the three genera were closely related.

Like *H. maculosa*, *N. cornuta* bears paired tergal spurs on abdominal segment six, although shorter and blunter. Crampton (1931) compared the spurs of *N. cornuta* with those found on abdominal segments six and seven of males of the eomeropid *Nothiothauma reedi* (MacLachlan 1877), assuming that the processes on A7 function as stabilizing guides for the distal abdominal segments when brought forward.

Males of *L. ritsemae* also have extended abdominal segments 6–8; however, there, segment seven is much longer than segment six [*Holcorpa*: segments six and seven similar length]; segments seven and eight are similar in length [*Holcorpa*: eighth segment about 150% the length of seventh], segment seven is not curved [*Holcorpa*: distinctly curved], segment six lacks the paired spurs [*Holcorpa*: present], and the base of segment nine is also extended [*Holcorpa*: not]. Furthermore, in *Holcorpa*, both sexes possess a lengthened abdomen, whereas the female abdomen of *L. ritsemae* is not unusually extended.

In fact, *L. ritsemae* is not the only species of *Leptopanorpa* bearing an extended abdomen: *L. nematogaster* (MacLachlan 1869), *L. filicauda* (Liefstinck 1936) and *L. robusta* (Liefstinck 1936) also bear such extended A6–A8 (and the base of A9, to varying degrees) (Liefstinck 1936: Fig. 8 and Plates 8, 9). An entire range of degrees of lengthening can be seen among the males of various *Leptopanorpa* species, from somewhat lengthened (e.g., *L. javanica* (Westwood 1842) and *L. pi* (Weele 1909)), to medium-lengthened (e.g., *L. sarangana* (Liefstinck 1936), and those then called *L. erythrura* Liefstinck 1936 (now recognized as a junior synonym of *L. cingulata* Enderlein 1921)), through the species mentioned above (Liefstinck 1936: Plates 8, 9; note also the tergal process on A3). In all of these species, the length and shape of particular abdominal segments are altered similarly (to varying degrees), not in the manner seen in *Holcorpa*. The configuration of the anal veins of *Leptopanorpa* and *Neopanorpa* is distinctive (Willmann 1989: 105), also not as in *Holcorpa*.

Willmann (1989) and Willmann & Novokshonov (1998) separated *Holcorpa* from all known Panorpidae by character states (1)–(4). It is also possibly distinct by

(6), morphology of abdominal tergum and sternum six, which, in panorpid and panorpid males are joined form a tube (as are some other abdominal segments), seamlessly in Panorpidae, but with an evident seam in Panorpididae (Willmann & Novokshonov 1998). In the male specimen of *H. maculata*, preservation precludes determination of the existence of such a seam, however, in the holotype of *H. dillhoffi*, this is possibly preserved, although, if so, faintly, not with enough clarity for certainty.

Willmann (1989) further distinguished *Holcorpa* from Panorpidae by (7), Rs_{3+4} very short; and (8), only one crossvein between Cu_1 and Cu_2 as in Panorpididae, not Panorpidae. However, Rs_{3+4} length in *Holcorpa* does not appear to be particularly useful, distinctive relative to that of Panorpidae and Panorpididae, and the number of crossveins seems rather uncertain by poor preservation on specimens of *H. maculosa*—note that Scudder (1878) and Carpenter (1931) disagreed on the presence of crossveins at all in the holotype. In examination of the specimens of *H. maculosa* for this study, few crossveins were detected with confidence (Figs. 1B, 3C–D), not as many as Carpenter illustrated in his reconstruction (1931: plate XXXIII; reproduced in Carpenter 1992: Fig. 214.1 and by Willmann 1989: Fig. 147a). However, examination of the more distinctly preserved but somewhat damaged and incompletely forewing of *H. dillhoffi* indicates that Willmann's assessment of character state (8) may in fact be correct, and might further separate *Holcorpa* from Panorpidae. This, however, should be confirmed in future specimens.

Holcorpa then shares (4) and (5) and possibly (6) and (8) with Panorpididae, and is separated from this family by character states (1)–(3).

Other characters by which *Holcorpa* might be evaluated relative to Panorpidae and Panorpididae (Byers & Thornhill 1983; Penny 2006) are either undeterminable in known *Holcorpa* fossils by preservation, but may be known in future specimens (Panorpidae: tarsal claws toothed; Panorpididae, not toothed); or will surely never be determinable in fossil insects (panorpid larvae are saprophagous, eruciform, and live on the soil surface; panorpid larvae are phytophagous, scarabaeiform, and subterranean). Willmann (1989) concluded that Panorpidae and Panorpididae are sister taxa by morphological characters. Results of a recent molecular analysis were consistent with both Panorpidae and Panorpididae as monophyletic, yet could not resolve their relationship relative to Bittacidae (Pollmann *et al.* 2008).

Willmann (1989) agreed with previous authors (above) that if the media with five branches in the

A



B



Figure 2
Holcorpa dillhoffi **n. sp.** holotype (male) RBCM.EH2008.018.0001: A, photo; B, drawing. A-B to scale = 5 mm.

forewing of *Holcorpa* is a symplesiomorphy with “Orthophlebiidae”, and the media with five branches in the hind wing is derived, this would suggest that *Holcorpa* was basal to Panorpididae + Panorpidae, although, alternatively, this could possibly also be derived in both the fore- and hind wings. The Eocene Australian Austropanorpidae and the Lower Jurassic Siberian Muchoriidae also had four branches of the media in both the fore- and hind wings. Willmann

(1977) suggested that Austropanorpidae might be sister to Panorpidae + Panorpididae if this condition is homologous, although later (1987, 1989) indicated that it may have been a more basal offshoot of the “Orthophlebiidae”. The position of Muchoriidae within the Panorpini is uncertain (Willmann 1987).

The lengthened abdominal segments 6–8 and paired tergal processes on abdominal segment six also occurred in Orthophlebiidae from the Late Jurassic of Karatau,

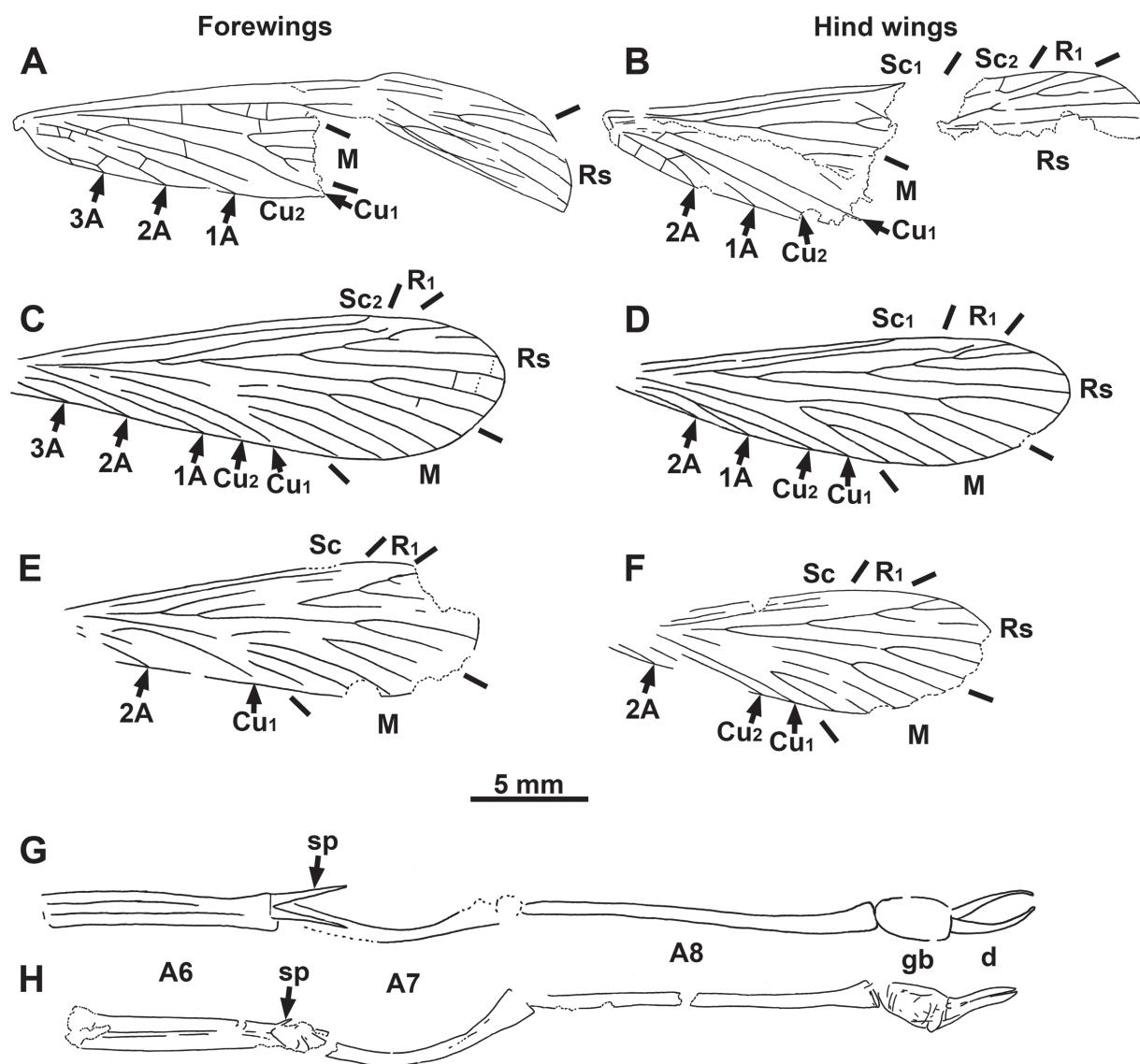


Figure 3

Holcorpa species, comparison of wings, A–F; comparison of male abdomen, segment A6 to apex, G–H. **A**, *H. dillhoffi* n. sp. male forewing; **B**, *H. dillhoffi* n. sp. male hind wing; **C**, *H. maculosa* male forewing; **D**, *H. maculosa* male hind wing; **E**, *H. maculosa* female forewing; **F**, *H. maculosa* female hind wing; **G**, *H. maculosa* male abdomen; **H**, *H. dillhoffi* n. sp., male abdomen. All to scale = 5 mm. Abbreviations: A6–A8: abdominal segments 6 through 8; sp: spurs; gb: genital bulb; d: dististyli.

Kazakhstan (Willmann & Novokshonov 1998). *Orthophlebia elenae* (Willmann & Novokshonov 1998) had a somewhat extended abdomen in both the male and female, and the abdomen was further extended in the male of *Orthophlebia longicauda* (Willmann & Novokshonov 1998) (female not known), with segment 8 longest (Willmann & Novokshonov 1998). *O. longicauda* also bore paired tergal spurs on the rear of abdominal segment 6, similar in position and shape to those of *Holcorpa*. Character state (1) is then the primary difference between *Holcorpa* and Orthophlebiidae (and other families of the orthophlebiid grade), in which the forewing has five branches, like *Holcorpa*, but the hind wing has four. Choristidae also has five branches of the media in the forewing and four in the hind wing.

Willmann & Novokshonov (1998) suggested that *O. longicauda* and *O. elenae* may form a monophyletic group by their shared, distinctive, large metatarsal organ on hind legs of the male; they specifically excluded *Holcorpa* from this proposed clade, as the male *H. maculata* lacks this organ as seen in published photographs, confirmed here by examination of this specimen (not determinable on the male *H. dillhoffi* holotype by preservation).

It then appears most likely that a strikingly lengthened abdomen arose independently at least three times in the Panorpini: in *Holcorpa*, and in restricted

cases within Jurassic Orthophlebiidae and extant male Panorpidae.

The Eocene Dinopanorpidae, also known from McAbee, also has a media with five branches in both the fore- and hind wings, and apparently also shares character state (4) with *Holcorpa* (Archibald 2005), suggesting a close relationship between them. *Holcorpa* is easily separated from the Dinopanorpidae, however, by character state (5). In Dinopanorpidae, R_1 is extended, almost reaching the wing apex, curving posteriad to reach the margin, a condition that Cockerell (1924: 2) found “remarkable for ending practically parallel with the costa, forming an extremely acute angle” and Carpenter (1972: 86) “unique in the known Mecoptera, extinct and Recent, as noted by Cockerell (1924); in other members of the order, R_1 is much shorter and is curved anteriorly at its termination.” Further, in Dinopanorpidae the female abdomen is not lengthened (the male abdomen is not known). Wing shape further separates them: in *Holcorpa* spp. forewings, the costa and subcosta are relatively parallel and close in the basal quarter, whereas dinopanorpid forewings bear an expanded costal space in the basal quarter, like the condition found in the Choristidae (and occurring repeatedly in the Neuropterida), where the costa and subcosta are bowed apart (only slightly in the smallest dinopanorpid species such as *Dinokanaga*

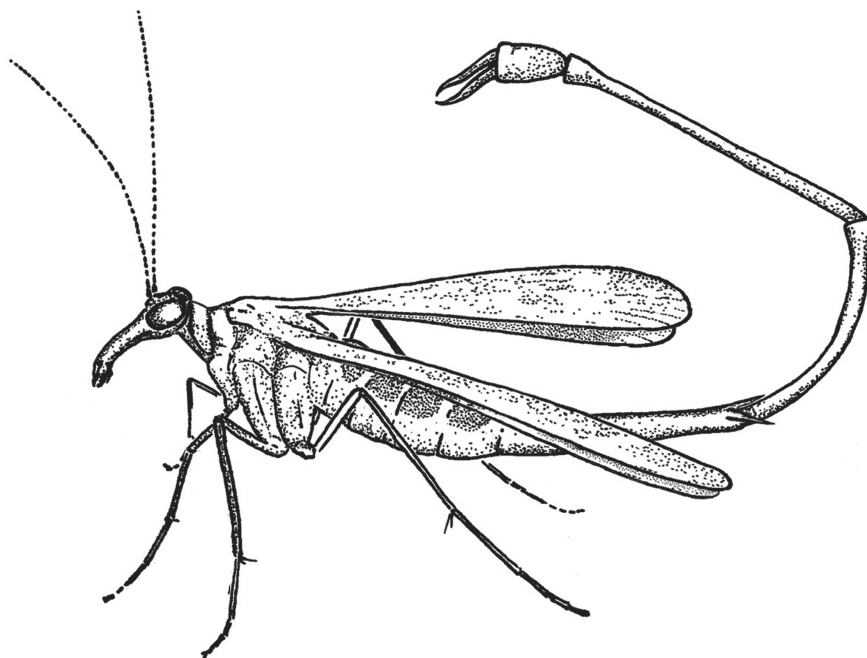


Figure 4
Reconstruction of *Holcorpa* sp. male habitus.

webbi (Archibald 2005)); also, the general shape of the wing differs in that the greatest width tends to be more distal in *Holcorpa* spp. than in dinopanorpid spp. (cf. Archibald 2005: Fig. 3 and Fig. 3, here).

These character states then support placement of *Holcorpa* in its own family; provide further support for the phylogenetic model discussed by previous authors (above) wherein Holcorpidae arose from the orthophlebiid grade and may be sister to Panorpidae + Panorpididae (+ Austropanorpidae?); and further suggests that Dinopanorpidae is (most?) closely related (its position relative to Muchoriidae remains obscure).

Genus *Holcorpa* Scudder 1878 (Figs. 1–4)

Type species. *Holcorpa maculosa* Scudder 1878, by monotypy.

Diagnosis. As for family.

Description, male. As in diagnosis, Figs. 1–3, and the following.

Head. Antennae long (full length not known by preservation).

Thorax. Apparently generalized panorpoid morphology, but poorly known. **Forewing.** Colouration: dark with varying light spots or fascia; length about 19–25 mm, width about 5–6 mm; ovate, widest at about three quarters length; Sc_2 terminates on C at pterostigma (Sc_1 not detected); Rs: Rs_{1+2} with four pectinate branches (but see genus Discussion), Rs_{3+4} two branches; M: with five branches, M_4 branched M_{4a} , M_{4b} ; Cu_1 curved basally, then straight, terminates on posterior margin mid-wing, Cu_2 aligned with Cu_1 parallel with Cu_1 to margin just before mid-wing; 1A: mostly straight with minor bends at crossveins; 2A: curved basally, then straight; 3A little known; crossveins: few preserved, likely more. **Hind wing.** As for forewing, except: colouration varying; length a few mm shorter, width about 0.5 mm narrower; Sc_1 terminates on anterior margin, meets C at low angle distinctly basad position of Sc_2 termination in forewing at pterostigma (Sc_2 not detected in hind wing); R: branching nearer base than in forewing; Cu_2 joined with 1A near base; 1A: after separation rather straight to margin; 2A: rather straight, then gently curved toward posterior margin; 3A: not detected; crossveins: little known as preserved. **Abdomen.** A6 with two tergal spurs; A6, 7 length about 10 mm, A7 curved upward; A8 length about 15–16 mm, slightly expanded cone-like at distal end. Male: genital bulb enlarged, length about 3 mm, width about 2 mm; dististyli long, about 3.5 mm, slender, basal tooth not detected. **Female.** As provided for *H. maculosa* by Carpenter (1931).

Distribution. As for family.

Included species. *H. maculosa* Scudder, *H. dillhoffi* n. sp.

Biology. As for family.

Holcorpa maculosa Scudder 1878 (Figs. 1, 3A–D, G)

Diagnosis. See that of *Holcorpa dillhoffi*.

Description, male and female. See Carpenter (1931), except as revised below.

Type material. Holotype: MCZ 247 (part only), Fig. 1A–B,

preservation mostly complete, but with distal abdomen missing, much of body indistinct; in the collection of the MCZ. Labelled (front): Type (red label); 247 (black ink on rock); 63 (black ink on rock). Collected by Mrs. Fisher at Florissant, Colorado (specific quarry not mentioned), 1877. Allotype: AMNH 18887, American Museum of Natural History (part); UCM 4494, University of Colorado Museum (counterpart), Fig. 1C–D, well-preserved, complete male; collected by G. N. Rohwer at Florissant, Colorado, station 14, in 1907.

Distribution (range and age). Florissant Formation, Florissant, Colorado; Priabonian (details above).

Biology. The Florissant forest was dominated by Fagaceae (*Fagopsis* leaves the most abundant) (Manchester 2001). Mean annual temperature (MAT) is estimated as lower mesothermal (~13–14 °C) by leaf physiognomy (Gregory & McIntosh 1996), to mid-mesothermal (~17 °C) by nearest living relative analysis (Leopold & Clay-Poole 2001), with few, if any frost days are indicated by the presence of palms. Florissant was at high elevation (estimates summarized by Meyer 2001).

Discussion. In re-examining the allotype of *H. maculosa*, the terminal portion of R_1 is found to be more sharply curved around the pterostigma (Figs. 1B, 3C–D) than illustrated by Carpenter (1931: plate XXXIII; and reproduced in the references cited above), not with the shallow, gentle curve as shown in Carpenter's drawing. This shape is also seen clearly in the hind wing of *H. dillhoffi* (Fig. 2B, 3B).

Further differences were seen in re-examination of *H. maculosa* beyond this and the number of crossveins detected as noted above. Carpenter depicted Rs in the right forewing with five branches, whereas in the three other wings, it is shown with six branches. This could, of course, be an adventitious condition, but it seems more likely that the apical-most branch was simply not detected by preservation, as the fore and hind wings do overlap on this side and discernment of such characters there is difficult (see Fig. 1A–B).

Although they might appear homologous at first, in the forewing, the distinctly evident portion of the subcosta ends distally with Sc_2 terminating on C, while on the hind wing, it is actually the terminus of Sc_1 that similarly joins C. In the hind wing, a short portion of Sc_2 joins with R_1 (although this portion is not preserved in any current fossil, it is apparent in some other families, e.g., see Fig. 3 of Willmann 1989) and terminates at the pterostigma (see *H. dillhoffi* Fig. 3B). Here, the length of the subcosta in the forewing (i.e., terminating with Sc_2) was found to be distinctly longer than the “evident” subcosta on the hind wing (i.e., the terminus of Sc_1). Carpenter's drawing, however, shows these to be closer in length. The length of the Sc terminating with Sc_1 in the hind wing of *H. maculosa* was seen to be similar relative to wing size as in *H. dillhoffi* (Fig. 3B, D).

In the hind wing, 3A was not detected, contrary to Carpenter.

***Holcorpa dillhoffi* n. sp.**
(Figs. 2–3E–F, H)

Diagnosis. May be separated from *H. maculosa* most easily by any of the following. Forewing R branches to Rs, R₁ distinctly greater than 1/3 wing length [*H. maculosa*: distinctly less than 1/3]; male forewing length 24–25 mm [*H. maculosa*: 21 mm, female 19 mm], male body length about 60 mm (total, reconstructed length) [*H. maculosa*: about 55 mm reconstructed, female about 30 mm as preserved, incomplete]; forewing mostly dark basally, hind wing hyaline basally, both mostly dark distally [*H. maculosa*: forewing, hind wing hyaline basally, both mostly dark distally]; forewing with scattered light spots with indistinct borders in basal portion, without distinctive large light spots in apical anterior portion, hind wing with at least one small spot in apical anterior portion [*H. maculosa*: without such basal spots, with such apical, distal spots]; A6 spurs mostly missing by preparation, but apparently form wider angle than those of *H. maculosa*.

Description, male. As in genus description, Diagnosis, and the following. **Forewing.** Width about 5 mm as preserved (wing somewhat compressed); Rs: indeterminate number of branches preserved; M₁₊₂ preserved but not M₁, M₂, region; crossveins detected as preserved as in Fig. 2B, likely more. **Hind wing.** Basal half, apical anterior portion preserved, length, width not known with any precision, but confidently larger than hind wing of *H. maculosa*; Rs: four pectinate branches preserved, total number indeterminate (possibly 6?); M: little-preserved; 3A not detected; crossveins detected as in Fig. 2B, very likely more than evident by preservation.

Material examined. Holotype, RBCM.EH2008.018.0001 (part only). Male, body somewhat complete, but missing a portion of A5. Three wings preserved: one forewing, one hind wing, preserved as described above and see Fig. 2; one forewing (by colouration) missing apical and posterior regions. Collected IX.1999 by Richard Dillhoff. Housed in the collection of RBCM, labelled Holotype, *Holcorpa dillhoffi*, Archibald 2009.

Distribution (range and age). The McAbee locality, unnamed formation of Kamloops Group Okanagan Highlands lacustrine shales 10 kilometres east of Cache Creek in south-central British Columbia, ~51 Ma, Ypresian.

Etymology. The specific epithet is a patronym formed from the surname of the collector and donor of the holotype, Richard Dillhoff, honouring his contributions to paleoentomology in the donation of this and other specimens.

Biology. McAbee had an upland forest dominated by Fagaceae (*Fagus* leaves the most abundant) similar to the modern eastern deciduous forests of North America, but with elements that are extinct or that today persist in East Asia (e.g., *Metasequoia*) or in low latitudes (e.g., palms) (D.R. Greenwood personal communication; Dillhoff *et al.* 2005; Greenwood *et al.* 2005; Moss *et al.* 2005). It had a mesic climate

with upper microthermal MAT of about 10 °C by leaf physiognomy (both CLAMP and leaf margin analysis) and about 13 °C by nearest living relative of flora analysis, with mild winters (Greenwood *et al.* 2005; Moss *et al.* 2005). Although McAbee was an upland, it may not have been at as high an elevation as Florissant (discussion / review of paleoelevation in Greenwood *et al.* 2005 and references therein; of paleoelevation relative to Florissant and comparative communities / environments in Archibald *et al.* 2005 and references therein).

Acknowledgements. I thank Rick Dillhoff for the donation of RBCM.EH2008.018.0001 to the author and Richard Hebda (curator) and Joan Kerik (collections manager) of the RBCM for subsequent acceptance of this specimen into the RBCM collections and facilitating research; Dena Smith, Eugene Hall and Toni Culver of UC for loan of 4494; David Grimaldi and Bushra Hussaini of the AMNH for the loan of AMNH 18887; Stephen Fisher for German translation; Sara Ashworth for help with digital photography; Vladimir Makarkin for obtaining Russian literature, translation, and helpful discussion; John Oswald for discussion of the ICZN; and André Nel and Julián Petrulevičius, for further helpful comments. The research was completed during a Natural Sciences and Engineering Research Council of Canada (NSERC) postdoctoral fellowship. I am also grateful for partial support provided through NSERC grants to Rolf Mathewes (Simon Fraser University) and David Greenwood (Brandon University).

References

- Archibald S.B. 2005. New Dinopanorpidae (Insecta: Mecoptera) from the Eocene Okanagan Highlands (British Columbia, Canada; Washington State, USA). *Canadian Journal of Earth Sciences* 42: 119–136.
- Archibald S.B., Rasnitsyn A.P., Akhmetiev M.A. 2005. The ecology and distribution of Cenozoic Eomeropidae (Mecoptera), and a new species of *Eomerope* Cockerell from the Early Eocene McAbee locality, British Columbia, Canada. *Annals of the Entomological Society of America* 98: 503–514.
- Byers G.W., Thornhill R. 1983. Biology of the Mecoptera. *Annual Review of Entomology* 28: 203–228.
- Carpenter F.M. 1931. Affinities of *Holcorpa maculosa* Scudder and other Tertiary Mecoptera, with descriptions of new genera. *Journal of the New York Entomological Society* 39: 405–414.
- Carpenter F.M. 1972. The affinities of *Eomerope* and *Dinopanorpa*. *Psyche* 19: 79–87.
- Carpenter F.M. 1992. Superclass Hexapoda, p. i–ii, 279–655 in: Kaesler R.L. (ed.), *Treatise on invertebrate paleontology. Part R, Arthropoda 4, vol. 4*. Geological Society of America, Boulder, Colorado.
- Cockerell T.D.A. 1924. Fossil insects in the United States National Museum. *Proceedings of the United States National Museum* 64: 1–15.
- Cockerell T.D.A. 1927. *Zoology of Colorado*. University of Colorado Press, Boulder, Col. 262 p.
- Crampton G.C. 1931. The genitalia and terminal structures of the male of the archaic mecopteran, *Nothiothauma reedi*, compared with related Holometabola from the standpoint of phylogeny. *Psyche* 38: 1–21.
- Dillhoff R.M., Leopold E.B., Manchester S.R. 2005. The McAbee flora of British Columbia and its relation to the Early-Middle Eocene Okanagan Highlands flora of the Pacific Northwest, *Canadian Journal of Earth Sciences* 42: 151–166.

- Ewing T.E. 1981.** Regional stratigraphy and structural setting of the Kamloops Group, south-central British Columbia. *Canadian Journal of Earth Sciences* **18**: 1464-1477.
- Evanoff E., McIntosh W.C. Murphey P.C. 2001.** Stratigraphic summary and $^{40}\text{Ar}/^{39}\text{Ar}$ geochronology of the Florissant Formation, Colorado. p. 1-16 in: **Evanoff E., Gregory-Wodzicki K., Johnson K. (eds)**, *Fossil Flora and Stratigraphy of the Florissant Formation, Colorado. Proceedings of the Denver Museum of Nature and Science*, series **4** (1). Denver Museum of Nature and Science, Denver, Colorado.
- Greenwood D.R., Archibald S.B., Mathewes R.W., Moss P.T. 2005.** Fossil biotas from the Okanagan Highlands, southern British Columbia and northeastern Washington State: climates and ecosystems across an Eocene landscape. *Canadian Journal of Earth Sciences* **42**: 167-185.
- Greenwood D.R., Wing S.L. 1995.** Eocene continental climates and latitudinal gradients. *Geology* **23**: 1040-1048.
- Gregory K.M., McIntosh W.C. 1996.** Paleoclimate and paleoelevation of the Oligocene pitch-pinnacle flora: Sawatch Range, Colorado. *Geological Society of America Bulletin* **108**: 545-561.
- Grimaldi D., Engel M.S. 2005.** *Evolution of the Insects*. Cambridge University Press, NY, 755 p.
- Hong Y.-C., Zhang Z.-J. 2004.** New taxonomy of Orthophlebiidae. *Geological Bulletin of China* **23**: 802-808 (in Chinese).
- Hong Y.-C., Zhang Z.-J. 2007.** Reclassification of fossil Orthophlebiidae (Insecta: Mecoptera). *Entomotaxonomia* **29**: 26-36.
- International Trust for Zoological Nomenclature. 1999.** *International Code of Zoological Nomenclature, fourth edition*. International Trust for Zoological Nomenclature, London.
- Leopold E.B., Clay-Poole S.T. 2001.** Florissant leaf and pollen floras of Colorado compared: climatic implications. p. 17-70 in: **Evanoff E., Gregory-Wodzicki K., Johnson K. (eds)**, *Fossil flora and stratigraphy of the Florissant Formation, Colorado. Proceedings of the Denver Museum of Nature and Science*, series **4** (1). Denver Museum of Nature and Science, Denver, Colorado.
- Lieftink M. 1936.** Studies in oriental Mecoptera. 1. The genus *Leptopanorpa* in Malaysia. *Treubia* **15**: 271-320.
- Manchester S.R. 2001.** Update on the megafossil flora of Florissant, Colorado p. 137-162 in: **Evanoff E., Gregory-Wodzicki K., Johnson K. (eds)**, *Fossil flora and stratigraphy of the Florissant Formation, Colorado. Proceedings of the Denver Museum of Nature and Science*, series **4** (1). Denver Museum of Nature and Science, Denver, Colorado.
- Martynova O.M. 1962.** Order Mecoptera. Scorpion flies, p. 283-294 in: **Rohdendorf B.B. (ed.)**, *Fundamentals of paleontology: reference book for paleontologists and geologists of the U.S.S.R. 9, Arthropods, tracheates and chelicerates* [English translation of: *Osnovy Paleontologii: Spravochnik dlya paleontologov i geologov SSSR 9, Chlenistonogie, Tracheiny i Khe-litserovye*. Izdatel'stvo Akademii Nauk SSSR, Moscow], Smithsonian Institution, Washington, D.C.
- Meyer H.W. 2001.** A review of paleoelevation estimates from the Florissant flora, Colorado, p. 205-216 in: **Evanoff E., Gregory-Wodzicki K., Johnson K. (eds)**, *Fossil Flora and Stratigraphy of the Florissant Formation, Colorado. Proceedings of the Denver Museum of Nature and Science*, series **4**(1). Denver Museum of Nature and Science, Denver, Colorado.
- Moss P.T., Greenwood D.R. Archibald S.B. 2005.** Regional and local vegetation community dynamics of the Eocene Okanagan Highlands (British Columbia - Washington State) from palynology. *Canadian Journal of Earth Sciences* **42**: 187-204.
- Novokshonov V.G. 2002.** Order Panorpidia Latreille, 1802, p. 194-199 in: **Rasnitsyn A.P., Quicke D.L.J. (eds.)**, *History of insects*. Kluwer Academic Press. Dordrecht, The Netherlands.
- Penny N.D. 1975.** Evolution of the extant Mecoptera. *Journal of the Kansas Entomological Society* **48**: 331-348.
- Penny N.D. 2006.** A review of our knowledge of California Mecoptera. *Proceedings of the California Academy of Sciences* **57**: 365-372.
- Pollmann C., Misof B., Sauer K.P., 2008.** Molecular phylogeny of panorpodid scorpionflies: An enigmatic, species-poor family of Mecoptera (Insecta). *Organisms, Diversity & Evolution* **8**: 77-83.
- Scudder S.H. 1978.** An account of some Insecta of unusual interest from the Tertiary rocks of Colorado and Wyoming. *Bulletin of the United States Geological and Geographical Surveys of the Territories* **4**: 519-544.
- Willmann R., 1977.** Zur systematischen Stellung von *Austropanorpa* (Insecta, Mecoptera) aus dem Alttertiär Australiens. *Paläontologische Zeitschrift* **51**: 12-18.
- Willmann R., 1987.** The phylogenetic system of Mecoptera: *Systematic Entomology* **12**: 519-524.
- Willmann R., 1989.** Evolution und phylogenetisches System der Mecoptera (Insecta: Holometabola). *Abhandlungen der senckenbergischen naturforschenden Gesellschaft* **544**: 1-153.
- Willmann R., Novokshonov V. 1998.** Neue Mecopteren aus dem oberen Jura von Karatau (Kasachstan) (Insecta: 'Orthophlebiidae'). *Paläontologische Zeitschrift* **72**: 281-298.
- Zherikhin V.V. 1970.** Zoogeograficheskie svyazi paleogenovykh nasekomykh [Zoogeography of Paleogene insects], p. 29-88 in: **Bei-Bienko G.Ya. (ed.)**, *Doklady na dvadzat' vtorom ezhegodnom chtenii pamyati N. A. Kholodkovskogo, 4 aprelya 1969* [22nd Annual report on lectures in memory of N.A. Kholodkovsky, 4 April 1969]. Nauka Press, Leningrad (In Russian).