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ABSTRACT—The early Eocene green lacewings (Neuroptera, Chrysopidae) of the Okanagan Highlands deposits of McAbee, and Driftwood Canyon, British Columbia (Canada) and Republic, Washington (U.S.A.) are treated in detail for the first time. At least six genera are present, one unnamed, three new, with at least 10 new species, six named: *Protochrysa fuscobasalis* n. sp. (McAbee) (Limaiinae, the youngest known record of the subfamily), *Okanaganochrysa coltsunae* n. gen. n. sp. (McAbee), *Adamsochrysa aspera* n. gen. n. sp. (McAbee), *A. wilsoni* n. gen. n. sp. (Republic), *Archaeochrysa profracta* n. sp. (McAbee), and *Pseudochrysopa harveyi* n. gen. n. sp. (Driftwood Canyon) (all Nothochrysinae, the latter provisionally). The four unnamed species include one assigned to *Pseudochrysopa*, two likely belonging to *Adamsochrysa*, and one of an unknown nothochrysine genus. Microtholi are detected on the abdominal sclerites of *Adamsochrysa wilsoni*, and the spermatheca and spermathecal duct in the abdomen of *Pseudochrysopa harveyi*, the first reported occurrences of these preserved in fossil Chrysopidae. Structures were detected on the apical wing margins of some species that appear similar to trichosors, which are unknown in Chrysopidae, but are present in some other neuropteran families. This is the richest described assemblage of the family anywhere in the fossil record. Okanagan chrysopids were also morphologically and presumably ecologically diverse, including large species with rich venation and well as those with simplified venation and the smallest known fossil species. This is the oldest reported occurrence of the family in North America.

INTRODUCTION

THE CHRYSOPIDAE, green lacewings, is the second largest family of modern Neuroptera, with over 1,200 species distributed globally except in highest latitudes. Only the ant lions (Myrmeleontidae) have more species within the order. They are mostly crepuscular or nocturnal inhabitants of a wide variety of habitats worldwide, and feed mainly on aphids. Together with the brown lacewings (Hemerobiidae, that feed on similar prey), green lacewings are the most abundant Neuroptera in deciduous forests, both in terms of species and individuals (e.g., Duelli et al., 2002). They are usually a distinctive green color with copper-colored or golden eyes, hence the name Chrysopidae from the Greek *chrysos* for golden and *ops*, eyes. Brooks and Barnard (1990) provided an overview and revision of the modern Chrysopidae to the genus level.

Their fossil record extends to the Jurassic but they have not been reported in North America older than the Eocene. Chrysopidae was listed and briefly mentioned as occurring in the early Eocene Okanagan Highlands of far-western North America (Wehr and Barksdale, 1996; Archibald and Makarkin, 2006; Archibald, 2009), but the oldest previously treated in any detail are from the late Eocene of Florissant, Colorado, where eight species in four genera have been described (Scudder, 1885, 1890; Cockerell, 1908, 1909, 1914; Carpenter, 1935; Adams, 1967). They are represented in the Oligocene of Creede, Colorado (Carpenter, 1935; Carpenter et al., 1938; Adams, 1967) and the Ruby River basin (Lewis and Lee, 1992) and Canyon Ferry Reservoir (CoBabe et al., 2002) of Montana, and the middle Miocene of Stewart Valley, Nevada (Scudder et al., 1986).

Here we treat the early Eocene Okanagan Highlands Chrysopidae in detail, describing a rich assemblage of at least six genera and 10 species, which includes three new named genera and six new named species. This represents their earliest known occurrence in North America. Microtholi were identified on one specimen, and the spermatheca and spermathecal duct were clearly preserved on another, organs that have not been previously reported in fossil Chrysopidae. Some specimens show structures that appear similar to trichosors, which are known in the wings of some Neuroptera, but not previously seen in Chrysopidae.

The fossils reported here are from three of the seven major insect-bearing sedimentary basins of the Okanagan Highlands, a series of fossiliferous early Eocene upland deposits of lacustrine shales scattered across about a thousand kilometers of south-central British Columbia, Canada into north-central Washington state, U.S.A. (Fig. 1). These localities are Ootsa Lake Group shale at Driftwood Canyon, BC, Kamloops Group shale at McAbee, BC, and exposures of Klondike Mountain Formation shale in and near the town of Republic, Washington, U.S.A. The biota, climates, ages and ecologies of these localities were characterized and reviewed by Greenwood et al. (2005), Moss et al. (2005), and Archibald et al. (2011). Although the flora of individual sites differ in detail, they had a generalized Okanagan Highlands forest that has been characterized as the antecedent of the modern Eastern Deciduous Forest, but which also included extinct lineages (e.g., *Paleomyrtinia*, see below), elements that range in East Asia today (e.g., *Metasequoia*), and others that are today restricted to low latitudes (e.g., palms) (Greenwood et al., 2005). All had upper microthermal mean annual temperature values (Greenwood et al., 2005), no significant winter frost days and mesic precipitation. These sites span about 2 to 4.5 million years of the latter portion of the early Eocene: McAbee is the oldest, ^{40}Ar/^{39}Ar age of 52.90 ± 0.83 Ma; Driftwood Canyon, U-Pb age of 51.77 ± 0.34 Ma (Mortensen and Archibald, work in progress cited in Moss et al., 2005 and Archibald et al., 2010); and Republic is the youngest, ^{40}Ar/^{39}Ar age of 49.4 ± 0.5 Ma (Wolfe et al., 2003).

SYSTEMATIC PALEONTOLOGY

We examined 24 specimens collected by SBA and various institutional and private collectors (donated to institutions as

FIGURE 1—Map of chrysopid-bearing fossil localities of the Okanagan Highlands referred to in the text. Solid dots=Driftwood Canyon, McAbee, and Republic; open circle=Vancouver, BC.

indicated). Drawings were done directly from the fossils and checked against photographs. Most specimen photographs are composites of close-up images, in one case (Fig. 21.1) taken from better-preserved portions of both the part and counterpart. Some fossils were photographed wetted with ethanol.

Terminology for wing venation employed here generally follows that of Brooks and Barnard (1990), except "Cu1" of these authors is our CuA, "Cu2"' is CuP in accordance with common practice in other neuropteran families, "R" (distad branching with Rs) is our R1, and "posterior median crossveins" are branches of pseudomedia, as they are not true crossveins. We use the terminology for veinlets, spaces, and designation of crossveins as defined by Oswald (1993). Principal crossveins in the basal part of wing are designated by the longitudinal veins with which they connect, and are numbered in sequence from the wing base, e.g., 1icu, 2icu, basal and second crossveins connecting CuA and CuP; 1r-m, 2r-m, basal, and second crossveins between R (Rs) and M (MA).

Venation abbreviations used are: 1A-3A, anal veins; C, costa; *c1*, first (basal) intracubital cell; *c2*, second intracubital cell; Cu, cubitus; CuA, anterior cubitus; CuP, posterior cubitus; *im*, basal intramedian cell; M, media; MA, anterior branch of media; MP, posterior branch of media; Psm, pseudomedia (formed by the alignment of sections of branches of MA and Rs and the crossveins connecting them); Psc, pseudocubitus (formed by the alignment of sections of branches of MA, MP, and Rs, and the crossveins connecting them); R, radius; R1, first branch of radius; Rs, radial sector; Rs1, most proximal branch of Rs; Sc, subcosta.

Institutional abbreviations used are BM, Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington, U.S.A; CNM, Canadian National Museum of Natural Sciences, Ottawa, Canada; MCZ, Museum of Comparative Zoology, Cambridge, MA, U.S.A; RBCM, Royal British Columbia Museum, Victoria, BC, Canada; SR, Stonerose Interpretive Center, Republic, Washington, U.S.A; TRU, Thompson Rivers University, Kamloops, BC, Canada.

Order NEUROPTERA LINNAEUS, 1758
Family CHRYSOPIDAE Schneider, 1851
Subfamily LIMAIINAE Martins-Neto and Vulcano, 1989
Genus PROTOCHRYSA Willmann and Brooks, 1991

Type species.—*Protochrysa aphrodite* Willmann and Brooks, 1991, by monotypy.

Diagnosis.—Revised: separated from other limaiine genera by some distal veinlets of R1 forked (all simple in other Limaiinae).

Species included.—Three species from the early Eocene of Europe and North America: *Protochrysa aphrodite*, *Protochrysa* sp. from Denmark (Fur Formation) (Rust, 1999; see below), *P. fuscobasalis* n. sp. from British Columbia, Canada (McAbee).

Remarks.—The second species from the early Eocene Fur Formation, Denmark assigned to *Protochrysa* was briefly described, illustrated, and named *P. athene* (Rust, 1999, p. 285; pl. 24, fig. a), although this appeared only in a dissertation and the name is therefore unavailable (ICZN, 1999, Articles 8.1.2 and 8.1.3), as noted by Nel et al. (2005), who considered it *in litteris* and referred to this specimen as "*Protochrysa* sp."

Willmann and Brooks (1991) did not assign *Protochrysa* to a subfamily when they proposed the genus, and neither did Adams (1996), who discussed it only as "pre-nothochrysine." Nel et al. (2005) then assigned it to the Mesozoic subfamily Limaiinae, which they elevated to family level. These authors provided a diagnosis for the Limaiinae based on the following forewing character states (slightly modified here): 1) Sc terminates at C well basad wing apex (Sc is indeed short, but not terminated at C, see below); 2) numerous veinlets present in the space between C and R1 (i.e., numerous veinlets of R1); 3) R1 terminates at or near the wing apex; 4) only two gradate series of crossveins in the radial space (inner and other); 5) Psm consists of the almost unmodified proximal portion of the inner (anterior) gradate series of crossveins (few cases where Psm is rather distinct, see below) and distally continuous with that gradate series; 6) Psc more defined than in Mesochrysopidae; 7) the cell *im* is elongate and narrow; and 8) the crossvein between cell *im* and CuA (2m-cu) is in a very distal position (Fig. 2.4–2.6). Limaiinae had been similarly characterized by Makarkin (1997).

All of these character states are found in *Protochrysa* and exclude it from the Chrysopinae and the Apochrysinae with certainty. Some, however, are found in the majority of both Limaiinae and Nothochrysinae, such as the absence of a well-developed Psm (character 5), which, however, is distinct in both the limaiine *Mesypochrysa magna* Makarkin, 1997 (Makarkin, 1997, fig. 1) and the nothochrysine *Nothochrysa* McLachlan, 1868 (Adams, 1967, fig. 3). The arrangement of crossveins in the radial space (character 4) and the structure of Psc (character 6) are also not informative: the radial crossveins are arranged in a similar manner in the majority of Chrysopidae, and the basal portion of the Psc is similarly constructed in both subfamilies. R1 is long in *Protochrysa* (terminating just before the wing apex) as in most Limaiinae (character 3; in the majority of those, R1 terminates just beyond the wing apex); however, this is not strongly diagnostic, as it also occurs in some Nothochrysinae (e.g., *Adamsochrysa wilsoni* n. gen. n. sp., below). These characters are, therefore, not useful in distinguishing between these two subfamilies.

Characters 7 (the shape of *im*), 8 (the position of 2m-cu), and a combination of characters 1, 2, and 3 (the relative lengths of Sc and R1 and the numerous veinlets of R1), however, are useful in this regard. In *Protochrysa*, *im* is long, with the sections of MA

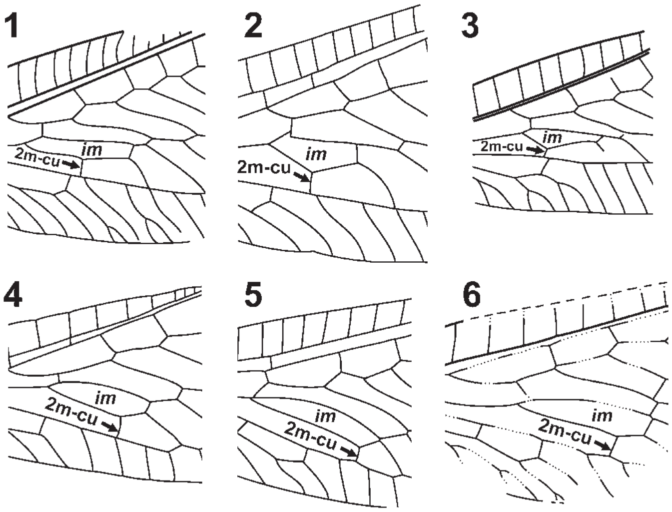

FIGURE 2—Configuration of intramedian cell (*im*) and the position of the crossvein 2m-cu in the forewing of the early Eocene and Early Cretaceous Chrysopidae; re-drawn, based on original figures as cited. *1–3*, early Eocene Nothochrysinae: *1*, *Stephenbrooksia mulifurcata* Willmann, 1993; *2*, *Cimbrochrysa moleriensis* Schluter, 1982; *3*, *Danochrysa madseni* Willmann, 1993; *4–6,* Early Cretaceous Limaiinae: *4*, *Lembochrysa miniscula* Ren and Guo, 1996; *5*, *Mesypochrysa magna* Makarkin, 1997; *6*, *Baisochrysa multinervis* Makarkin, 1997. All not to scale.

and MP bounding it mostly subparallel, but tapering to a point or nearly so basally, as is always the case in Limaiinae; in known Nothochrysinae, its shape is quite different: broadly variable, but always angulate, although it may be long in some genera (e.g., *Stephenbrooksia* Willmann, 1993) (Fig. 2). In all Limaiinae known to us (including the oldest, undescribed species from the Middle Jurassic of Daohugou, China), the crossvein 2m-cu is located in the distal part of *im* and Sc is relatively short and either fused with R1 (or closely approaches it) or its termination point is undetectable within the heavily pigmented pterostigma (character 1); as a result, the long R1 has numerous veinlets distally (character 2), as is the case in *Protochrysa*. Together, the shape of *im*, the position of 2m-cu and the relative lengths of Sc and R1 confidently place *Protochrysa* in the subfamily Limaiinae.

The monotypic extant genus *Leptochrysa* (Adams and Penny, 1992) is known from a single female specimen from Peru and bears a number of traits that are distinctive within the modern Chrysopidae. For example, it is unique in that microtrichia cover the whole of the wing membrane, whereas this is restricted to the posterior base of the forewing in all other extant Chrysopidae. Detection of microtrichia is almost always precluded in compression fossils by preservation, but they do appear to be absent in examined well-preserved Limaiinae specimens from the Barremian Yixian Formation of China, where fine-level preservation suggests that they should be visible if present (Q. Yang, personal commun. to VNM, 2011). Adams and Penny (1992a, 1992b) placed its only species, *Leptochrysa prisca* (Adams and Penny, 1992), in the Nothochrysinae. Like *Protochrysa*, however, *Leptochrysa* bears character states that suggest that this is an uncomfortable fit. For example, there is a proximal crossvein between Rs and MA in the hind wing, which is not known in any modern Chrysopidae, but is found in early Eocene Nothochrysinae and in most Limaiinae. More interesting is the relative lengths of Sc and R1, which is similar to the configuration found in *Protochrysa*, with R1 having numerous veinlets and Sc not extending beyond the distinct pterostigma (cf. Adams and Penny, 1992a, fig. 10), suggesting a limaiine affinity. Further, the cell *im* is distinctively shaped, tapering basally, although broad and rather short, with the very short crossvein 2m-cu located in the distal half of *im*. Although the broad and short shape of *im* is not known in Limaiinae, its tapering basally is, and further, the placement of the crossvein 2m-cu is as in Limaiinae (proximad *im* or in proximal half of *im* in all other Nothochrysinae, extant or extinct). It is quite possible that *Leptochrysa* belongs to Limaiinae, although the shape of *im* does provide doubt. If so, it is the single known living limaiine, and the only one known after the early Eocene species reported here. If it is a nothochrysine, it is certainly strongly different from other members of the subfamily, both extant and fossil.

Some of the species-level variation within *Protochrysa* is noteworthy. *P. fuscobasalis* bears some character states that appear to be derived within the Limaiinae, such as 1) its three-branched CuP, which it shares with the monotypic nothochrysine *Stephenbrooksia* and *Danochrysa* Willmann, 1993 (both early Eocene, Fur Formation, Denmark), the Early Cretaceous limaiine *Caririchrysa skulda* Martins-Neto, 2003 (Crato Formation, Brazil) and the monotypic *Drakochrysa* Yang and Hong, 1990, also Early Cretaceous (Laiyang Formation, China), whose subfamily affinity is uncertain (although its venation is rather similar to that of some nothochrysine genera); 2) two basal subcostal crossveins (if it is not an anomaly of the holotype); and 3) two crossveins between MA an MP proximal to Psc (1im, 2im). This species is noteworthy also by the presence of two crossveins between MP and CuA proximal to Psc (2m-cu, 3m-cu). There is only one crossvein in the majority of limaiine and nothochrysine genera. The known exceptions are the extant *Dictyochrysa* Esben-Petersen, 1917 and *Adamsochrysa* n. gen., and the very odd Early Cretaceous genus *Paralembochrysa* Nel et al., 2005 from the Yixian Formation of Liaoning Province, NE China, which was considered by Nel et al. (2005a) as "Chrysopoidea familia incertae sedis (maybe Chrysopidae)," and was subsequently included in Chrysopidae by Ren and Makarkin (2009). Finally, 1A and 2A are deeply forked in *P. fuscobasalis*, a condition characteristic of most limaiine genera. *Protochrysa aphrodite* differs in having a two-branched CuP, single basal subcostal crossvein, single crossvein each between MA and MP (1im) and between MP and CuA (2m-cu) is proximal to Psc, and 1A and 2A is simple (Willmann and Brooks, 1991, fig. 2).

PROTOCHRYSA FUSCOBASALIS new species
Figure 3

2006 *Protochrysa* ARCHIBALD AND MAKARKIN, p. 126.
2007 Chrysopidae sp. 4 ARCHIBALD, p. 111.
2011 Chrysopidae ARCHIBALD ET AL., fig. 2J.

Diagnosis.—May be distinguished from *P. aphrodite* by three-branched CuP (two-branched in *P. aphrodite*) or by two crossveins each between MA, MP, between MP, CuA proximal to Psc (one in *P. aphrodite*).

Description.—Holotype UCCIPR L-18 F-1525 (Fig. 3.1–3.3): Forewing. Length 17.0 mm; width 5.3 mm. Costal space relatively narrow; 22–23 simple subcostal veinlets (proximal to pterostigma), rather widely spaced. Pterostigma distinct, fuscous. Sc relatively short, entering margin within pterostigma. Two crossveins in proximal part of subcostal space. R1 entering margin slightly before wing apex, with about 18 apical veinlets, of which at least eight forked near margin. Space between R1, C broad. R1 space rather narrow basally and apically, somewhat dilated medially, with 17 crossveins. Rs zigzagged, with 16 branches. Basal crossvein between Rs, M very short, connecting stem of Rs, MA. M dividing into MA, MP distal to origin of Rs. Between MA, MP three crossveins. *im* long, tapering basally. Psm not developed. Two m-cu crossveins. Cu dividing into CuA, CuP,

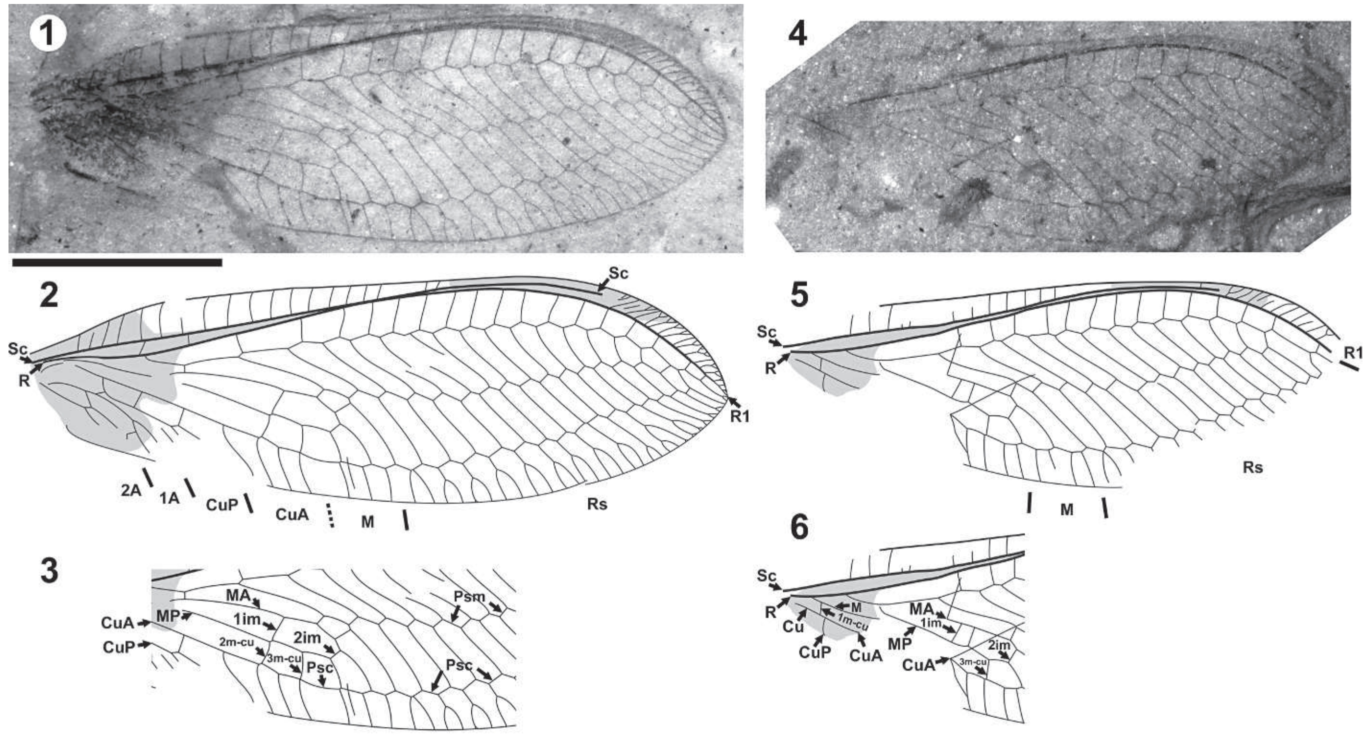

FIGURE 3—*Protochrysa fuscobasalis* n. sp.: *1–3,* holotype UCCIPR L-18 F-1525, photograph, drawing, labeled drawing, respectively; *4–6*, UCCIPR L-18 F-1528, photograph, drawing, labeled drawing, respectively. Scale=5 mm.

two crossveins between them. CuA with six simple branches. CuA continuing into short Psc, then into outer gradate series of crossveins. CuP with two branches, forked proximal to crossvein 2icu. 1A, 2A deeply forked. 3A poorly visible. Two gradate series of crossveins, slightly convergent apicad; 16 crossveins in inner series, 17 in outer; one intra-serial crossvein between Rs1, MA. Wing membrane dark basally.

Specimen UCCIPR L-18 F-1528 (Fig. 3.4–3.6): Forewing ~13.5 mm long as preserved (estimated length 15 mm), 5.5 mm wide. Venation similar to that of holotype except: Rs with 13 preserved branches (14 estimated in complete wing); three intramedian crossveins before Psc (two most proximal rather close to each other); short 1m-cu preserved; 13 crossveins in inner series of crossveins; preserved veinlets of R1 simple. This fossil is on a piece of shale approximately 25×20 cm, which also bears UCCIPR L-18 F-1529 (placed in *Okanaganochrysa coltsunae* n. gen. n. sp., see below), a feather, several leaves (*Betula*, ?*Prunus*), a *Dipteronia* fruit, small seeds, conifer needles, and at least ten new insect species in seven orders (Archibald et al., 2011, fig. 2).

Etymology.—From Latin *fuscus*, fuscous, and *basalis*, basal, in reference to dark coloration of forewing basal portion.

Type.—Holotype: UCCIPR L-18 F-1525; a well-preserved nearly complete forewing; deposited in the TRU collection. Other material examined: UCCIPR L-18 F-1528a, b; a rather poorly preserved and slightly crumpled, incomplete forewing; deposited in the TRU collection.

Occurrence.—McAbee, British Columbia, Canada; early Eocene.

Subfamily NOTHOCHRYSINAE Navás, 1910

Diagnosis.—Revised: Nothochrysinae may be characterized by the following character states (based on Adams, 1967 and Brooks and Barnard, 1990, supplied here with addition characters): in the forewing, (A) Psm consists of slightly modified proximal portion of inner (anterior) gradate series of crossveins (few exceptions, e.g., in *Nothochrysa*, Psm is distinct) and/or distally continuous with that gradate series (shared with Limaiinae; extending to outer gradate series in Chrysopidae, Apochrysinae); (B) tympanal organ is absent (unknown in Limaiinae; present in Chrysopidae, Apochrysinae); (C) the jugal lobe is well developed (shared with Limaiinae; absent or reduced in Chrysopidae, Apochrysinae); (D) the crossvein 2m-cu located proximad *im* or in proximal half of *im* (shared with Chrysopidae; located in distal half of *im* in Limaiinae; inapplicable to Apochrysinae); (E) frenulum present in hind wing (probably shared with Limaiimae [not clearly determined]; absent or reduced in Chrysopidae, Apochrysinae); (F) in both wings, Sc is only somewhat shorter than R1, veinlets of R1 are not numerous (shared with Chrysopinae; Sc much shorter than R1 with numerous veinlets of R1 in Limaiinae, Apochrysinae).

Remarks.—This subfamily is considered by most authors to be more primitive than the other two extant subfamilies (Chrysopinae and Aphochrysinae), possessing many plesiomorphic conditions (Adams, 1967; Brooks and Barnand, 1990). As a result, no defining apomorphies have been established for Nothochrysinae (Brooks, 1997). The presence of five or six rings of flagellar setae could be apomorphic for the subfamily (Brooks and Barnard, 1990, Adams and Penny, 1992a), but this might have also been present in Limaiinae (the antennae in this subfamily are poorly preserved in known specimens, as reported), and, therefore, may be plesiomorphic. Some authors believed that the subfamily is likely paraphyletic (e.g., Willmann and Brooks, 1991; Adams and Penny, 1992a).

Genus OKANAGANOCHRYSA new genus

Type species.—*Okanaganochrysa coltsunae* new species, by monotypy.

Diagnosis.—As for species.

Etymology.—From the Okanagan Highlands, and *chrysa*, a

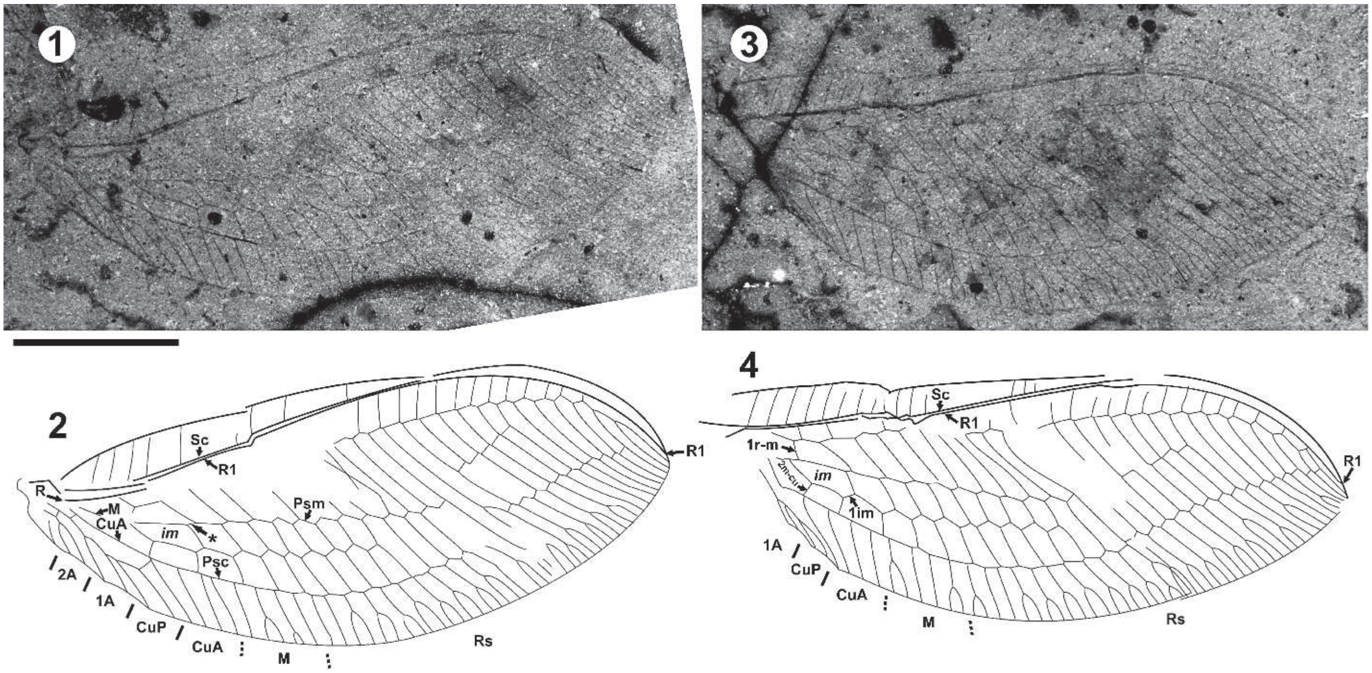

FIGURE 4—*1–4*, *Okanaganochrysa coltsunae* n. gen. n. sp., holotype UCCIPR L-18 F-1530, two disarticulated forewings: *1, 3*, photographs; *2, 4*, drawings. Asterisk is the basalmost crossvein of the anterior gradate series connecting Rs to *im* (see genus diagnosis). Scale=5 mm.

traditional ending of chrysopid genera, derived from the Greek *chrysos*, gold. Gender feminine.

Remarks.—A nothochrysine affinity of this genus is based of the presence of character states (A), distinguishing it from Chrysopinae and Apochrysinae, and (D) distinguishing it from Limaiinae.

Okanaganochrysa n. gen. and *Adamsochrysa* are noteworthy, as in these genera, the basalmost crossvein of the anterior (inner) gradate series connects Rs1 and *im*, whereas in other chrysopid genera, this crossvein is always positioned distad this cell. *Okanaganochrysa* also resembles the Danish Fur Formation genera *Cimbrochrysa* Schlüter, 1982, *Danochrysa* and *Stephenbrooksia* by the rather similar shape of *im*, the distal shift of 2m-cu, and Psc being smoothly and slightly curved, not zigzagged (cf. Schlüter, 1982, fig. 1b; Willmann, 1993, figs. 1a, 2a). *Okanaganochrysa* is unlike other Cenozoic North American genera (i.e., those described from Florissant and Creede; those reported from other localities await description) by the much more distal position of crossvein 2m-cu; in these genera this is placed either proximad 1r-m (connecting Rs and *im*), or nearly opposite this, or very rarely (as in *Archaeochrysa fracta* (Cockerell, 1914)) slightly distal to 1r-m (Adams, 1967).

OKANAGANOCHRYSA COLTSUNAE new species
Figures 4, 5

2007 Chrysopidae sp. 3 ARCHIBALD, p. 111.
2011 Chrysopidae ARCHIBALD ET AL., fig. 2G.

Diagnosis.—Basalmost crossvein of anterior gradate series connecting Rs1 to *im* placed well proximal to 1im (Fig. 4) (shared with species of *Adamsochrysa* n. gen.; placed distal to *im* in other species of Nothochrysinae); two gradate series of crossveins in distal portion of wing (four series in species of *Adamsochrysa*).

Description.—Holotype UCCIPR L-18 F-1530 (Fig. 4.1–4.4): Forewings. Preserved lengths 20 mm, 20.8 mm (estimated complete lengths 21–22 mm), widths 8.3 mm (maximum). Costal space moderately broad, with simple subcostal veinlets relatively closely spaced. Distal part of Sc not preserved. R1 long, entering wing margin just before apex, its veinlets not preserved. Space between R1, costal margin in apical portion narrow. Crossvein 1sc-r not preserved. Origin of Rs located relatively close to wing base, proximal to *im*; part of Rs proximad 1r-m, 1r-m nearly equal in length; 24–25 branches of Rs. R1 space (between R1, Rs) narrow basally, distally, somewhat dilated medially; crossveins closely spaced. M forked distal to origin of Rs. *im* subtriangular. Basal crossvein 1r-m at nearly right angle to *im*, connects Rs, *im* just distal to forking of M. Most proximal crossvein of inner gradate series very short connecting Rs1, distal half of *im*. Intramedian crossvein 1im (closed *im* apically) rather short. One m-cu crossvein preserved (2m-cu), located rather far distal to fork of M, clearly proximal to crossvein 1r-m. Psm rather well-developed, zigzagged. Psc well-developed, not zigzagged proximally. CuA probably with four simple branches. CuP deeply forked (CuP, 1A appear fused for quite long distance probably due to crumpled wing base). 1A, 2A deeply forked. 3A only fragmentary preserved. One intracubital crossvein preserved (2icu), located at most-proximal branch of CuA. Three gradate series of crossveins: inner series proximally running as straight, zigzagged line (as part of Psm) then bent to anterior, with 19–20 crossveins; intermediate series rather short (eight to nine crossveins) parallel to basal part of inner series; outer series nearly parallel to inner series, with up to 26 well-visible crossveins (others included into Psc). Wing membrane apparently hyaline throughout.

Specimen UCCIPR L-18 F-1529 (Fig. 5): Apical portion of a forewing about 10 mm long, 8.3 mm wide as preserved, in all ways similar to the holotype.

Etymology.—The specific epithet is a patronymic formed from the surname Coltsun, maiden name of Sylvia O'Sullivan, mother of Terrence O'Sullivan, collector of the holotype.

Type.—Holotype UCCIPR L-18 F-1530a, b (part and counterpart); two nearly complete forewings lying next to each other on the rock (the same rock, as discussed above, see UCCIPR L-18 F-1525); deposited in the TRU collection.

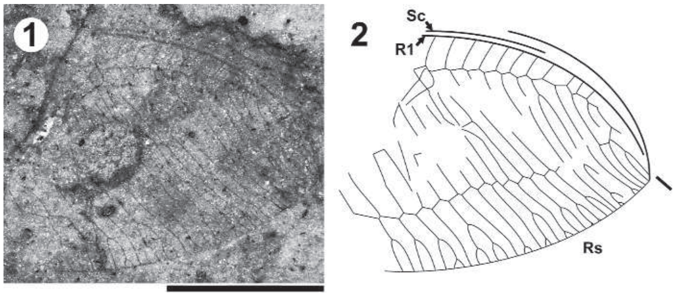

FIGURE 5—*Okanaganochrysa coltsunae* n. gen. n. sp., specimen UCCIPR L-18 F-1529: *1*, photograph; *2*, drawing. Scale=5 mm.

Other material.—Specimen UCCIPR L-18 F-1529a, b (part and counterpart); deposited in TRU; an apical fragment of forewing.

Occurrence.—McAbee, British Columbia, Canada; early Eocene

Remarks.—The preserved portion of UCCIPR L-18 F-1529 is sufficiently similar to the holotype that we assign it to this species. This wing is somewhat damaged. Some parts the wing membrane are crumpled, and in other parts the membrane may be torn and bits with veins on it may be displaced.

Genus Adamsochrysa new genus

Type species.—*Adamsochrysa aspera* new species.

Other species.—*A. wilsoni* new species, *Adamsochrysa* species A, Adamsochrysa species B (the latter two provisionally).

Diagnosis.—The forewing venation of *Adamsochrysa* n. gen. is most similar to that of *Dictyochrysa*, but easily distinguished from it by any of: much more proximal position of basalmost crossvein of anterior gradate series connecting Rs-system with *im* (this crossvein placed well distad intramedian cell in *Dictyochrysa*); vast majority of radial crossveins form four to five distinct gradate series (majority of these crossveins form reticulation in *Dictyochrysa*); radial crossveins not extending to forks of Rs branches (extending to forks of Rs in *Dictyochrysa*).

Etymology.—From the surname of Prof. Dr. Phillip Anthony Adams (1929–1998), a prominent American neuropterologist, and *chrysa*, a traditional ending of chrysopid genera. Gender feminine.

Occurrence.—McAbee, British Columbia, Canada; Republic, Washington, U.S.A.; early Eocene.

Remarks.—The nothochrysine affinity of this genus is based on the presence of the character states (A), distinguishing it from Chrysopinae and Apochrysinae, and (D) and (F) distinguishing it from Limaiinae.

This Eocene North American genus is probably most closely related to the extant Australian/ Tasmanian genus *Dictyochrysa*, whose venation is shown in Kimmins (1952, fig. 2), New (1980, figs. 42–45), and Brooks and Barnard (1990, fig. 527). These genera share a unique character state within Nothochrysinae, i.e., the crossveins in the radial space are either arranged in four or more gradate series, or they form a reticulation (in *Dictyochrysa*). These crossveins are arranged in other nothochrysine genera in two or three gradate series.

The forewing venation of the genus *Adamsochrysa* is similar to that of *Okanaganochrysa* n. gen. (see above), but easily distinguished from it by the greater number of gradate series in the distal half of the forewing (four to five in the former, two in the latter).

Adamsochrysa aspera new species
Figures 6–10

2005 *Chrysopa* Grimaldi and Engel, p. 351, fig. 9.29.
2007 Chrysopidae sp. 1 Archibald, p. 111.
2007 Chrysopidae sp. 2 Archibald, p. 111.

Diagnosis.—May be distinguished from other species of the genus by regular arrangement of crossveins in forewing radial space (irregular in *A. wilsoni* n. gen. n. sp.); wide, short *im* (elongate in *A. wilsoni* n. gen. n. sp.; *A*. sp. B); trichosor-like structures absent (present in *A*. sp. A).

Description.—Holotype CMNIF25 (Fig. 6.1, 6.2): Forewing. Length 29.0 mm; width 10.6 mm (length/width ratio 2.74). Costal space moderately broad proximally with simple subcostal veinlets relatively widely spaced, several (probably six) veinlets forked before pterostigmal region. Sc long, terminating on apical margin. R1 long, entering wing margin at apex, its veinlets poorly preserved. Space between Sc, R1, between Sc, costal margin in apical portion narrow. Numerous (up to 16) subcostal crossveins before pterostigma. Origin of Rs located relatively far from wing base, slightly proximal to *im*; part of Rs proximad 1r-m slightly longer than 1r-m; 24 branches of Rs. R1 space (between R1, Rs) somewhat dilated medially, narrow distally; crossveins closely spaced. M forked slightly distal to origin of Rs. *im* broad, seven-sided. Basal crossvein 1r-m connects Rs, *im* in proximal part *im*. Proximal-most crossvein of inner gradate series long, connecting Rs1, distal half of *im*. Two intermedian crossveins (1im, 2im); crossvein 1im (closed *im* apically) relatively short. Four m-cu crossveins preserved, basal 1m-cu oblique; 2m-cu, 3m-cu located in proximal part of *im*, 2m-cu slightly proximal to crossvein 1r-m. Psm weakly-developed, zigzagged. Psc well-developed, smooth proximally, zigzagged distally. CuA probably with four branches. CuP only proximally preserved. One intercubital crossvein preserved (1icu), located relatively close to origin of CuP. 1A, 2A deeply forked. Four complete gradate series of crossveins extending through most of radial space; additional short series between second, third series proximally in radial space. Wing membrane apparently hyaline throughout.

Specimen CMNIF105 (Fig. 6.3, 6.4): Forewing. Length 29.0 mm; width 10 mm (length/width ratio 2.90). Costal space moderately broad proximally, with simple subcostal veinlets relatively widely spaced (one veinlet forked) before pterostigmal region. Termination of Sc not preserved, apparently long. R1 long, apparently entering wing margin at apex, its veinlets not preserved. Two subcostal crossveins before pterostigma preserved. Origin of Rs located relatively far from wing base, distal of basal 1sc-r; apparently 22 branches of Rs. R1 space somewhat dilated medially, narrow distally; crossveins closely spaced (one forked). Basal 1m-cu crossvein oblique Psc well-developed, smooth proximally, zigzagged distally. CuP originated just proximad 1m-cu. Four gradate series of crossveins in radial space partially preserved.

Specimen UCCIPR L-18 F-983 (female) (Fig. 7): Head relatively small. Antennae: scapus strongly enlarged; pedicellus only slightly stouter than first flagellomere; proximal flagellar segments elongate, 2–2.5 times as long as wide (boundaries between other segments not clearly visible); palpi relatively long. Thorax: prothorax short; mesothorax morphology not distinct. Legs covered with dense, short hairs; tibial apical spurs not detected. Abdomen complete; shape of terminal segments somewhat unclearly preserved, but in general appear similar to that of extant *Dictyochrysa*.

Forewing. Length 30.5 mm as preserved (estimated complete 31.5 mm); width 11 mm (length/width ratio 2.86). Costal space moderately broad with simple subcostal veinlets relatively widely spaced proximally, several veinlets (one in left wing, seven in right wing) forked before pterostigmal region. Termination of Sc, R1 not preserved, but R1 long. No subcostal crossveins detected. Origin of Rs located relatively far from wing base, probably proximal to *im*. Rs with >22 branches. R1 space somewhat

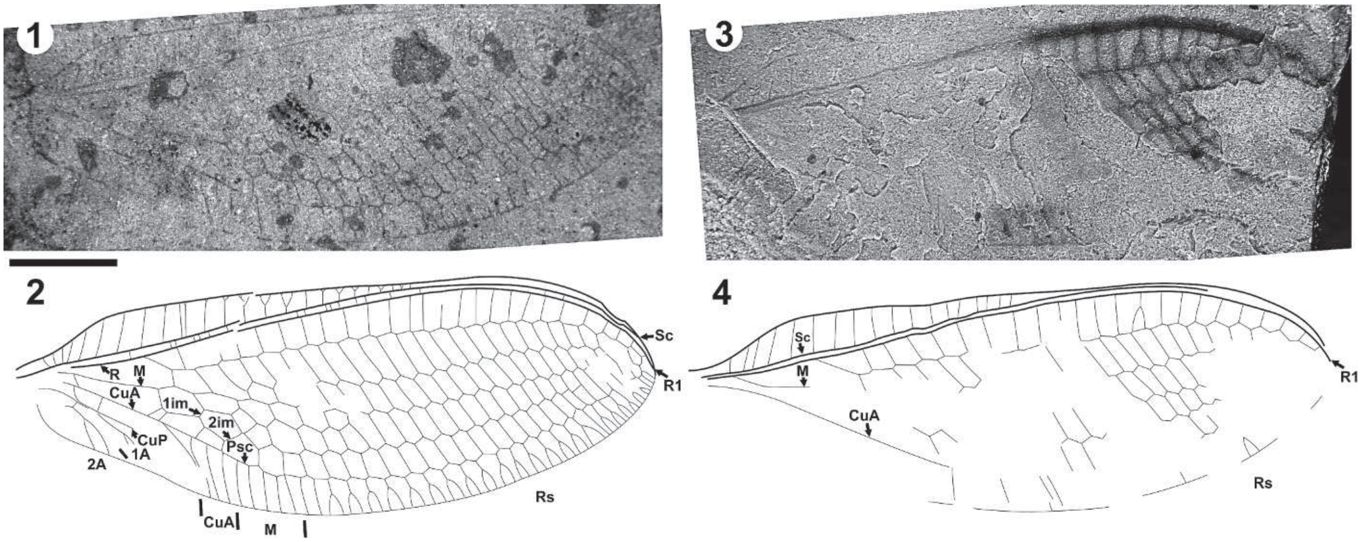

FIGURE 6—*Adamsochrysa aspera* n. gen. n. sp. forewings: *1, 2*, holotype CMNIF25, photograph and drawing, respectively; *3, 4*, CMNIF105, photograph and drawing, respectively. Scale=5 mm.

dilated medially, narrow distally; crossveins closely spaced. *im* short, broad. Three intermedian crossveins (1im to 3im); crossvein 1im (closed *im* apically) relatively long, oblique. Two m-cu crossveins preserved; 2m-cu connects *im*, CuA. Psm weakly developed, zigzagged. Psc well-developed, smooth proximally, zigzagged distally. CuA probably with four or five branches. CuP with three branches (right wing); with two branches, proximal branch of which deeply forked (left wing). Two intercubital crossveins preserved (1icu, 2icu); *c1* clearly shorter than *c2*. 1A, 2A deeply forked; some of their branches shallowly forked (one branch of 1A in left wing; three branches of 1A, 2A in right wing). 3A not preserved. Four compete regular gradate series of crossveins; additional short series between second and third series proximally in radial space. Wing membrane apparently hyaline throughout.

Hind wing. Narrower than forewing; length 25.8 mm (as preserved; estimated complete ~27–28 mm); width 8.7 mm. Costal space narrow, with simple subcostal veinlets relatively widely spaced before pterostigmal region. Termination of Sc not preserved. R1 long, entering wing margin just before apex, its veinlets rather widely spaced. R1 space narrow distally, somewhat dilated medially. Psc relatively well-developed, slightly zigzagged. Four complete regular gradate series of crossveins.

Specimen UCCIPR L-18 F-1531 (Fig. 8.1, 8.2): Forewing. Preserved length 20 mm (estimated complete ~30 mm); preserved width 11.3 mm (estimated complete 11.3–11.5 mm). Costal space moderately broad proximally, with simple subcostal veinlets relatively widely spaced before pterostigmal region. Termination of Sc, R1 not preserved, but these apparently long. Subcostal crossveins not preserved. Rs with >23 branches. R1 space narrower basally, somewhat dilated medially; crossveins rather closely spaced. Psm weakly developed, zigzagged. Psc well-developed, smooth proximally, zigzagged distally. Four compete gradate series of crossveins in radial space; additional short irregular series between second and third series proximally in radial space.

Specimen UCCIPR L-18 F-1532 (Fig. 8.3, 8.4): Head, antennae, thorax, legs present, but poorly preserved. Hind wing. Length 22 mm as preserved (23 mm estimated complete), 8.0 mm wide. Costal space narrow. Termination of Sc, R1 not preserved, but they appear surely long. R1 space nearly equal in width throughout, with 20 crossveins preserved. Branches of Rs (~21 in number) more oblique than in forewing. Four regular compete gradate series of crossveins. Basal portion of wing poorly preserved.

Specimen UCCIPR L-18 F-1533 (Fig. 9.1–9.3): Head, thorax poorly preserved. Legs covered with dense, short hairs. Abdomen very incomplete, terminal segments not preserved.

Forewing. Preserved length 24 mm (estimated complete ~29 mm), preserved width about 10 mm (estimated width 10.5–10.8 mm). Costal space moderately broad proximally, with simple subcostal veinlets relatively widely spaced (one veinlet forked) before pterostigmal region. Termination of Sc, R1, subcostal crossveins not preserved. Basal 1m-cu crossvein oblique. Psc well-developed, smooth proximally, zigzagged distally. CuP originated just proximad 1m-cu. Four gradate series of crossveins in radial space partially preserved.

Hind wing. Fragments, indistinctly preserved.

Specimen UCCIPR L-18 F-1534 (Figs. 10.1–10.6, 26): Body not preserved.

Forewing. One, length ~26 mm (estimated complete 28 mm); width 11.2 mm (length/width ratio 2.50; possibly slightly crumpled). Second forewing very crumpled. Costal space moderately broad proximally. Termination of Sc, subcostal crossveins not preserved. R1 long, entering wing margin just before apex. R1 space (between R1, Rs) somewhat dilated medially, narrow distally; crossveins closely spaced. M forked distal to origin of Rs. *im* broad, five-sided. Rs with >20 branches. Proximal-most crossvein of inner gradate connecting Rs1, distal half of *im*. Three intramedian crossveins (only visible in one wing). 2m-cu connecting proximal part of *im*, CuA. Psc well-developed, smooth proximally, zigzagged distally. CuA probably with four branches. CuP with two long pectinate branches. 1A rather deeply forked. Four gradate series of crossveins in radial space partially preserved.

Hind wings preserved as crumpled, torn portions only.

Etymology.—From the Latin adjective *asper*, meaning hard or difficult; referring to difficulties at times in obtaining specimens.

Types.—Holotype CMNIF25 (part and counterpart); a rather well-preserved, almost complete, forewing; deposited in the CMN collection.

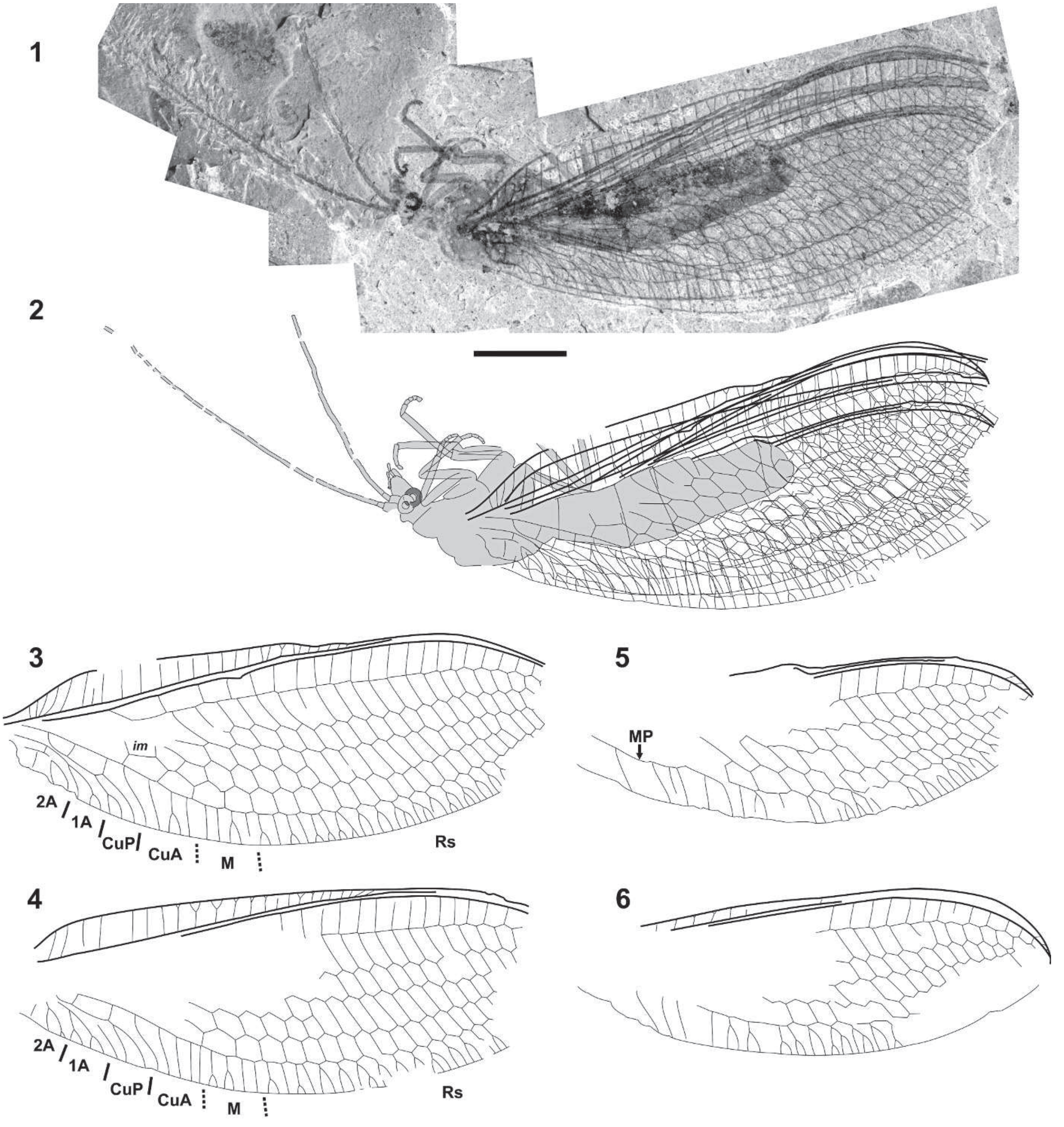

FIGURE 7—*Adamsochrysa aspera* n. gen. n. sp., specimen UCCIPR L-18 F-983: *1,* photograph; *2*, drawing the specimen as preserved; *3, 4,* drawings of forewing venation; *5, 6*, drawing of hind wing venation. Scale=5 mm.

Other material.—Six specimens. UCCIPR L-18 F-983 (part only); a beautifully preserved almost complete specimen in lateral position with all wings overlapping; deposited in the TRU collection (not the MCZ fossil insect collection as stated by Grimaldi and Engel, 2005, p. 351). CMNIF105 (part and counterpart); a poorly preserved incomplete forewing; deposited in the CMN collection. UCCIPR L-18 F-1531 (only part); an incomplete forewing; deposited in the TRU collection. UCCIPR L-18 F-1534a, b (part and counterpart); a poorly preserved incomplete fore and hind wings overlapped; deposited in the TRU collection. UCCIPR L-18 F-1533; a very incomplete and crumpled specimen with articulated wings; deposited in the TRU collection. UCCIPR L-18 F-1532a, b (part and counterpart); head, thorax, some legs, a hind wing indistinctly preserved, venation visible under ethanol with oblique lighting; deposited in the TRU collection.

Occurrence.—McAbee, British Columbia, Canada; early Eocene.

Remarks.—The holotype of *Adamsochrysa aspera* is a unique fossil chrysopid by the presence of numerous proximal subcostal

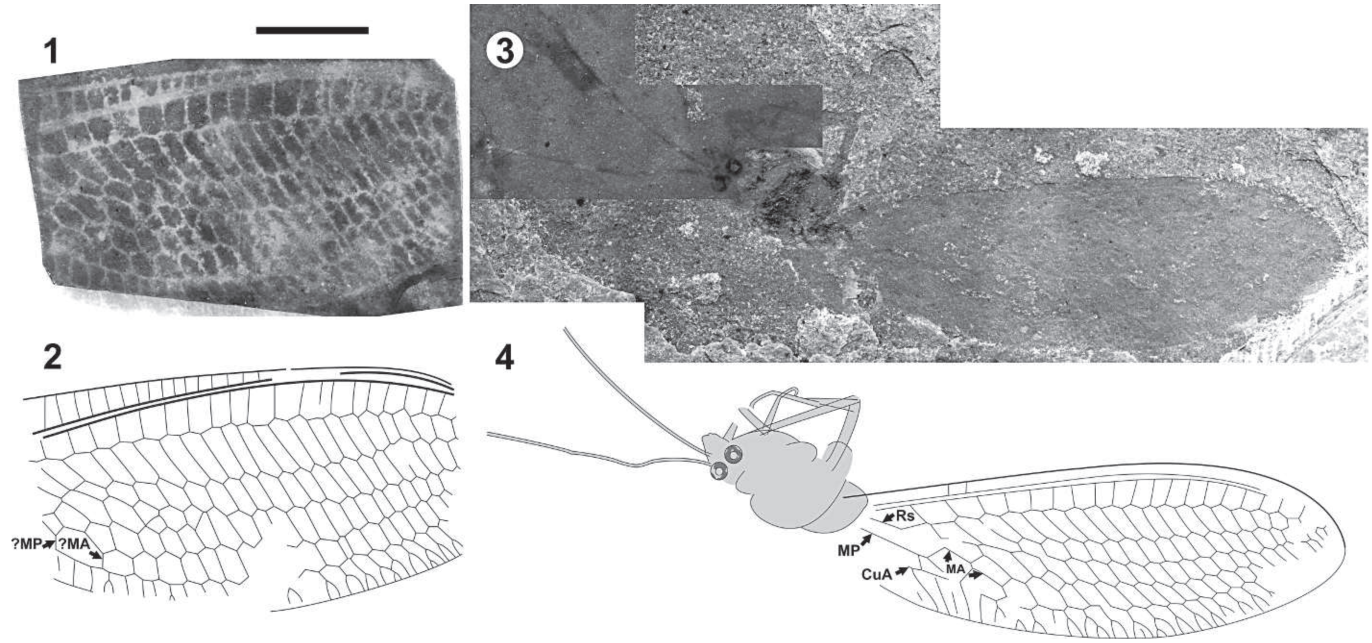

FIGURE 8—*Adamsochrysa aspera* n. gen. n. sp.: *1, 2,* UCCIPR L-18 F-1531, forewing photograph and drawing, respectively; *3, 4*, UCCIPR L-18 F-1532, body and a hind wing composite photograph (anterior portion wetted with ethanol) and drawing, respectively. Scale=5 mm.

crossveins in the forewing. The only other known species of Chrysopidae possessing this character state is the extant *Kimochrysa impar* Tjeder, 1966 from Southern Africa (Tjeder, 1966, fig. 785). Interestingly, two other *Kimochrysa* species (also from Southern Africa) have only one proximal subcostal crossvein, which is usual for the family. These numerous proximal subcostal crossveins were not, however, detected in the other specimens that we assign to this species. It's possible that their apparent absence is an artifact of preservation in these, or, alternatively, that they were not in fact present on these insects, and that they represent a separated species. We consider it most likely, however, that these crossveins are adventitious on the holotype.

Unfortunately, specimens CMNIF105, UCCIPR L-18 F-983, UCCIPR L-18 F-1531, UCCIPR L-18 F-1534, and UCCIPR L-18 F-1533 have incompletely preserved forewings, impeding detailed comparison. The venation of these specimens differs in detail but agrees in general with that of the holotype (e.g., same both shape of *im* and configuration of gradate series in the radial space) sufficiently that we consider them conspecific. Specimen UCCIPR L-18 F-1532 is assigned to this species preliminary, as its forewing is unknown.

The length/width ratio of the forewing in *A. aspera* ranges between 2.50 and 2.90. This variation might be at least partially accounted for by sexual dimorphism. In *Nothochrysa* specimens examined by Brooks and Barnard (1990), forewing length/width ratio ranged from 2.9 to 3.2, although a potential sexual difference was not mentioned. Shape dimorphism in wing morphology is little known in Neuroptera in general, although the forewings of males were usually somewhat wider than those of females in Dilaridae (Adams, 1970) and, to a lesser extent, in most species of Hemerobiidae (Makarkin and Kholin, 1995). Sexual dimorphism in forewing shape has been observed in Chrysopidae (the late P. Adams, personal commun. to VNM, 1994), although not characterized. Specimen UCCIPR L-18 F-983 has a length/width ratio of 2.86 and is known to be a female; if the pattern observed in Dilaridae and Hemerobiidae is shared in this family, this would suggest that the wider wings assigned to *A. aspera* here (i.e., whose length/width ratio is considerably less) belong to males.

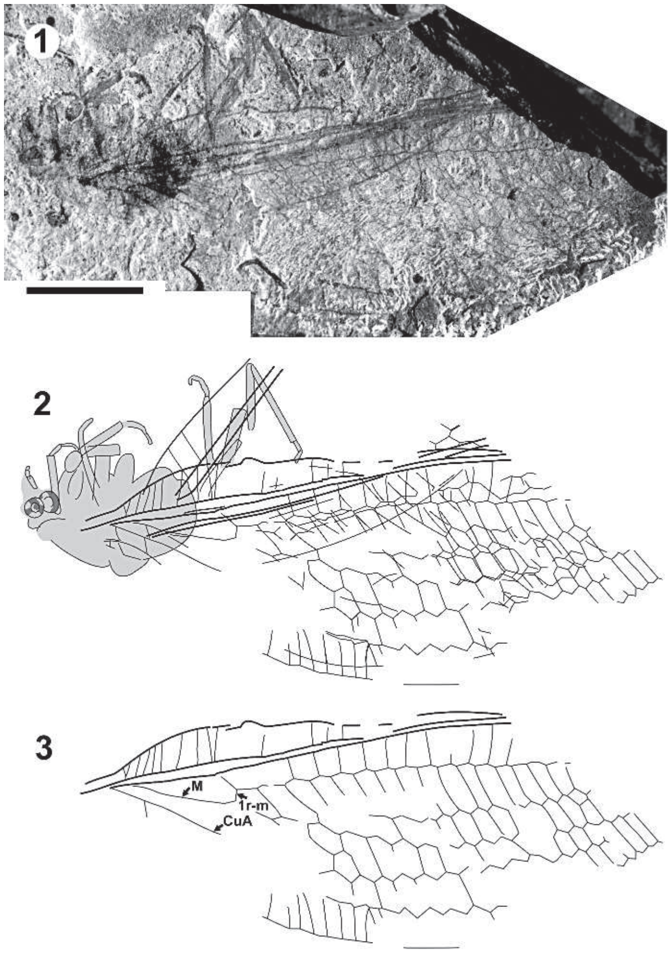

FIGURE 9—*Adamsochrysa aspera* n. gen. n. sp., UCCIPR L-18 F-1533: *1*, photograph; *2*, drawing of the specimen; *3*, drawing of the forewing. Scale=5 mm.

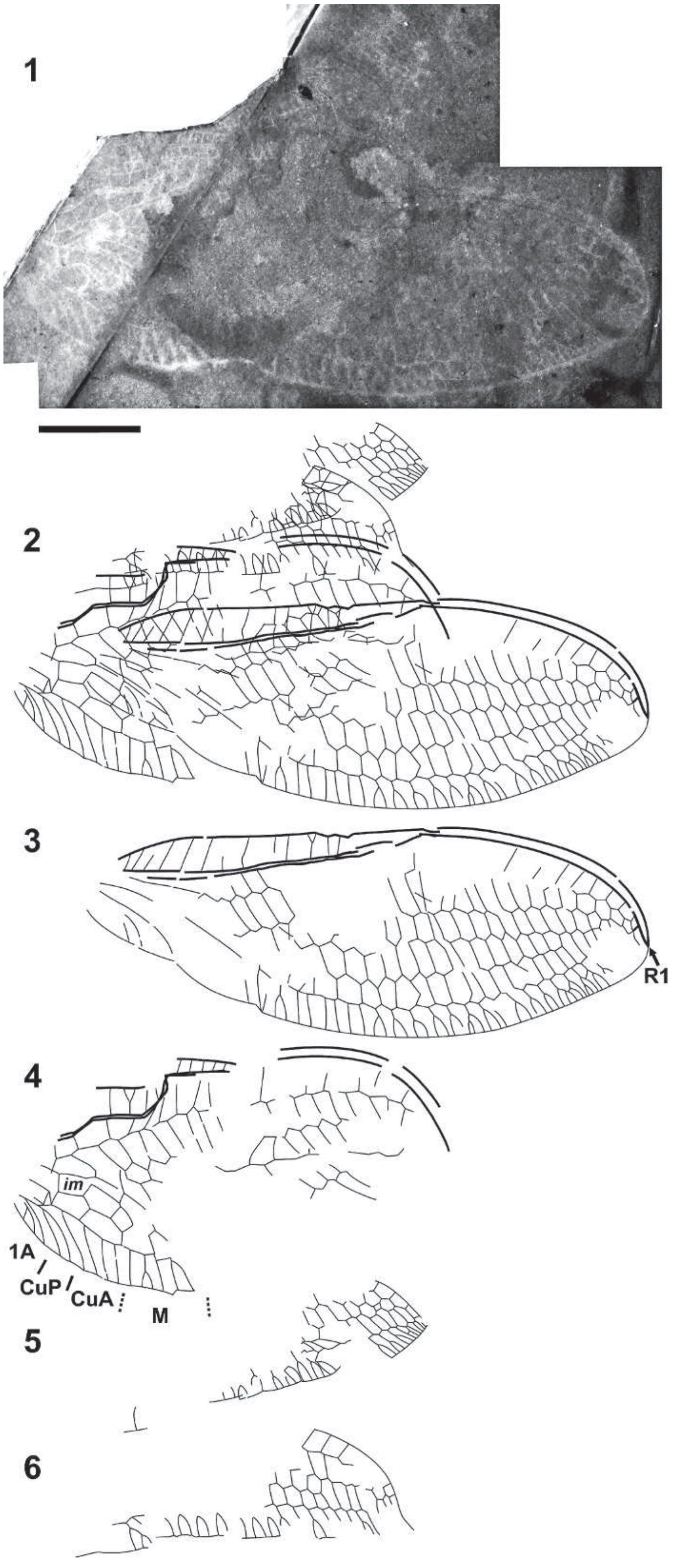

FIGURE 10—*Adamsochrysa aspera* n. gen. n. sp., UCCIPR L-18 F-1534: *1*, photograph; *2*, drawings of the specimen as preserved; *3, 4,* drawings of the forewings; *5, 6*, drawings of hind wings. Scale=5 mm.

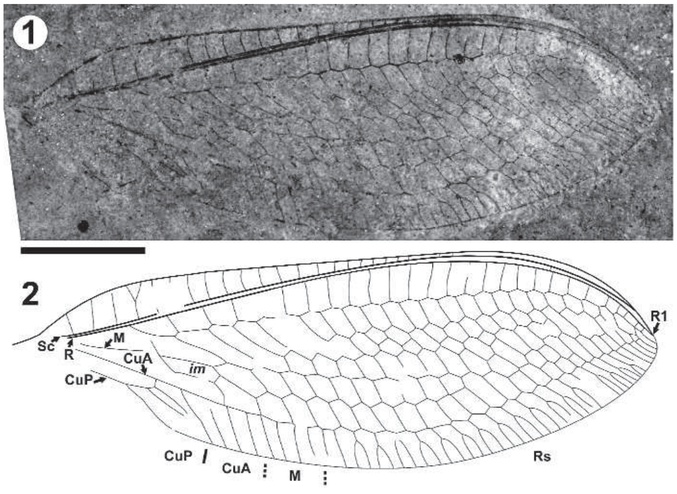

FIGURE 11—*Adamsochrysa wilsoni* n. gen. n. sp., holotype, SR06-23-01, forewing: *1,* photograph; *2,* drawing. Scale=5 mm.

Adamsochrysa wilsoni new species
Figure 11

Diagnosis.—May be distinguished from other species of the genus by irregular arrangement of crossveins in forewing radial space (regular in *A. aspera* n. gen. n. sp.); elongated *im* (short, broad in *A. aspera*); proximal branches of Rs, M entering Psc at acute angle (at more obtuse angle in *A.* sp. A); MP, CuA parallel in cell adjoining *im* sharing MP (clearly divergent in *A.* sp. B).

Description.—Forewing. Length 24.8 mm; width 8.6 mm. Costal space moderately broad, with simple subcostal veinlets relatively widely spaced (one veinlet forked) before pterostigmal region, very closely spaced after. Sc long, terminating on apical margin. R1 long, entering wing margin just before apex, its veinlets not evident as preserved. Space between Sc, R1, between Sc, costal margin in apical portion narrow. Subcostal crossvein not detected (possibly by preservation). Origin of Rs located relatively close to wing base, proximal to *im*; part of Rs proximad 1r-m, 1r-m nearly equal in length; 24 branches of Rs. R1 space (between R1, Rs) narrow basally, distally, somewhat dilated medially; crossveins closely spaced. M forked distal to origin of Rs. *im* elongate, subtrapezoid. Basal crossvein 1r-m connects Rs, *im* just at forking of M. Most proximal crossvein of inner gradate series long, connecting Rs1, distal half of *im*. Single intermedian crossvein 1im (closed *im* apically) rather long; m-cu crossveins not preserved, but 2m-cu should be located far distal to fork of M, clearly proximal to crossvein 1r-m (judging from curvature of MP at this point). Psm rather weakly developed, zigzagged. Psc well-developed, not zigzagged proximally. CuA probably with four to five simple branches. CuP with two long branches. Anal veins not preserved. One intracubital crossvein preserved (2icu), located proximal to 2m-cu. Five–six gradate series of crossveins, mostly irregular; outer (posterior) series compete, regular, nearly parallel to hind wing margin, with up to 20 well-visible crossveins (others included into Psc); other series incomplete. Wing membrane apparently hyaline throughout.

Etymology.—The specific epithet is a patronym formed from the surname of the collector of the holotype, Gregg Wilson.

Type.—Holotype SR06-23-01 (part only); an almost complete forewing; deposited in the SR collection.

Occurrence.—Republic, Washington, U.S.A., locality B4131; early Eocene.

Adamsochrysa (?) species A
Figure 12

1996 Chrysopidae Wehr and Barksdale, p. 29.

Description.—Thorax incompletely preserved (mostly crumpled mesothorax). Four large fragmentary disarticulated abdom-

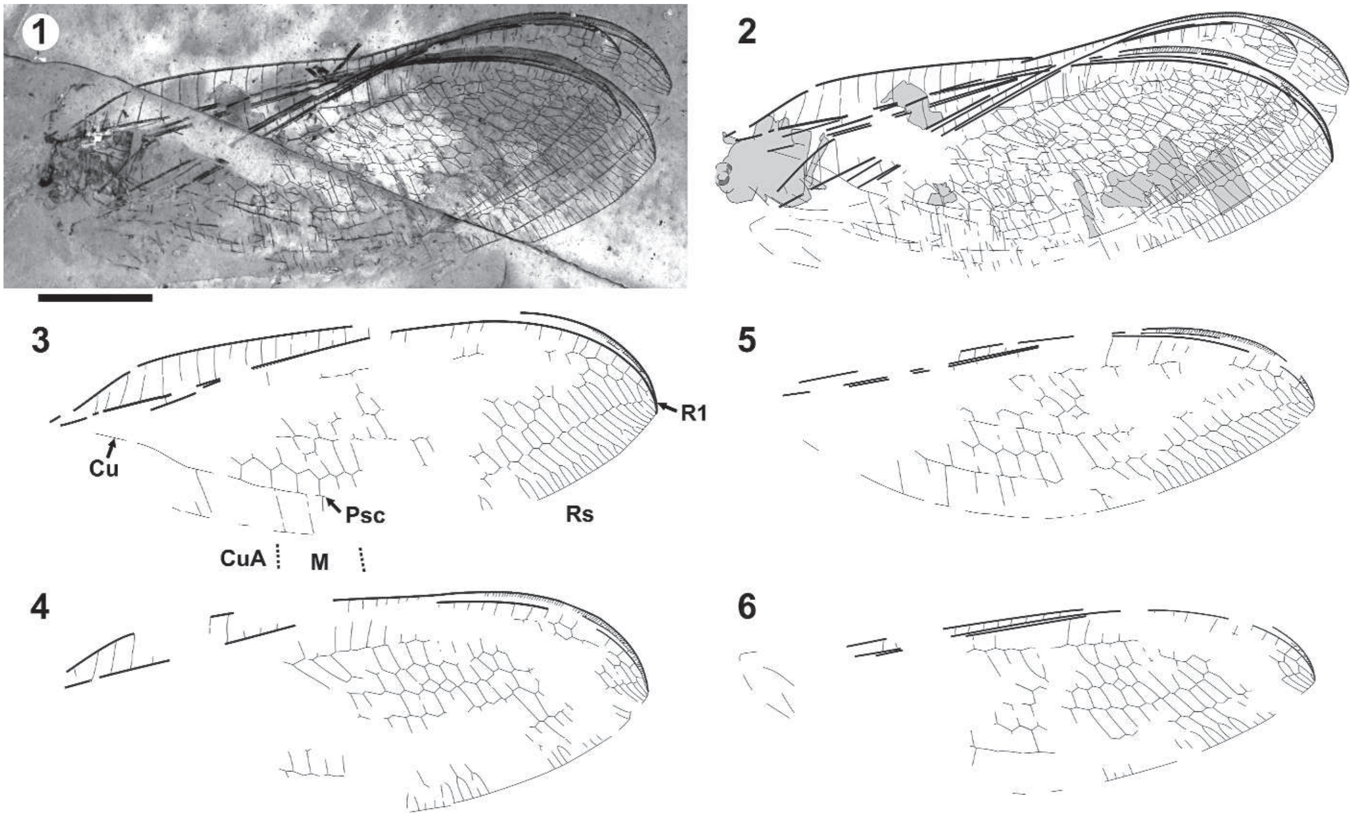

FIGURE *12*—*Adamsochrysa* (?) sp. A, UWBM 77571: *1*, photograph; *2*, drawing of the specimen as preserved; *3, 4*, drawing of the forewings; *5, 6*, drawings of hind wings. Scale=5 mm.

inal sclerites preserved, microtholi present on three of these (Fig. 26.1). All wings incompletely preserved.

Forewing. Length 26.6 mm; width 9.0 mm (as preserved; estimated complete 9.2 mm). Costal space moderately broad, with simple subcostal veinlets relatively widely spaced before pterostigmal region, very closely spaced after. Sc long, terminating on apical margin. R1 long, entering wing margin at apex, its veinlets closely spaced. Space between Sc, R1, between Sc, costal margin narrow apically. Basal subcostal crossvein located at level of most dilated costal space (opposite fifth subcostal veinlets). R1 space somewhat dilated medially, narrow distally. Psm rather weakly developed, zigzagged. Psc well-developed, not zigzagged proximally. Four to five irregular gradate series of crossveins preserved; outer (posterior) series regular. Costal margin rather stout with few hairs detected, presumably more missing. Hairs on margin in pterostigmal region arranged in transverse rows, at tips of veins/veinlets and one between them; each row probably with three to four visible (probably six total including those presumed hidden on opposite side). Hind wing margin thinner than costal margin, with hairs arranged in two to four rows between pairs of vein tips at slight thickenings of margin; each row with three visible (presumably four to five including those likely hidden on opposite side). Wing membrane apparently hyaline throughout.

Hind wing. Narrower than forewing, with apex sub-acute; length 23.5 mm (as preserved; estimated complete ~24 mm); width 8.0 mm. Costal space narrow, with simple subcostal veinlets relatively widely spaced before pterostigmal region, very closely spaced after. Sc long, terminating on apical margin. R1 long, entering wing margin at apex, its veinlets closely spaced. R1 space narrow basally, distally, somewhat dilated medially. Psm, Psc relatively well-developed, slightly zigzagged. Four to five irregular gradate series of crossveins preserved; outer (posterior) series regular, complete.

Material.—Specimen UWBM 77571 (part only); a male (?) in lateral position with well-preserved overlapping incomplete wings, a small portion of the thorax and head, and at least four disarticulated and fragmentary abdominal segments.

Occurrence.—Republic, Washington, U.S.A., locality A0307; early Eocene; deposited in the BM collection.

Remarks.—This specimen is somewhat similar to *Adamsochrysa wilsoni* n. gen. n. sp. but differs from it by forewing shape (forewing apex more obtuse) and a few details of venation (number and arrangement of gradate series, proximal branches of Rs and M entering Psc at more obtuse angle). Although the shape differences might be explained by sexual dimorphism (see above), the differences in the venation appear to be specific. Unfortunately, the venation of proximal (most critical) part of both fore- and hind wings is almost entirely not preserved. Therefore, although this specimen likely represents a new species of *Adamsochrysa*, we refrain from naming it. The presence of trichosor-like structures in this specimen (see below), which were not detected and presumed absent in other specimens of *Adamsochrysa*, indicates that it may belong to distinct genus.

Small, brown spots on the abdominal sclerites of this specimen (Fig. 25.8, 25.9) appear to be microtholi, i.e., minute, dome-like structures (Tjeder, 1966) of unknown function found in males of almost half of chrysopid genera (Brooks and Barnard, 1990). Within the Nothochrysinae, Brooks (1997) recognized their presence in what he termed the *Nothochrysa*-group, i.e., *Triplochrysa* Kimmins, 1952, *Dictyochrysa*, *Nothochrysa*, *Hypochrysa* Hagen, 1866 and *Aesthenochrysa* Adams and Penny, 1992. Tjeder (1966) recorded them in at least some species of *Kimochrysa* Tjeder, 1966 and *Pimachrysa* Adams, 1957. They occur on the tergites of all *Dictyochrysa* species and in the species

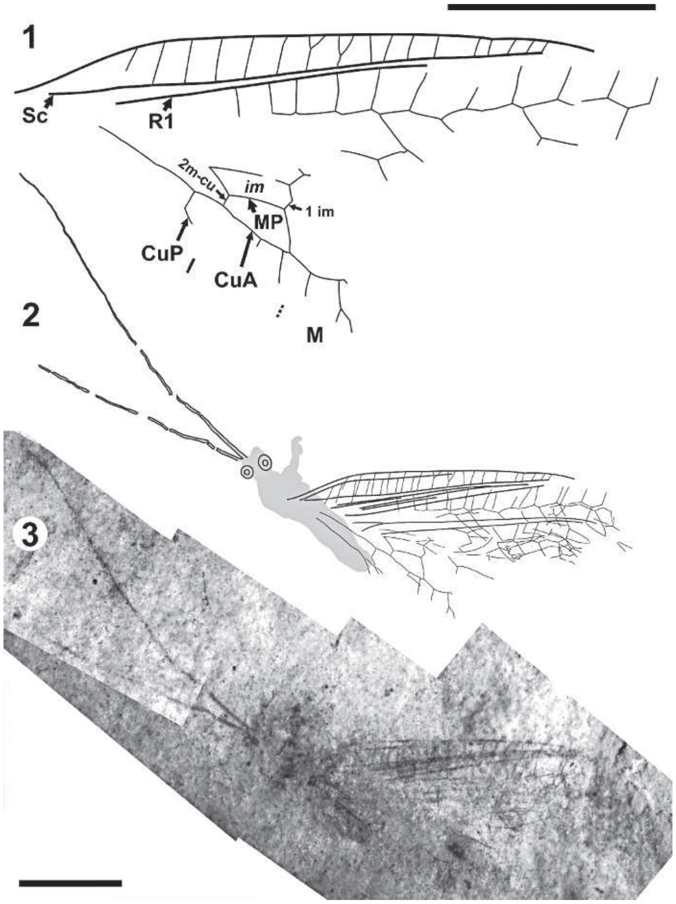

FIGURE 13—*Adamsochrysa* (?) sp. B, RBCM.EH2012.003.0008.001: *1*, drawing of the forewing; *2*, drawing of the specimen as preserved; *3*, photograph. Scale=5 mm.

of *Kimochrysa* where they are present, and only on the sternites of *Nothochrysa*, *Hypochrysa*, and *Pimachrysa* species (Tjeder, 1966; Brooks and Barnard, 1990). They have not been reported in *Pamochrysa* Tjeder, 1966 and *Leptochrysa*, although the latter is only known from a female. Microtholi are reported here for the first time in fossil Chrysopidae.

Although Wehr and Barksdale (1996) didn't specify specimens representing Republic taxon occurrences in their checklist, UWBM 77571 is surely the specimen referred to as establishing Chrysopidae at Republic, as it was the only member of the family known from the Klondike Mountain Formation at the time.

ADAMSOCHRYSA (?) species B
Figure 13

Description.—*Specimen RBCM.EH2012.003.0008.001*. Body poorly preserved; no details visible. Antennae long (preserved portion ~18 mm); flagellomeres elongate, probably about two times long as wide (poorly preserved). Forewing. Length ~16 mm (as preserved; estimated complete ~25–27 mm). Costal space moderately dilated, with subcostal veinlets rather widely spaced (two forked in one forewing). R1 space dilated in middle, with crossveins rather widely spaced. *im* rather elongate, pentagonal. Most proximal crossvein of inner gradate series long, connecting Rs1, distal half of *im*. Intermedian crossvein 1im (which closes *im* apically) rather short; 2m-cu located in proximal haft of *im*. Branches of Rs spaced rather widely; one preserved crossvein in proximal part of inner gradate series long.

Hind wing. Fragmentary, venation mostly indistinctly preserved; R1 space, basal portions of Rs branches in middle portion of wing similar to those of forewing; otherwise unclear.

Material.—RBCM.EH2012.003.0008.001 (part only); a mostly indistinctly preserved and somewhat torn, but almost complete specimen, with possibly at least portions of all four wings; deposited in the RBCM collection.

Occurrence.—Driftwood Canyon, British Columbia, Canada (public exposure near top); early Eocene.

Remarks.—The relatively dense venation and size of specimen RBCM.EH2012.003.0008.001 excludes it from the genus *Pseudochrysopa* n. gen. and the long crossvein in the proximal part of the inner gradate series from Nothochrysinae species A (both also from Driftwood Canyon). We assign this species tentatively to *Adamsochrysa* based on the similar configuration of *im* of this species and *A. wilsoni* n. gen. n. sp., and by the basal-most crossvein of anterior gradate series connecting Rs1 to *im*, which is placed within *im* and long (short in *Okanaganochrysa*). It clearly differs from *A. wilsoni* as indicated in the diagnosis of that species.

ADAMSOCHRYSA (?) species indeterminate
Figure 14

Description.—Forewing. Length 26.2 mm as preserved (estimated complete ~27–27.5 mm); width ~8.8 mm as preserved (estimated complete ~9–9.2 mm). Costal space moderately wide, most dilated at level of basal crossvein sc-r. Subcostal veinlets simple, rather closely spaced. Terminal part of Sc unclear. Subcostal space narrow; basal crossvein sc-r preserved. R1 entering margin at or just after wing apex. R1 space broad, with closely spaced crossveins. Rs little zigzagged, with closely spaced branches. Only inner gradate series of crossveins in radial space partially preserved. Cells between Rs, inner gradate series in middle part of forewing elongate, narrow.

Material.—Specimen UCCIPR L-18 F-1526 (part only); a poorly preserved incomplete pair of overlapping forewings; deposited in the TRU collection.

Occurrence.—McAbee, British Columbia, Canada; early Eocene.

Remarks.—The size and preserved venation of this specimen most resembles those found in species of *Adamsochrysa* n. gen., however, we only tentatively associate it with this genus by the lack of sufficient generic features as preserved.

Genus ARCHAEOCHRYSA Adams, 1967

Type species.—*Palaeochrysa creedei* Carpenter, 1935, by original designation.

Diagnosis.—Revised: May be distinguished from other nothochysine genera by presence of basal crossveins 1r-m connecting Rs and MA in hind wing (shared with *Danochrysa*, *Stephenbrooksia*, absent in all other fossil and extant genera [except for *Leptochrysa*, see above]), Rs originating close to wing base, nearly at level of 1icu in forewing (far from wing base, well distad 1icu in *Danochrysa*, *Palaeochrysa*, *Tribochrysa*), and CuP forked once in forewing (forked at least twice in *Danochrysa*, *Stephenbrooksia*).

Species included.—Four species from the Eocene and Oligocene of North America: *Archaeochrysa profracta* n. sp. from early Eocene of British Columbia (McAbee); *A. fracta* (Fig. 15.1, 15.2) and *A. paranervis* Adams, 1967 from late Eocene of Florissant, Colorado, and *A. creedei* (Carpenter, 1935) from Oligocene of Creede, Colorado.

Remarks.—This genus was considered by Adams (1967) to be the most primitive among Cenozoic chrysopids, in particular because of the presence of the proximal crossvein between Rs and MA in the hind wing. This is now known to also occur in *Stephenbrooksia* and *Protochrysa*, i.e., in all early Eocene

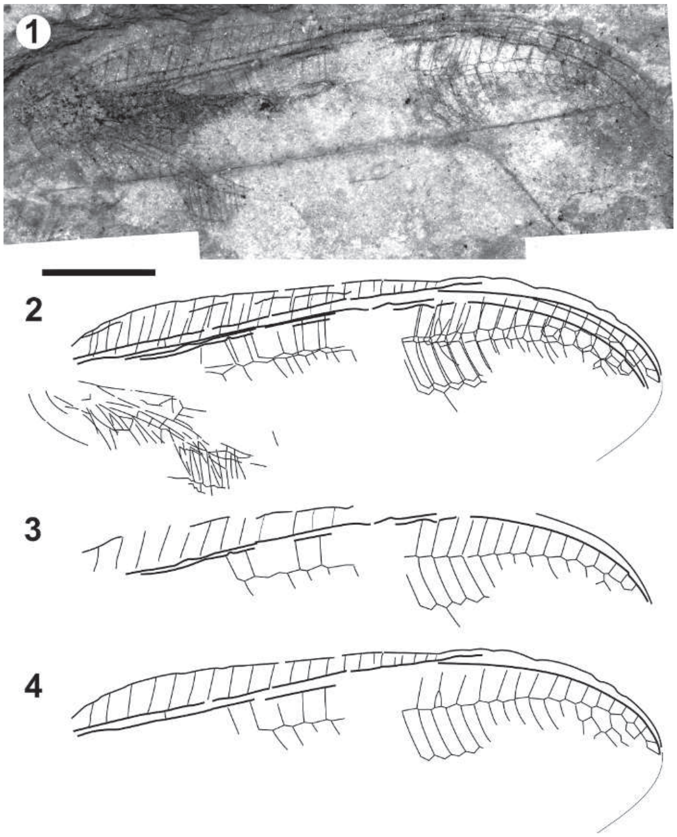

FIGURE *14*—*Adamsochrysa* sp. indet., UCCIPR L-18 F-1526, two forewings: *1*, photograph of the specimen as preserved; *2, 3,* drawings. Scale=5 mm.

Chrysopidae where the basal portion of the hind wing is well preserved. This crossvein is lost in all extant Chrysopidae (except the nothochrysine *Leptochrysa* from Peru) and in all younger fossil Chrysopidae where the hind wing is known (MA is fused for a short distance with Rs). In this connection, it is interesting to note that MA and Rs are also fused in the Mesozoic genera *Mesypochrysa* Martynov, 1927 and *Paralembochrysa*. In *Mesypochrysa*, the basal portion of MA is completely fused with R and the stem of Rs and appears like the proximal branch of Rs; in *Paralembochrysa*, MA is fused for a short distance with Rs1. In the hind wing of other Mesozoic genera, MA is connected with Rs by a crossvein (i.e., *Baisochrysa* Makarkin, 1997, *Lembochrysa* Ren and Guo, 1996, *Drakochrysa*).

ARCHAEOCHRYSA PROFRACTA new species
Figure 15.3–15.6

Diagnosis.—Forewing similar to that of *A. fracta*, distinguished from it by more proximal position of crossvein 1r-m (at proximal extremity of *im* in *A. profracta*, within *im* in *A. fracta*) and proximal-most branch of CuA (proximal to 2m-cu in *A. profracta*, distal to 2m-cu in *A. fracta*).

Description.—Forewing. Length 12 mm as preserved (estimated complete 12.5 mm); width 4.6 mm. Costal space moderately wide, most dilated at level of proximal-most r1-rs crossvein. Subcostal veinlets simple, 19 in number (proximal to pterostigma), rather closely spaced. Pterostigma distinct, fuscous; incorporated veinlets, crossveins unclear. Terminal part of Sc unclear. Subcostal space narrow; basal crossvein sc-r between two proximal-most r1-rs crossveins. R1 incomplete, probably entering margin near or at wing apex. R1 space broad, with 21 crossveins. Rs little zigzagged, with 13 branches. Basal crossvein between Rs, M very short, connecting stem of R, stem of MA near origin of MA. M dividing into MA, MP far distal to origin of Rs. MA strongly ached, rather smooth; MP zigzagged; MA, MP weakly divergent toward Psc. Between MA, MP one crossvein before Psc. *im* rather long, tapering basally. Psm weakly developed, strong zigzagged. Crossvein 2m-cu (between *im*, CuA) shifted distally, placed almost in middle of *im*, distinctly distal to proximal-most branch of CuA. CuA with two–three simple branches. CuA continuing into well developed Psc, which continues into outer gradate series of crossveins. CuP deeply forked far proximal to crossvein 2icu. Two crossveins between CuA, CuP. 1A forked; 2A, 3A simple. Two gradate series of crossveins parallel.

Hind wing. Length ~11.5 mm; width ~4 mm (estimated). Costal space poorly preserved. Subcostal space narrow, no crossvein detected. R1 space broad, with 14 crossveins preserved. Rs zigzagged, with 11 branches; all (except probably distal-most) forked once or twice after outer gradate series. Basal crossvein between Rs, M not detected, probably connecting stem of Rs, MA near origin of MA. M probably divided into MA, MP distal to origin of Rs (poorly preserved). MA strongly zigzagged. MP straight, continuing course of M before of outer gradate series. Two crossveins between MA, MP: proximal long, distal short. Psm, Psc strongly zigzagged. One distal crossvein detected between M, Cu. CuA with three branches. CuP, Anal veins poorly preserved. Two gradate series of crossveins nearly parallel to each other, hind margin; proximal-most crossvein of inner series very short.

Etymology.—From the Greek *pro*, before, and *fracta*, referring to its great similarity to the late Eocene species *Archaeochrysa fracta*.

Type.—Holotype UCCIPR L-18 F-1527 (part only); a well-preserved nearly complete forewing and hind wing overlapped; deposited in the TRU collection.

Occurrence.—McAbee, British Columbia, Canada; early Eocene.

Remarks.—The congeneric relationship of *Archaeochrysa profracta* n. gen. n. sp. and *A. fracta* is assured by the amazing similarity of their venation, in spite of their considerable difference in size (Fig. 15.2, 15.5). The type species of the genus (*A. creedi*) differs from them in having a very narrow costal space, but otherwise its venation is similar. It is quite possible that the genus *Archaeochrysa* is paraphyletic.

Genus PSEUDOCHRYSOPA new genus

Type species.—*Pseudochrysopa harveyi* new species, by monotypy.

Diagnosis.—This genus may be easily distinguished from other nothochrysine genera by the proximal-most branches of Rs, MA touching at anterior gradate series, i.e., basal-most crossvein in anterior gradate series absent.

Etymology.—From Greek *pseudos*, false, and *Chrysopa*, a genus-group name, in reference to superficial resemblance to some chrysopine genera. Gender feminine.

Remarks.—The nothochrysine affinity of this genus should be considered provisional because of its specialized venation. Only two nothochrysine features are present: Psm does not extend to the outer gradate series (character A), and 2m-cu is located in the proximal half of *im* (character D); others characters are not available for assessment. However, the preserved venation most resembles that of the modern nothochrysine genus *Pimachrysa* (five species from the southern regions of North America and Mexico). The forewing lengths of these genera are also similar, i.e., 7.5–11.3 mm in *Pimachrysa* (one species is larger with the forewing 14.0 mm long) (Adams, 1967), and ~8.2–10.3 mm in *Pseudochrysopa* n. gen.

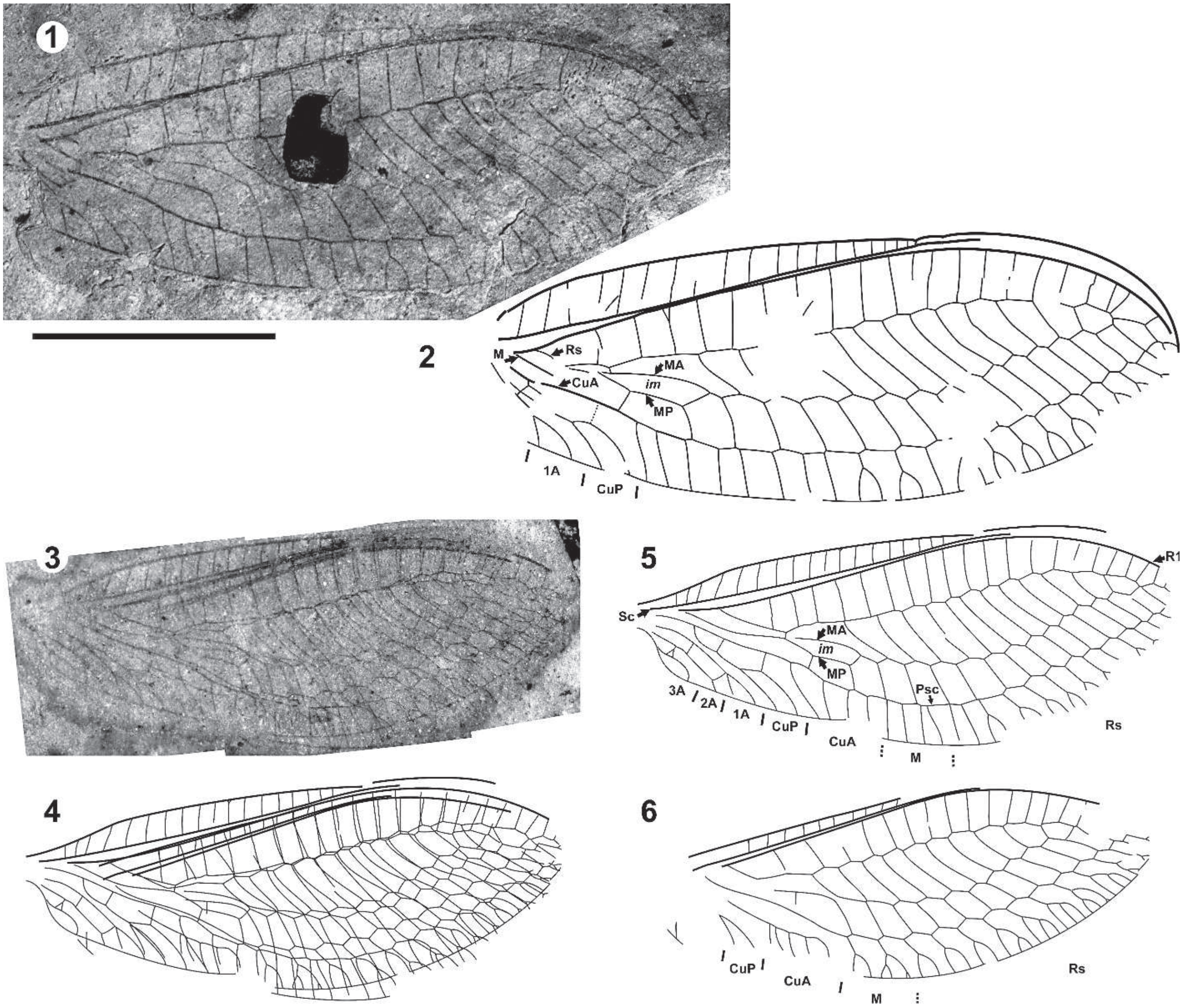

FIGURE 15—Wings of *Archaeochrysa*: *1, 2, Archaeochrysa fracta* Adams, 1967 forewing, photograph and drawing, respectively; *3–6, Archaeochrysa profracta* n. sp., holotype, UCCIPR L-18 F-1527: *3, 4*, a forewing and hind wing overlapping, photograph and drawings as preserved, respectively; *5*, drawing of forewing; *6*, drawings of hind wing. Scale=5 mm.

Pseudochrysopa harveyi new species
Figures 16–19

Diagnosis.—The species is distinguished from *Pseudochrysopa* species A by the presence of the crossveins between R1, Rs distal to origin of distal-most branch of Rs (absent in *Pseudochrysopa* sp. A); or by deep forks of apical branches of Rs (shallow in *P*. sp. A).

Description.—Holotype RBCM.EH2012.003.0001.001 (female) (Fig. 16): Head rather short, with long palpi; antennal scape big, bulbous; pedicel larger than any flagellar segments. Thorax: pronotum relatively large; mesothorax poorly preserved. Legs covered with relatively long hairs; basitarsus longest segment of tarsus. Abdomen complete, rather well-preserved, but terminal segments not clearly preserved. Spermatheca, spermathecal ducts clearly visible when wetted with ethanol, with long, thin spermathecal duct coiled basally (Fig. 17) (terminology of Tauber, 2010).

Forewing. Length 10.3 mm; width 3.5 mm. Costal space moderately wide. Subcostal veinlets simple, widely spaced. Pterostigma indistinct. Sc, subcostal space, subcostal crossveins not preserved. R1 relatively short, entering margin well before wing apex; its distal veinlets widely spaced. R1 space broad, especially basally, with seven crossveins, rather regularly spaced. Rs zigzagged, with six to seven branches. Rs1, MA touching at anterior gradate series (i.e., basal-most crossvein in anterior gradate series lost). Basal crossvein 1r-m relative short, connecting stem of Rs, MA near origin of MA. M dividing into MA, MP far distal to origin of Rs. MA, MP not divergent toward Psc, both deeply forked. Between MA, MP one crossvein (1im) before Psc. *im* elongate, trapezoidal. M, Cu approach each other basally. One crossvein between M, CuA (2m-cu) connecting *im*, CuA in proximal part of *im*. Psm not present. CuA with three simple branches. Psc not developed. CuP deeply forked. Anal veins poorly preserved. Two gradate series of crossveins, slightly convergent apically; five crossveins in inner series, nine in outer. Hairs on apical portions of costal, hind margin arranged in several transverse rows between pairs of vein tips at slight thickenings of margin (trichosor-like structures, see below) (Fig. 25.7); hind

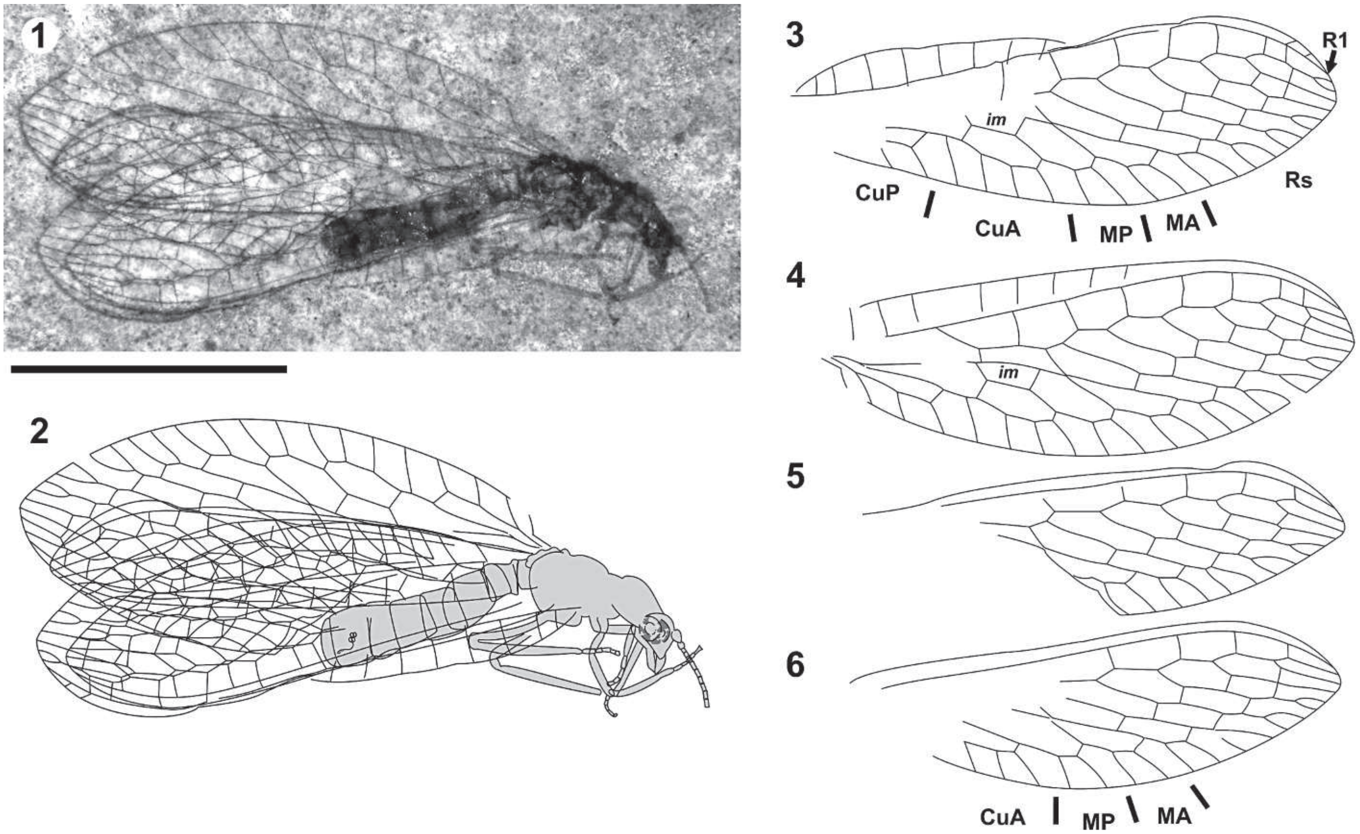

FIGURE 16—*Pseudochrysopa harveyi* n. gen. n. sp., holotype, RBCM.EH2012.003.0001.001: *1*, photograph; *2*, drawing of whole specimen with some features of the body indistinct; *3, 4,* forewing drawings; *5, 6*, drawings hind wings. Scale=5 mm.

margin far from apex lacks such slight thickenings and hairs on margin appear more or less sporadically.

Hind wing. Length ~9 mm; width 2.7 mm, clearly narrower than forewing, sub-acute. Costal space poorly preserved. Sc not preserved. R1 entering margin well before wing apex. Subcostal space not preserved. Crossveins in R1 space widely spaced. Rs zigzagged, with six branches. MA, MP deeply forked. CuP with two simple branches. Anal veins not preserved. Two gradate series of crossveins nearly parallel to hind margin; inner series with four crossveins, outer series with seven crossveins. Hairs on wing margins arranged similarly to forewing, including presence of trichosor-like structures on apical portions of costal, hind margins (Fig. 25.11).

Specimen RBCM.EH2012.003.0002.001 (Fig. 18): Head, thorax not preserved. Abdomen complete but poorly preserved. The anterior end is hidden by a mass with a seed cluster (upper left, Fig. 18.1) that is similar to the fruit of *Paleomyrtinia*, a guava-like plant (Myrtaceae) (K. Pigg, personal commun. to SBA, 2012, see Pigg et al., 1993).

Forewing length 7.5 mm as preserved (estimated complete ~8.2 mm); width 2.7 mm. Costal space moderately wide. Subcostal veinlets simple (one forked in left wing), widely spaced. Pterostigma indistinct. Sc, subcostal space, subcostal crossveins not preserved. R1 relatively short, entering margin well before wing apex. R1 space broad, especially basally, with seven crossveins, irregularly spaced. Rs zigzagged, with seven branches. Rs1, MA touching at anterior gradate series (i.e., basalmost crossvein in anterior gradate series lost). Basal crossvein 1r-m short, connecting stem of Rs, MA near origin of MA. M dividing into MA, MP far distal to origin of Rs. MA, MP not divergent toward Psc. Between MA, MP one crossvein (1im) before Psc. *im* elongate, trapezoidal. M, Cu convergent basally. Psm not present. Crossvein 2m-cu connects *im*, CuA in proximal part of *im*. CuA with three simple branches. Psc not developed. CuP deeply forked. Two gradate series of crossveins, slightly convergent apically; five crossveins in inner series, eight in outer.

Hind wing length estimated from preserved portion ~7.2 mm (estimated complete ~7.5 mm); width ~2.2 mm, clearly narrower than forewing. Costal space poorly preserved. Sc not preserved.

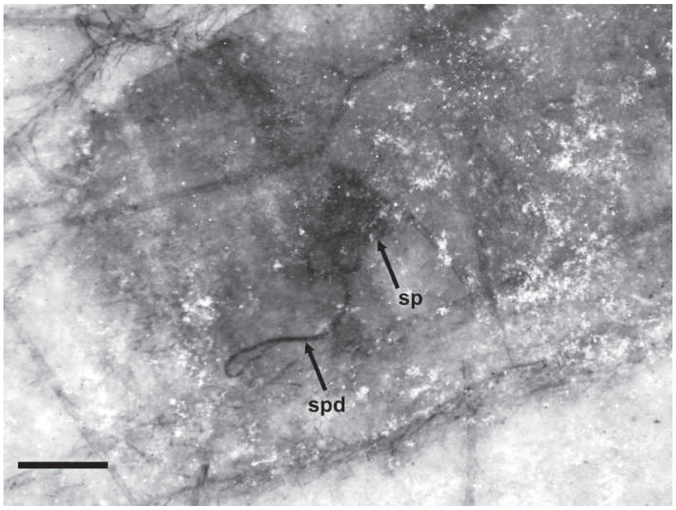

FIGURE 17—*Pseudochrysopa harveyi* n. gen. n. sp., RBCM.EH2012.003.0001.001. Apex of abdomen wetted with ethanol, showing spermatheca (sp) and spermathecal duct (spd). Scale=200 μm.

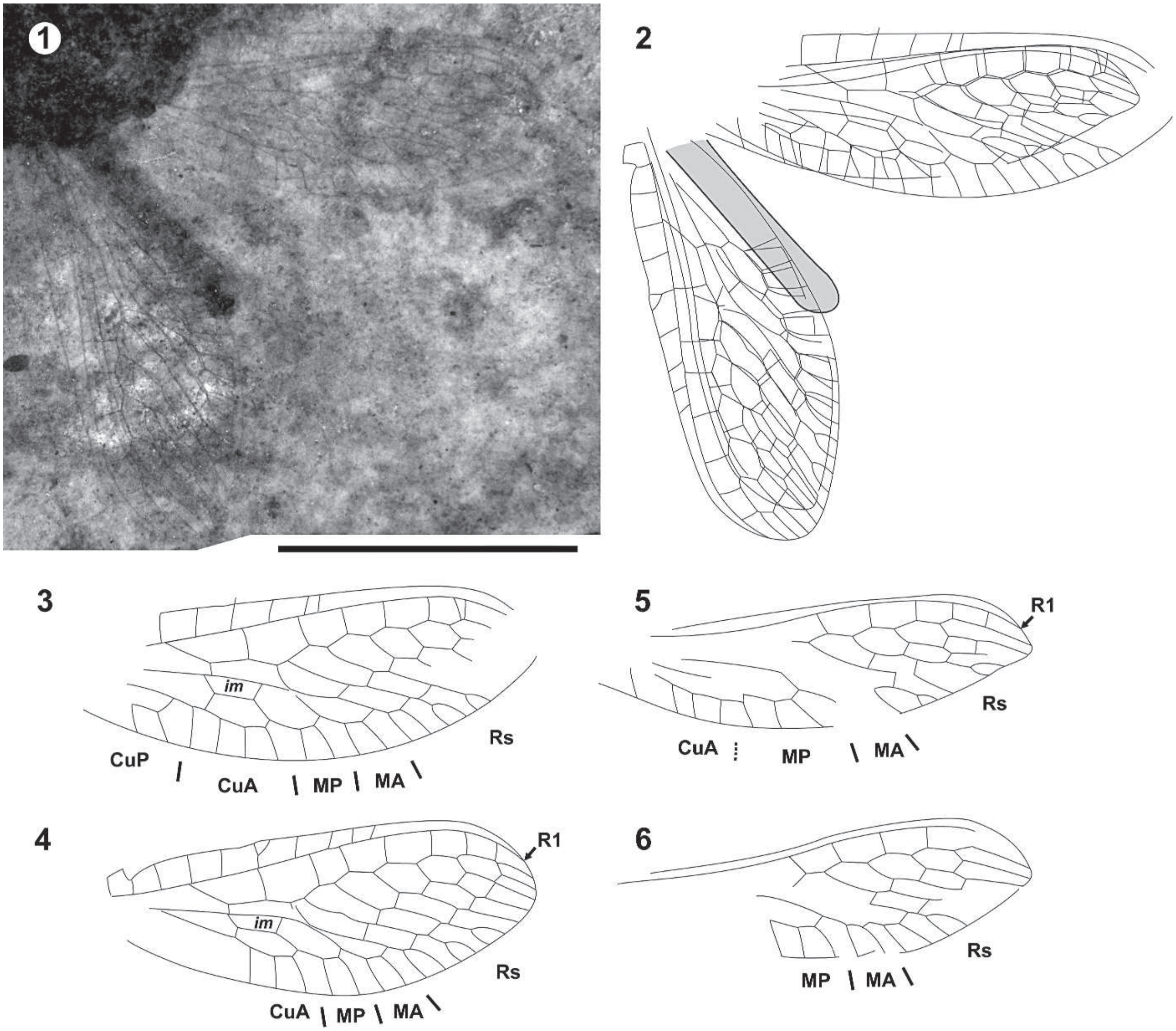

FIGURE 18—*Pseudochrysopa harveyi* n. gen. n. sp., RBCM.EH2012.003.0002.001: *1*, photograph; *2*, drawing of the specimen as preserved; *3, 4,* drawings of forewings; *5, 6*, drawings of hind wings. Scale=5 mm.

R1 entering margin well before wing apex. Subcostal space not preserved. R1 space broad, with five crossveins preserved, widely spaced. Rs zigzagged, with five branches. MP deeply forked. CuP with three simple branches. Anal veins poorly preserved. Two gradate series of crossveins nearly parallel to hind margin; inner series with up to four crossveins preserved (probably five when complete), outer series with up to six crossveins preserved (probably seven when complete).

Specimen RBCM.EH2012.003.0005.001 (Fig. 19): Forewing. Small crumpled fragment, length about 6 mm as preserved (estimated complete ~7 mm). Preserved venation similar to that of other two specimens.

Etymology.—The specific epithet is a patronym derived from the surname of Gordon Harvey, in recognition of his act of public service in donating the Driftwood Canyon locality to BC Parks in 1967.

Types.—Holotype RBCM.EH2012.003.0001.001 (part only); an almost complete specimen preserved in lateral position with all wings partly overlapped; deposited in the RBCM collection. Paratype RBCM.EH2012.003.0002.001 (part only); a poorly preserved incomplete specimen in dorsal aspect with fore- and hind wings overlapped pairwise; deposited in the RBCM collection.

Other material.—Specimen RBCM.EH2012.003.0005.001 (part only); a well-preserved fragmentary crumpled forewing; deposited in the RBCM collection.

Occurrence.—Driftwood Canyon, British Columbia, Canada; early Eocene.

Remarks.—The holotype and specimen RBCM.EH2012.003.0002.001 are confidently conspecific. Specimen RBCM.EH2012.003.0005.001 is tentatively assigned here; while its preserved characters are in agreement with this species concept, it is quite fragmentary and damaged.

This is the smallest known fossil chrysopid species.

PSEUDOCHRYSOPA (?) species A

Figures 20, 25.8

Description.—Specimen RBCM.EH2012.003.0003.001: Fore-

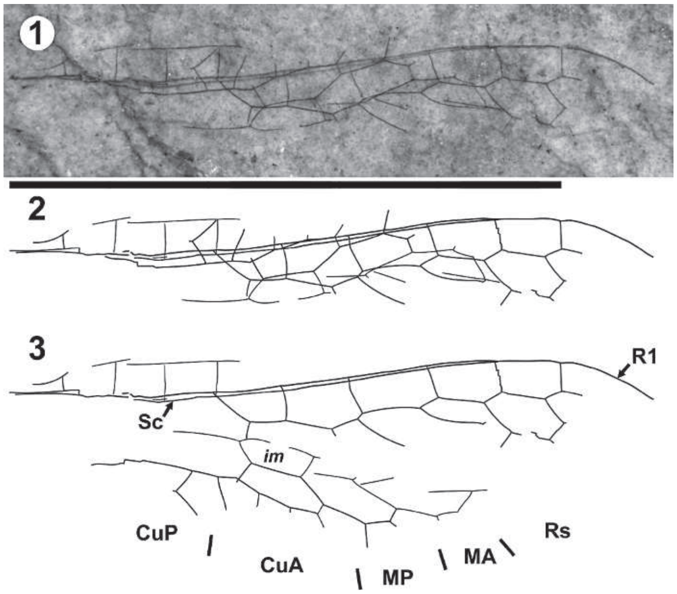

FIGURE 19—*Pseudochrysopa harveyi* n. gen. n. sp., RBCM.EH2012.003.0005.001: *1*, photograph; *2*, drawing of the specimen as preserved; *3*, reconstruction of the forewing venation. Scale=5 mm.

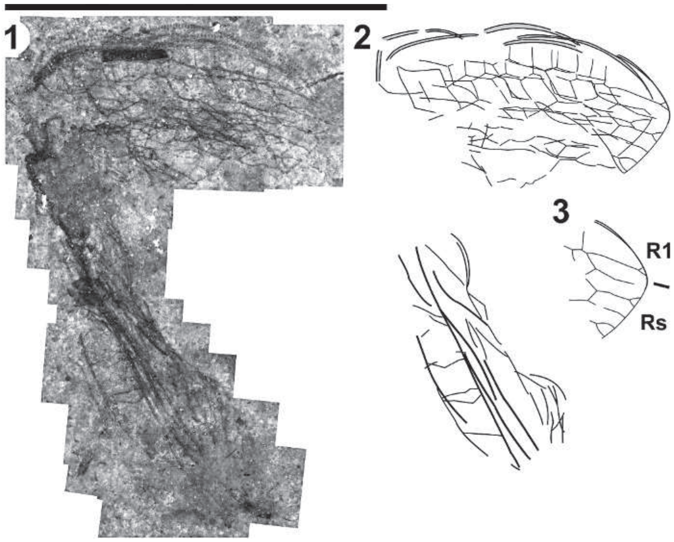

FIGURE 20—*Pseudochrysopa* (?) sp. A, RBCM.EH2012.003.0003.001: *1*, photograph; *2*, drawing of the specimen as preserved; *3*, forewing venation. Scale=5 mm.

wing. Only costal, apical portions distinctly preserved. Estimated length ~10 mm. Costal space dilated proximally with veinlets widely spaced. R1 entering wing margin well before apex. Crossveins between R1, Rs distal to origin of distal-most branch of Rs not detected. Apical branches of Rs with shallow forks. Apical-most crossvein between branches of Rs distinctly proximal to next crossvein of outer gradate series. Apical portion of costa wide; this and apical portion of hind margins possess trichosor-like structures with spots (apparently each with one hair) arranged in transverse rows resembling stripes (Fig. 25.6); more than one between tips two veins on outer margins (see below). Other details of wing venation unclear.

Material.—Specimen RBCM.EH2012.003.0003.001 (part only); a very crumpled specimen, with at least three wings mostly tangled together; deposited in the RBCM collection.

Occurrence.—Driftwood Canyon, British Columbia, Canada (public exposure near top); early Eocene.

Remarks.—We preliminary assigned this species to *Pseudochrysopa* n. gen. because of its small size and by R1 entering the wing margin well before apex. The species is distinguished from *Pseudochrysopa harveyi* n. gen. n. sp. by shallow forks of the apical branches of Rs (much deeper in *P. harveyi*), and the absence of the crossveins between R1 and Rs distal to origin of distal-most branch of Rs.

PSEUDOCHRYSOPA species indeterminate
Figures 21, 26.5–26.7

Description.—Specimen RBCM.EH2012.003.0004.001: Apical portion of forewing partially preserved. Estimated forewing length approximately 11 mm. Apical portions of costal, hind margins with trichosor-like structures with hair bases arranged in transverse rows resembling stripes (Fig. 26.5). R1 entering wing margin well before apex, with two veinlets; apex of R1, one of veinlets with very shallow forks. Widely spaced crossveins between R1, Rs; two crossveins distal to origin of distal-most branch of Rs. Stem of Rs rather deeply forked; each branch near margin with very shallow forks.

Apical portion of hind wing partially preserved, but very crumpled. R1 entering wing margin well before apex, with at least one simple veinlet. Between R1, Rs one crossvein distal to origin of distal-most branch of Rs. Stem of Rs divided into three minute branches. Apical portions of costal, hind margins with trichosor-like structures resembling stripes (Fig. 26.10); more than one between tips of veins ending on margin. Two nearly parallel gradate series. Apical-most crossvein between branches of Rs located well proximal to next crossvein of outer gradate series.

Material.—RBCM.EH2012.003.0004.001a, b (part and counterpart); a very crumpled specimen, basal portions (unclear of which wings) separated, torn, very damaged; deposited in the RBCM collection.

Occurrence.—Driftwood Canyon, British Columbia, Canada (public exposure near top); early Eocene.

Remarks.—The size and preserved venation of this specimen are similar to those of *P. harveyi* n. gen. n. sp. However, the presence of minute forks of R1 and Rs veinlets and branches near the margin are not found in that species. These minute forks, however, may be abnormalities of this specimen.

NOTHOCHYSINAE species A
Figure 22

Description.—Forewing. Length 8.2 mm as preserved (estimated complete 8.4 mm); width ~3 mm. Costal space moderately narrow. Subcostal veinlets simple, widely spaced. Pterostigma indistinct. Subcostal space quite narrow; subcostal crossveins not preserved. Terminal portions of Sc, R1 not preserved, but preserved portions R1 relatively long, possibly entering margin at or just after wing apex. R1 space broad, with nine preserved crossveins, rather irregularly spaced. Rs origin far from wing base; zigzagged, with eight branches. Rs1, MA connected by short crossvein at anterior gradate series (i.e., basal-most crossvein in anterior gradate series present). Basal crossvein 1r-m short, connecting Rs, *im* in proximal half. M forked distal to origin of Rs. MA, MP slightly divergent toward Psc. One crossvein (1im) between MA, MP, before Psc. *im* elongate, narrow. Long crossvein 2m-cu connecting *im*, CuA slightly distad fork of M. CuA with three simple branches. Psc poorly developed. CuP appears to have two pectinate branches (but proximal-most branch may be distal branch of 1A). Two crossveins between CuA, CuP. Anal veins poorly preserved. Two gradate series of crossveins; inner series somewhat sigmoid, with nine crossveins.

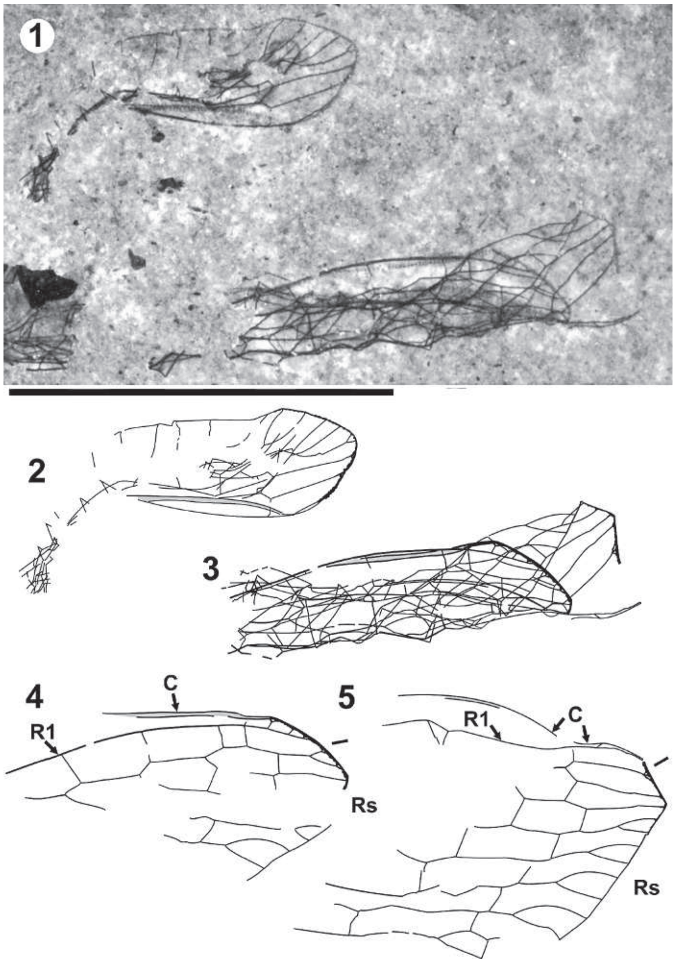

FIGURE 21—*Pseudochrysopa* sp. indet., RBCM.EH2012.003.0004.001: *1*, photograph of the part (A); *2*, drawing of the hind wing (?) as preserved; *3*, drawing of the fore and hind wings as preserved; *4,* reconstruction of the forewing venation; *5,* reconstruction of the hind wing venation; *4* and *5* only use veins and vein portions preserved, reconstructed by "graphically unfolding" the portions of wings crumpled together in *3*. Scale=5 mm.

Hind wing. Very crumpled: length 6.5 mm as preserved (estimated complete ~7.5 mm). Crossveins in R1 space regular; two gradate series of crossveins; branches of Rs widely spaced. Other details unclear.

Material.—Specimen RBCM.EH2012.003.0007.001 (part only); a forewing and hind wing, overlapped, well-preserved but crumpled; deposited in the RBCM collection.

Occurrence.—Driftwood Canyon, British Columbia, Canada (public exposure near top); early Eocene.

Remarks.—The forewing venation of this species is most similar to that of species in the genera *Tribochrysa* and *Palaeochrysa* from Florissant, Colorado, but it may not be confidently assigned to either of these because of the intermediate course of the inner series of gradate crossveins (somewhat sigmoid, not forming a broken curve as in *Tribochrysa*, nor smoothly curved as in *Palaeochrysa*). Its small size and general venation most resembles *Tribochrysa*, indicating that it might possibly belong to this genus. However, we refrain from this assignment due to the poor preservation of this, its only known specimen.

NOTHOCHRYSINAE species indeterminate
Figure 23

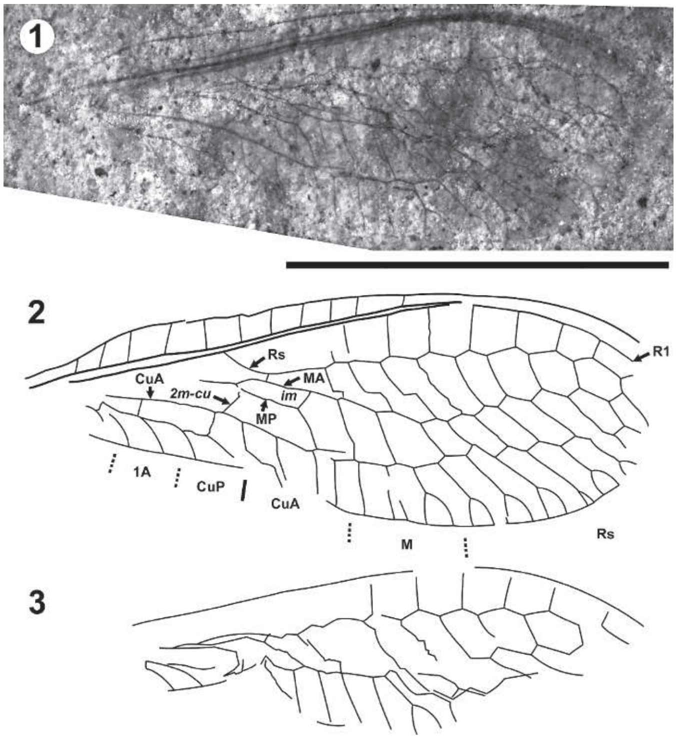

FIGURE 22—Nothochrysinae sp. A, RBCM.EH2012.003.0007.001: *1*, photograph; *2*, *3*, drawings of the forewing and hind wing, respectively. Scale = 5 mm.

Description.—Specimen UCCIPR L-18 F-1535 (Fig. 23): Body poorly preserved; no details visible. Forewing. Length ~15 mm as preserved (estimated complete 15.5–16 mm). Rs with >12 branches. Two gradate series of crossveins in radial space (partially preserved). 1A forked; 2A, 3A short, simple.

Material.—Specimen UCCIPR L-18 F-1535a, b (part and counterpart); a whole specimen in dorsal position with all the wings crumpled and overlapped; deposited in the TRU collection.

Occurrence.—McAbee, British Columbia, Canada; early Eocene.

Remarks.—Placement of UCCIPR L-18 F-1535 in the Nothochrysinae is assured by its long Sc. Little can be determined, however, of its generic affinity by poor preservation other than that it does not belong to *Adamsochrysa* n. gen. by the presence of only two gradate series of crossveins, nor to *Okanaganochrysa* n. gen., by its comparatively widely-spaced branches of Rs.

CHRYSOPIDAE species indeterminate
Figure 24

Description.—Specimen RBCM.EH2012.003.0006.001 (Fig. 24): Basal portion of forewing partially preserved. Costal space relatively broad, with subcostal veinlets quite closely spaced. Branches of CuA, CuP long. Other details of fore-, possibly hind wing venation unclear.

Material.—RBCM.EH2012.003.0006.001 (part only); a crumpled, fragmentary forewing; deposited in the RBCM collection.

Occurrence.—Driftwood Canyon, British Columbia, Canada (public exposure, near top); early Eocene.

Remarks.—The poorer preservation of RBCM.EH2012.003.0006.001 leaves even its subfamily placement impossible. Its size excludes it from *Pseudochrysopa* n. gen.

THE PRESENCE OF TRICHOSOR-LIKE ORGANS IN CHRYSOPIDAE

Structures on the apical portion of the costal margin and along the hind margin (Fig. 25) of the wings of some Okanagan

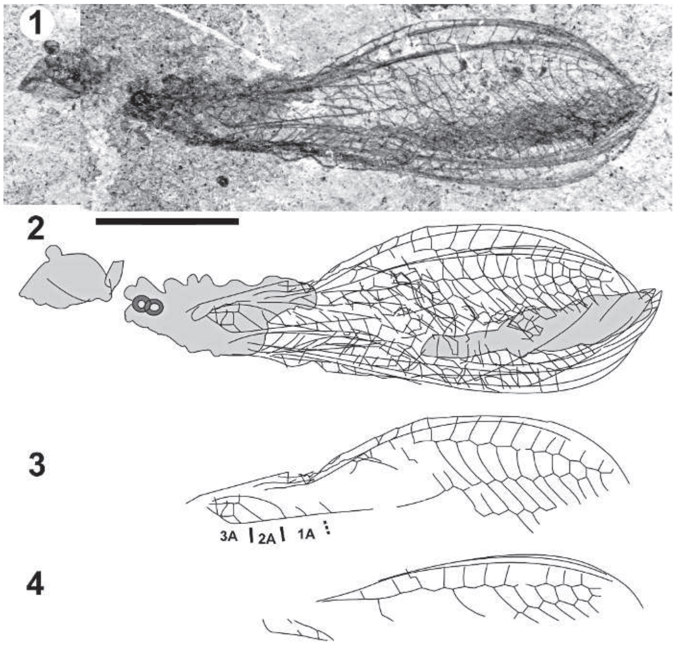

FIGURE 23—Nothochrysinae species indeterminate, UCCIPR L-18 F-1535: *1,* photograph, composite of part and counterpart; *2,* drawing of the specimen as preserved; *3, 4*, drawing of identified venation of forewings. Scale=5 mm.

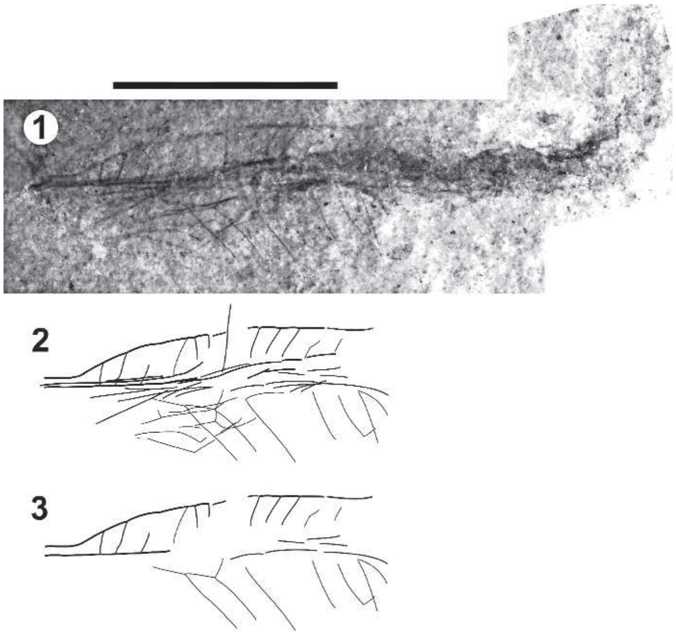

FIGURE 24—Chrysopidae sp. indet., RBCM.EH2012.003.0006.001: *1*, photograph of the specimen as preserved; *2*, drawing of the specimen as preserved; *3*, drawing of the forewing venation. Scale=5 mm.

Highlands species have morphology and placement suggestive of organs that Killington (1936) named trichosors, i.e., small setigerous swellings along the wing margin between the tips of veins and veinlets.

These structures are clearly evident on specimen UWBM 77581 (Fig. 25.3, 25.4, 25.8, 25.9), which likely belongs to *Adamsochrysa* n. gen., as well as on species assigned to or possibly belonging to *Pseudochrysopa* n. gen. (Fig. 25.5–25.7, 25.10, 25.11). In these, the apical portion of the costa is broad, bearing spots arranged in transverse rows that resemble stripes. Individual spots appear associated with hairs, apparently each representing the base of a single hair. In the apical hind margin, the marginal vein is narrower, but shows bead-like swellings that similarly possess hair base spots that are also clearly arranged in rows (see Fig. 25.9, 25.11). These thickenings along the hind margin appear similar to trichosors evident in other families, e.g., Nymphidae (see *Pronymphes* Krüger, 1923, Archibald et al., 2009, fig. 2), where there are more than one swelling between the tips of vein pairs. On the hind margin of the *Pseudochrysopa* wing, these structures appear restricted to the apical portion, whereas they extend much further from the apex in the wing of the possible *Adamsochrysa* species (UWBM 77571).

Trichosors occur in the majority of Neuroptera families both extant (i.e., Berothidae, Hemerobiidae, Ithonidae, Dilaridae, Mantispidae, Psychopsidae, Sisyridae, Nevrorthidae, Nymphidae, Osmylidae), and extinct (i.e., Archeosmylidae, Brongniartiellidae, Grammolingiidae, Kalligrammatidae, Osmylopsychopidae, Panfiloviidae, Permithonidae, Prohemerobiidae). Their absence is clearly a derived condition that occurs in most families of the Myrmeleontoidea (both extant and extinct) and a few others (i.e., Coniopterygidae, Mesochrysopidae and Ascalochrysidae). Trichosors are also thought to be absent in extant chrysopids and have never been reported in any fossil of the family. Indeed, the lack of trichosors has been referred to as a distinguishing characteristic of Chrysopidae (e.g., Barnard 1984). We examined wings of the extant nothochrysine *Hypochrysa elegans* (Burmeister, 1839), and of about 20 extant chrysopine species, and found no evidence of any structures resembling those that we detect in these fossils (e.g., see the chrysopine *Chrysoperla carnea*, Fig. 25.1, 25.2). In these, hairs in these regions appeared somewhat randomly spaced, not arranged in any discernible order (Fig 25.1, 25.2), other than at times rather zigzagged along the thinner hind marginal vein.

It is unclear if the occurrences of this structure are autapomorphies of these fossil genera (which appear not closely related), convergent not only between them, but also with trichosors (at least in general appearance, if not also in function); or if they are in fact trichosors, plesiomorphic here, lost in other known Chrysopidae. We believe that the latter assumption is more likely.

GREEN LACEWING COMMUNITIES ACROSS THE OKANAGAN HIGHLANDS

Six genera (five named) and at least 10 species (six named) of two subfamilies (Limaiinae and Nothochrysinae) are now known from the early Eocene Okanagan Highlands. This is a minimum number among the fossils reported here, as the poorly preserved specimens RBCM.EH2012.003.0006.001 and UCCIPR L-18 F-1535 might represent further genera and species. This assemblage is also notable for its wide morphological diversity, ranging from large species with enriched venation like those of *Adamsochrysa* n. gen., to *Pseudochrysopa* n. gen., with simplified venation. These represent a far wider range of taxa, morphology, and possibly ecological roles than might be expected for twenty-four specimens.

McAbee.—With thirteen fossils, McAbee is the richest locality for specimens (oldest: 52.90 ± 0.83 Ma). Chrysopidae ranks high amongst Neuroptera specimens recovered there: we have examined fifteen osmylids and four hemerobiids. McAbee also has the most taxonomically diverse chrysopid assemblage of the Okanagan Highlands, with twelve specimens belong to four species of *Protochrysa*, *Okanaganochrysa* n. gen., *Adamsochrysa* and *Archaeochrysa* (the poorly preserved thirteenth may represent another). The presence of Limaiinae in the McAbee community

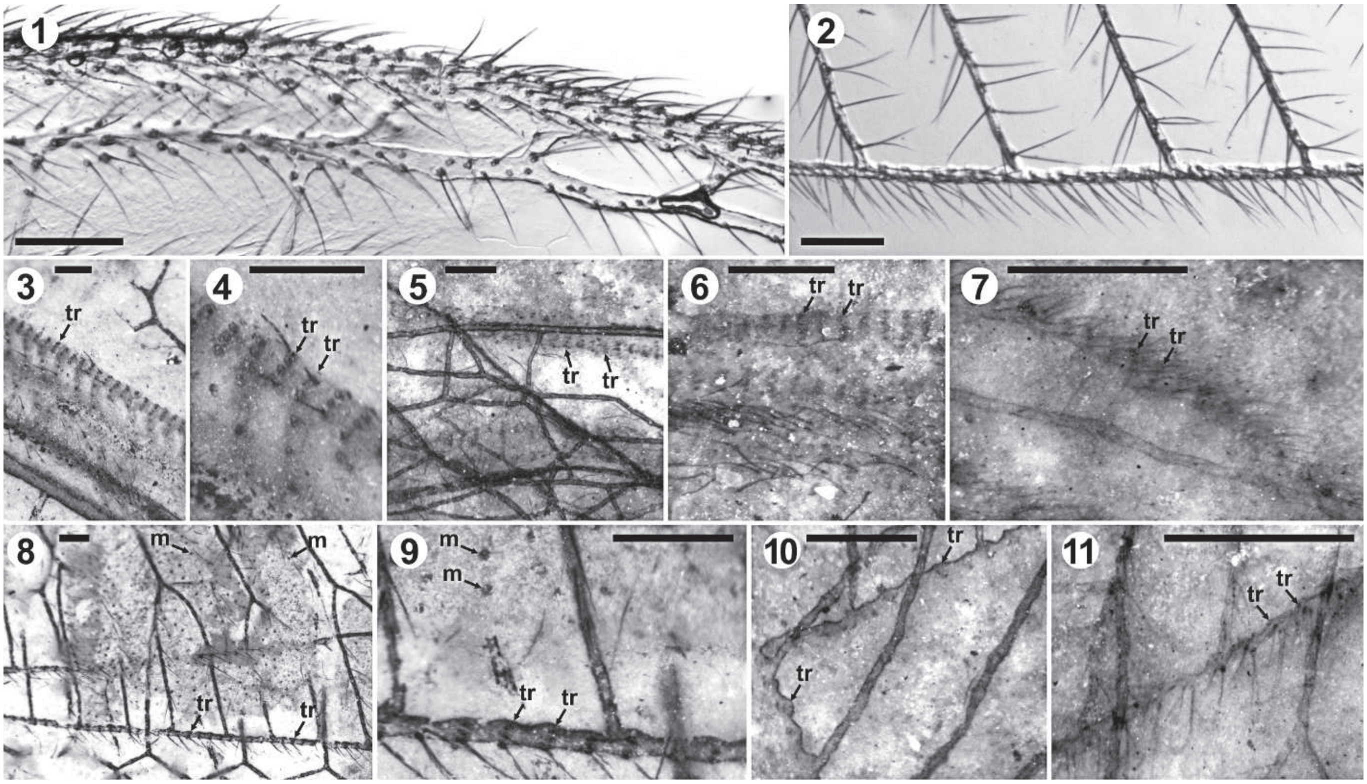

FIGURE 25—Extant (*1, 2*), and fossil Chrysopidae (*3–11*), showing trichosor-like structures (tr) on the apical wing margins of fossil species and their absence in extant species, and microtholi (m) on abdominal sclerites of a fossil species. *1, 2*, *Chrysoperla carnea* (Stephens, 1836), extant Chrysopidae: *1*, apical anterior wing margin showing hairs on C scattered randomly, not grouped in rows; *2*, posterior apical margin showing hairs spaced randomly, without grouping into rows on trichosor-like swellings; *3–11*, fossil Chrysopidae: *3–7*, apical anterior portion of fossil wings showing hair bases arranged in rows of trichosor-like structures (tr) on C: *3*, *Adamsochrysa* sp. A, UWBM 77571; *4*, close-up of *3*; *5*, *Pseudochrysopa* sp. indet., RBCM.EH2012.003.0004.001.A; *6*, *Pseudochrysopa* sp. A, RBCM.EH2012.003.0003.001; *7*, *Pseudochrysopa harveyi*, RBCM.EH2012.003.0001.001; *8–11*, abdominal sclerites showing microtholi (m) and trichosor-like stuctures (tr) evident as swellings along the wing margin with hairs arranged in rows: *8*, *Adamsochrysa* sp. A, UWBM 77571; *9*, close-up of *8*; *10*, RBCM.EH2012.003.0004.001.A; *11*, *Pseudochrysopa harveyi*, RBCM.EH2012.003.0001.001. All are forewings except for hind wings *10* and *11*. All scales=200 μm.

gives it an ancient aspect, although there are only two specimens, and new Chrysopidae are commonly found throughout the region.

Driftwood Canyon.—We examined eight specimens from Driftwood Canyon, of which three belong to *Pseudochrysopa harveyi* n. gen, n. sp.; two more that might also belong to this genus; one that most probably belongs to *Adamsochrysa* n. gen.; one that represents another genus and species (most likely related to *Tribochrysa*); and one that is too poorly preserved to assign to genus or species (at least three genera and four to five species in total). Chrysopidae far outnumbers other Neuroptera there: only a single specimen each has been reported of Osmylidae and Hemerobiidae (Makarkin et al., 2003). Most specimens from there are small; only one is large, with the enriched venation seen in McAbee *Adamsochrysa* species.

Republic.—Republic is the youngest (49.4 ± 0.5 Ma) of the series with the least specimens (two) and the least diverse Chrysopidae, with only two species of *Adamsochrysa*. Other Neuroptera are more numerous and diverse there: Ithonidae (sensu lato; including those belonging to the formerly recognized taxon Polystoechotidae) (31 specimens, mostly fragmentary), Osmylidae (13 specimens), Hemerobiidae (three specimens), and Nymphidae (one specimen) (Makarkin et al., 2003; Archibald and Makarkin, 2006; Archibald et al., 2009; Makarkin and Archibald, 2009; current research).

The variation of neuropteran taxonomic compositions across the Okanagan Highlands—notably the dominance of Ithonidae (s. l.) and rarity of Chrysopidae at Republic, and of Chrysopidae and Osmylidae at McAbee, which lacks these ithonids—does not seem explicable by taphonomic sorting and appears to reflect real community differences.

Almost all of the Chrysopidae that we examined are nothochrysines. This is consistent with the mesic forests that they lived in (Greenwood et al., 2005; Moss et al., 2005), the preferred habitat of the subfamily today.

Adamsochrysa is the most widely distributed genus in the Okanagan Highlands, occurring at all three localities (although tentatively at Driftwood Canyon). The other four genera are restricted to a single locality each. One genus (*Protochrysa*) is also known from the Eocene Fur Formation (below), and one (*Archaeochrysa*) is known from Florissant (Eocene) and Creede (Oligocene), Colorado, U.S.A. (below). The unattributed Nothochrysinae species A is most similar to the Florissant genus *Tribochrysa*, and may even belong to it; however, poor preservation prevents us from confirming this supposition.

Taphonomy.—Harding and Chant (2000) and O'Brien et al. (2002) presented a taphonomic model for Florissant Formation fossil insects and plants as entrapped in the mucous of annual diatom bloom mats. This would stabilize the insect body, decreasing decomposition, scavenging, and the chances of washing ashore, as well as promoting early diagenetic processes in fossilization by biofilm encasement (see O'Brien et al., 2008). This process should increase the relative representation of Neuroptera in fossil insect assemblages by lessening their loss due to sorting by their large surface area relative to body mass (Archibald and Makarkin, 2006 and references therein). Such diatomaceous shales have been identified at McAbee and some other Okanagan Highlands localities by their distinctive geochemical signatures (Mustoe, 2005). Although Driftwood Canyon has not been geochemically tested, general inspection of those sediments indicates preservation in diatomaceous laminae there as well. Republic has not been examined for evidence of diatom blooms.

The McAbee specimen UCCIPR L-18 F-1534 (*Adamsochrysa aspera* n. gen. n. sp.) is a good example of this type of fossilization. It is mostly encased within a siliceous lamina, and is hardly detectable until wetted with ethanol, when the wings are immediately, clearly visible as this lamina becomes transparent (Fig. 26). Specimens from Driftwood Canyon also show such preservation. They are more often crumpled and fragmentary (Figs. 20–22, 24) than are those from McAbee or Republic, indicating the likelihood of greater post-mortem disturbance or transport. Such damage would be consistent with wind or wave action on or near the water surface while encased in diatom bloom mucous. Preservation by biofilm-mediated diagenesis might also explain the exquisite preservation often seen in these deposits (e.g., Figs. 17, 25).

COMPARISON WITH OTHER EOCENE CHRYSOPIDAE ASSEMBLAGES

Fur Formation.—The diatom-rich sediment of the Fur Formation was deposited in a marine setting now exposed in many localities of the northern Jutland region of Denmark. It is in the earliest Eocene immediately above the Paleocene boundary; ash-bearing layers within the fossil bearing beds have been dated at 54.04 ± 0.14 to 54.52 ± 0.05 Ma by $^{40}\mathrm{Ar}/^{39}\mathrm{Ar}$ decay (Chambers et al., 2003).

The Fur Formation contains the only other early Eocene chrysopid assemblage comparable in number of taxa to that of the Okanagan Highlands. It has four known genera with five species, including two limaiines: *Protochrysa aphrodite* and *P.* sp.; and three nothochrysines: *Cimbrochrysa moleriensis* Schlüter, 1982, *Danochrysa madseni* Willmann, 1993 and *Stephenbrooksia multifurcata* Willmann, 1993 (Schlüter, 1982; Willmann and Brooks, 1991; Willmann, 1993; Rust, 1999). Fur Formation nothochrysine genera possess some plesiomorphic characters compared with those of Florissant and even some Okanagan Highlands taxa (*Pseudochrysopa*, Nothochrysinae species A). For example, in all Fur Formation genera, crossvein 2m-cu is in a more distal position (Fig. 2.1–2.3) than in all Florissant genera and in *Pseudochrysopa* and Nothochrysinae species A from Driftwood Canyon.

Protochrysa occurs at both the McAbee and in the Fur Formation, consistent with large-scale cross-North Atlantic Holarctic dispersal of plants and mammals during land bridge connections between North America and Europe associated with mild climates (discussed in Archibald and Makarkin, 2006).

Tadushi Formation.—The lacustrine deposits of the Tadushi Formation are distributed in restricted areas of eastern Primorye (Russian Far East). They were previously considered to be Paleocene (e.g., Rasnitsyn and Zherikhin, 2002), but K-Ar and Rb/Sr dating of an underlying formation gives an Eocene age (e.g., Otofuji et al., 1995; Popov and Grebennikov, 2001). Two specimens of undescribed Chrysopidae are known from this formation (current research of authors). One is a well-preserved but incomplete small forewing (estimated length 11 mm), with venation most similar to that of *Cimbrochrysa moleriensis* of the Fur Formation, particularly by the shape of the intramedian cell and relatively distal position of crossvein 2m-cu. This morphology does not appear in any Okanagan Highlands species. The other Tadushi Formation specimen is a fragmentary hind wing also belonging to a nothochrysine (judging from the long R1). Its generic affinity is mostly unclear by preservation but the dense veinlets of R1 resemble those of the Fur Formation's *Stephenbrooksia* and the Okanagan Highlands' *Adamsochrysa*. Although these Tadushi data are few, what there is more resembles the Fur Formation Chrysopidae than the closer Okanagan Highlands, connected by a forested land bridge across the Bering Straight at that time.

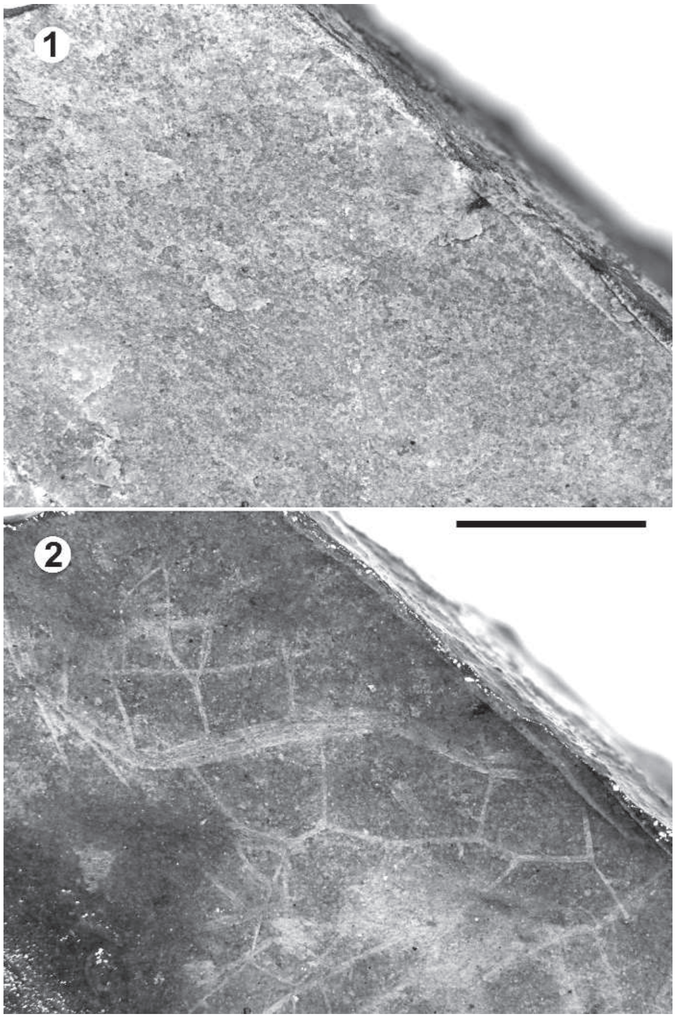

FIGURE *26*—Wings within silica layer that become visible with wetting in *Adamsochrysa aspera* n. gen. n. sp., UCCIPR L-18 F-1534a: *1*, dry; *2*, wetted with ethanol. Scale=5 mm.

Florissant.—This well-known locality is a classic North American fossil insect site, with extensive work since the 1870s by notable researchers such as Samuel Scudder, Theodore Cockerell, and Frank Carpenter (see review by Veatch and Meyer, 2008), and a paleoflora considered one of the best sampled in the continent (Leopold et al., 2008). It is currently dated as late Eocene, (34.07 ± 0.10 Ma) by $^{40}\mathrm{Ar}/^{39}\mathrm{Ar}$ decay (Evanoff et al., 2001). Like the Okanagan Highlands, it is thought to have been a cooler upland, as indicated by paleofloral analysis. Various estimates of paleoelevation have been provided in numerous studies (Meyer, 2007).

With the first chrysopid species description from these deposits published over 120 years ago (Scudder, 1890), Florissant had, until now, the most diverse described assemblage of the family in the fossil record. This included four genera with eight species of Nothochrysinae: *Archaeochrysa fracta*, *A. paranervis*, *Dyspetochrysa vetuscula* (Scudder, 1890), *Palaeochrysa concinnula* Cockerell, 1909, *P. stricta* Scudder, 1890, *P. wickhami* (Cockerell, 1914), *Tribochrysa firmata* Scudder, 1890 and *T. inaequalis*

Scudder, 1885 (Adams, 1967). Morphological diversity amongst these is low, with small details of wing venation separating Florissant genera. These do, however, possess character states that are clearly derived within the family (e.g., the proximal position of the crossvein 2m-cu in the forewings; the basal fusion of MA and Rs in the hind wings of three genera).

The Florissant Chrysopidae assemblage appears derived from that of the Okanagan Highlands, separated by about eighteen or so million years, depending on locality. Of the four Florissant genera, we find *Archaeochrysa* and possibly *Tribochrysa* there. A major change is the narrowing of morphological (e.g., absence of genera in which venation is enriched as in *Adamsochrysa* or reduced as in *Pseudochrysopa*) and possibly ecological variety within the Nothochrysinae, and the loss of the Mesozoic relicts (Limaiinae). Like McAbee, Chrysopidae (12 specimens) and Osmylidae (eight specimens) are the most abundant Neuroptera reported (Bather, 1909; Cockerell, 1913; Carpenter, 1943; Adams, 1967; Lahmers, 2011), which appears to represent a real community similarity. Unlike McAbee, however, Ithonidae (s. l.) and Nemopteridae (one specimen each) have been found at Florissant, while Hemerobiidae has not (Carpenter, 1960; Archibald and Makarkin, 2006).

Baltic amber.—This famous and well-studied source of knowledge of the late Eocene insects of northern Europe has been treated in detail in numerous publications (see review in Weitschat and Wichard, 2010). Although the occurrence of Chrysopidae in Baltic amber has been known for over a century and a half since the work of Göppert and Berendt (1845), no species have yet been described. A single illustrated adult specimen belongs to Chrysopinae judging from its forewing venation, which is most similar to that of the chrysopine tribe Belonopterygini (Weitschat and Wichard, 1998, pl. 56d). The affinities of four Baltic amber chrysopid larvae (Scheven, 2004, figs. on p. 68, 69; Weitschat, 2009, fig. 45; C. and H. W. Hoffeins, personal commun. to VNM, 2010) are unknown, but two probably belong to this subfamily judging from the presence of the lateral tubercles bearing long setae on the prothorax, and one might be assigned to Nothochrysinae because of the absence of these; differences in the structure of antennae and distal segment of labial palps that more confidently distinguish these subfamilies (see Díaz-Aranda and Monserrat, 1995) are not discernible in the photos of these larvae that we examined. Therefore, the representation and taxonomic composition of this assemblage appears to be very different from that of the Okanagan Highlands.

Chrysopids have not been reported from a number of other well-studied Eocene localities such as the Green River Formation (U.S.A.) and Messel (Germany). Taphonomic factors as discussed above would not operate differentially on Chrysopidae within Neuroptera, which has other families reported from Green River (three species of Ascalaphidae, and probably one specimen of Nemopteridae: Dayvault et al., 1995) and Messel (one species of Mantispidae: Wedmann and Makarkin, 2007). We are examining reasons for this differential occurrence in a separate work.

CONCLUSIONS

The Okanagan Highlands constitutes a remarkable record of the Chrysopidae at an important time of their evolution. This region—particularly at McAbee—contains an extraordinarily taxonomically, morphologically and likely ecologically diverse suite of the family. The richness of taxa and specimens described here in this first set of descriptions from the region already exceeds all other described localities or regional set of localities in the fossil record, including those that have been intensively studied for over a century. This assemblage reveals the family in transition, both biogeographically, as some of its members dispersed across the North Atlantic between Europe and North America; and taxonomically, as the last of the Mesozoic Limaiinae is seen and the beginnings of the modern dominance of Chrysopinae is still tens of millions of years in the future.

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