

New Early Eocene brown lacewings (Neuroptera: Hemerobiidae) from western North America

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Abstract—Two Early Eocene hemerobiid species from the Okanagan Highland deposits of western North America are described: *Wesmaelius mathewesi* **sp. nov.** (Quilchena, British Columbia, Canada) and *Cretomerobius wehri* **sp. nov.** (Republic, Washington, United States of America.). A poorly preserved specimen, possibly Hemerobiidae (Driftwood Canyon, British Columbia, Canada) is discussed. The systematic position of the genus *Cretomerobius* within the Hemerobiidae is unclear, but it appears to belong within (or possibly as the sister group to) the poorly differentiated Drepanacrinae–Megalominae–Drepanopteryginae grade of subfamilies. *Wesmaelius mathewesi* is the first fossil species to be assigned, although with some uncertainty, to this otherwise speciose and widely distributed extant genus. It also represents the oldest known material of the subfamily Hemerobiinae. *Mesohemerobius jeholensis* Ping is removed from the Hemerobiidae and treated as Neuroptera *incertae sedis*.

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Résumé—On trouvera ici la description de deux espèces d'hémérobies provenant des sédiments des terres hautes de l'Okanagan dans l'ouest de l'Amérique du Nord, *Wesmaelius mathewesi* **sp. nov.** (Quilchena, Colombie-Britannique, Canada) et *Cretomerobius wehri* **sp. nov.** (Republic, Washington, États-Unis d'Amérique). De plus, un spécimen mal conservé (Driftwood Canyon, Colombie-Britannique, Canada) qui est peut-être un hémérobie fait l'objet d'une discussion. La position systématique de *Cretomerobius* au sein des Hemerobiidae est incertaine, mais le genre semble appartenir au grade mal différencié des sous-familles Drepanacrinae–Megalominae–Drepanopteryginae ou alors il peut en être le groupe-soeur. *Wesmaelius mathewesi* est la première espèce fossile décrite dans ce genre contemporain, par ailleurs riche en espèces et à répartition étendue. C'est aussi le matériel fossile le plus ancien trouvé dans la sous-famille des Hemerobiinae. *Mesohemerobius jeholensis* Ping est retiré des Hemerobiidae et traité comme une espèce *incertae sedis* de Neuroptera.

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Introduction

The Hemerobiidae is one of the most speciose and widely distributed families in the order Neuroptera, containing some 600 extant species (Oswald 1993a). The oldest known hemerobiid fossil is *Promegalomus anomalus* Panfilov in Dolin *et al.* (1980), known from a complete but rather poorly preserved forewing from the Late Jurassic of Karatau, Kazakhstan. Panfilov (1980) created the monotypic family Promegalomidae for this species, which was subsequently synonymized with the Hemerobiidae by Oswald (1993a). Reexamination of the holotype by one of us (VM) has confirmed that Panfilov's drawing of the venation is substantially correct (Panfilov 1980, Fig. 91; however, the maculation shown in the drawing is entirely absent on the specimen), and so we agree that it properly belongs to the Hemerobiidae. *Mesohemerobius jeholensis*, another Late Jurassic (or Early Cretaceous) neuropteran, was described from China (Ping 1928) and discussed as a possible hemerobiid by Oswald (1993a). We now consider it inadvisable to assign this neuropteran to the Hemerobiidae because the presence of hemerobiid apomorphies (*i.e.*, multiple oblique radial branches (ORBs, equal to "radial sectors" of various authors)), although shown in Ping's (1928) venational drawing, cannot now be confirmed. Unfortunately, the primary type (and only known) specimen of this species appears to have been lost during the Second World War (D Ren, personal communication). We here move *M. jeholensis* to the status of Neuroptera *incertae sedis*. Early Cretaceous Hemerobiidae are only known with certainty from the single, almost complete, and well-preserved forewing of *Cretomerobius disjunctus* Ponomarenko, 1992 (from Bon-Tsagan, Mongolia). Two other neuropterans reported from the Early Cretaceous remain problematic. These insects, *Brasilopsychopsis kandleri* Rumbucher and *Cratopsychopsis maiseyi* Rumbucher, were described as hemerobiids from the Santana Formation of Brazil (Late Aptian / Early Albian) (Rumbucher 1995). The descriptions and illustrations of these taxa are inadequate to permit confirmation that they belong to this family. A reexamination of their type material (currently residing in a private collection (Bechly 1998)) will be required to verify their taxonomic placement. Late Cretaceous hemerobiids remain unknown. The only putative hemerobiid reported from this period — a reference to an undescribed species from the Cenomanian of Magadan Oblast in northeastern Siberia by Zherikhin (1980) — was subsequently described as a berothid (*Plesiorobius sibiricus* Makarkin (Neuroptera: Berothidae)) by Makarkin (1994).

The Tertiary record of hemerobiids is more diverse and numerous. Many species (14–17, depending on possible synonymy) have been referred to the extant genera *Notiobiella* Banks, *Drepanopteryx* Leach, *Neuronema* McLachlan, *Megalomus* Rambur, and *Hemerobius* Linnaeus, and four additional species have been described in the extinct monotypic genera *Prophlebonema* Krüger, *Prolachlanius* Krüger, *Prospadobius* Krüger, and *Bothromicromus* Scudder. The majority of these fossils are European (*i.e.*, from the Late Paleocene / Early Eocene of the "Mo-clay" deposits of Denmark (Henriksen 1922) and Havighorst, Germany (Illies 1941), Late Eocene / Early Oligocene of Isle of Wight, England (Jarzembowski 1980), Late Eocene Baltic amber (Pictet-Baraban and Hagen 1856; Krüger 1923), Middle Miocene of Stavropol, northern Caucasus, Russia (Makarkin 1991), and Late Pliocene of Murat, France (Nel 1990)). The assignment of almost all of these species to extant genera, and the validity of the extinct genera, however, needs confirmation. In addition, two fragmentary specimens have been described that are impossible to refer to the genus level (Jarzembowski 1980), several undescribed specimens have been reported from Baltic amber (Weitschat and Wichard 1998), and numerous undescribed specimens from the particularly fossiliferous Mo-clay (Larsson 1975; Rust 1999). An incomplete forewing from the Eocene of Geiseltal (Germany), which Pongrácz (1935) incorrectly considered belongs

to the hemerobiid genus *Bothromicromus*, has venation showing fundamental differences with this family (if Pongrácz's (1935) drawing is correct). This taxon cannot currently be placed to family and is removed here from the family Hemerobiidae and placed as Neuroptera *incertae sedis*. Only one fossil hemerobiid species has been described from the Tertiary of Asia (*i.e.*, *Drepanepteryx oedobia* Makarkin from one of the Late Oligocene / Early Miocene sites of the Sikhote-Alin Mountains, Russian Far East (Makarkin 1991)).

Few hemerobiid fossils are known from the New World. Two species have been reported from Miocene Dominican amber: an undescribed specimen referred to the genus *Hemerobius* (Poinar 1992, Fig. 71, but see Oswald 1999) and *Notiobiella thaumasta* Oswald, known from four well-preserved specimens that clearly belong to this extant pantropical genus (Oswald 1999; Poinar and Poinar 1999).

Only one fossil hemerobiid species has hitherto been described from continental North America: *Bothromicromus lachlani* Scudder from the Oligocene of Quesnel, British Columbia, Canada (Scudder 1878, 1890). Other, unnamed, hemerobiids were reported from Republic, Washington, by Wehr and Barksdale (1996), and from Quilchena, British Columbia, by Archibald and Mathewes (2000). In the present paper we provide names and formal descriptions for the specimens from the latter two sites, placing the Republic specimen in the extinct genus *Cretomerobius* and referring the Quilchena specimen to the extant genus *Wesmaelius*. One poorly preserved specimen from Driftwood Canyon (Smithers), British Columbia, we interpret as possibly a member of the Hemerobiidae. Despite the relatively wide distribution of hemerobiid fossils in Tertiary deposits, none have yet been found in the Late Eocene of Florissant, Colorado, which is well known for its extremely rich and long-studied fauna, including numerous neuropterans.

Material and methods

Of the more than 45 fossil neuropterans hitherto found at six Eocene Okanagan Highlands sites (current research), only three are hemerobiids. The Okanagan Highlands localities are a series of Early and Middle Eocene lacustrine shale sites (and one known fossiliferous amber occurrence) that extend about 1000 km through British Columbia and northern Washington State. In the Eocene this was an upland region characterized by microthermal temperatures (with a mean annual temperature $<13^{\circ}\text{C}$) (but see Quilchena locality, below), during the warmest period of the Cenozoic.

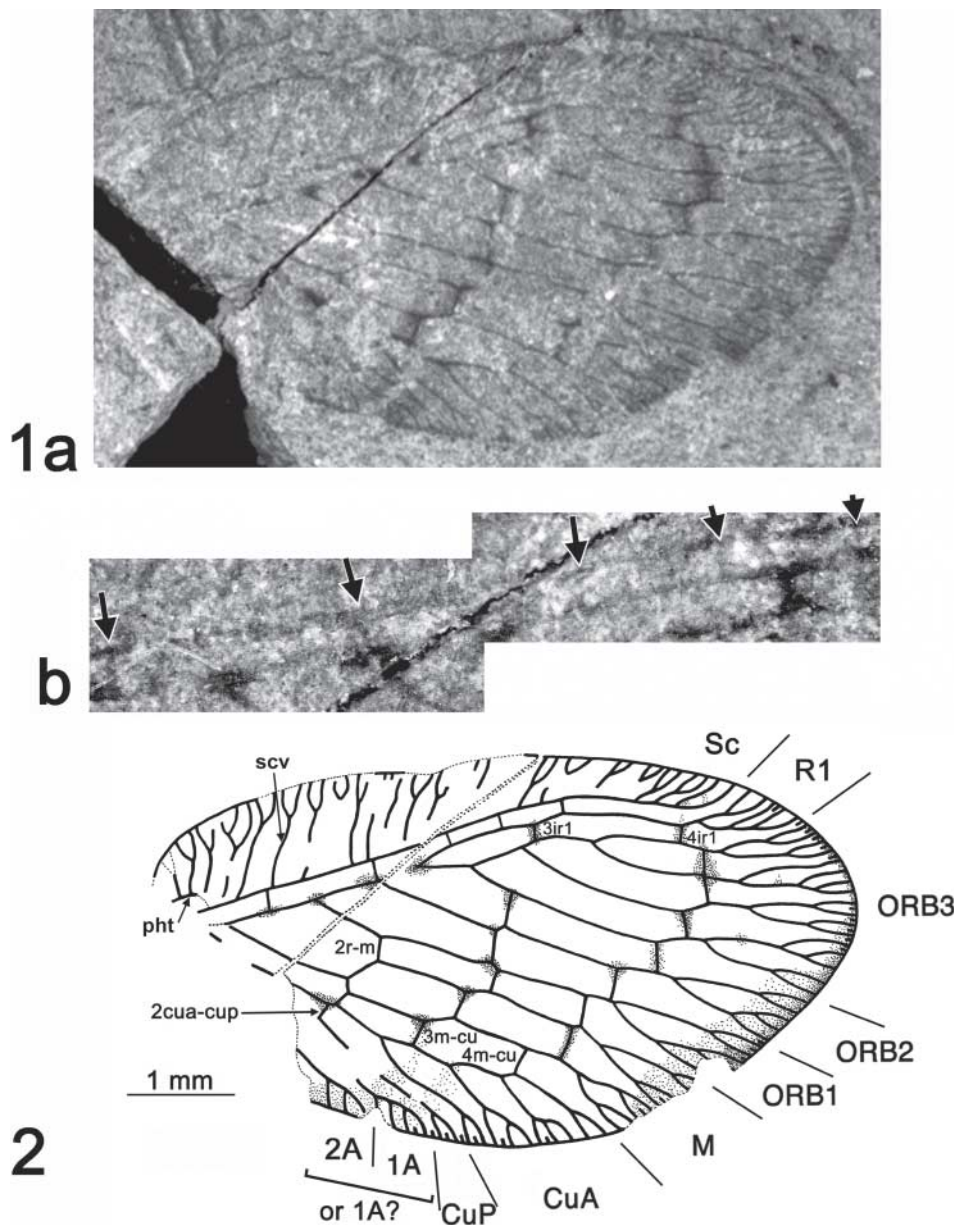
Insect fossils from all Okanagan Highland localities are preserved in a variety of lithologies, ranging from mudstones to sandstones; these specimens were found in fine-grained, easily splitting matrix, requiring minimal preparation (done at the Burke Museum, Seattle, Washington, and Simon Fraser University, Burnaby, British Columbia). A small amount of distilled water placed on the fossils at times made venation more clearly visible during camera lucida drawing.

The terminology of forewing venation, wing spaces, and cells employed here follows Oswald (1993a).

Taxonomic treatment

***Wesmaelius mathewesi* sp. nov. (Hemerobiidae, Hemerobiinae)** (Figs. 1–2)

Hemerobiidae sp.: Archibald and Mathewes 2000: 1448, Figure 6C.



FIGURES 1–2. *Wesmaelius mathewesi*, holotype Q-0092: 1a, forewing; 1b, detail of subcostal space (arrows indicate crossveins); 2, drawing of forewing. 1A–3A, anal veins; CuA, anterior cubitus; CuP, posterior cubitus; M, media; ORB1–ORB3, oblique radial branches of the radius (equal to “radial sectors” of authors); pht, proximal humeral trace; R1, first branch of radius; Sc, subcosta. A numerical prefix indicates the gradate series association of the crossvein and a letter indicates the longitudinal veins it intersects; “i” (or intra) indicates a crossvein joining different branches of the same longitudinal vein. Figures 1a and 2 have the same scale; Figure 1b enlarged to approximately 2.5 times Figure 1a.

Type material

Holotype: Q-0092 (part; no counterpart). Labeled: (front) “Q”; “Q-0092”; “HOLOTYPE: *Wesmaelius mathewesi* Makarkin, Archibald & Oswald”. Deposited in the fossil collection of Simon Fraser University (Burnaby, British Columbia, Canada). An incomplete forewing lacking the most basal portion, collected by Rolf Mathewes in 1976.

Etymology

The specific name is from the surname of Rolf Mathewes, in recognition of his work and support of paleontology at Quilchena.

Diagnosis

Wesmaelius mathewesi **sp. nov.** may be distinguished from all other species of the genus by (i) the narrow R1 space (wider in other species), (ii) the subparallel third and fourth gradate crossvein series (somewhat convergent towards CuA in other species), and (iii) both gradate series reaching the CuA (*i.e.*, both 3m-cu and 4m-cu present (in other species only one of these crossveins is present)).

Description

Forewing widely oval in shape with rounded apex, approximately 7.5 mm long and approximately 4.0 mm wide. Trichosors prominent. Costal space wide. All preserved subcostal veinlets branched, ending on costa. Humeral veinlet (basalmost subcostal veinlet) with proximal trace recurrent. True crossveins apparently lacking in costal space, but this space rather poorly preserved. Subcostal space moderately wide for entire length; crossveins rather poorly preserved, but five detected with certainty and others possible. R1 space narrow compared with other species of the genus. Three ORBs; ORB1 not forked proximal to the fourth gradate series; configuration of ORB2 similar to ORB1; ORB3 with three branches proximal to fourth (outer) gradate series. M appears fused basally with R1 for some distance (but see Discussion below). Basal portion of M parallel to bases of ORB1 and ORB2. M forked proximal to second gradate series. Origin of Cu not preserved. CuA pectinately branched, with three short branches. Origin and basal portions of CuP and anal veins not preserved. CuP with only single marginal fork (“shallowly” forked CuP), 1A and 2A pectinately branched near wing margin (alternative interpretation: 1A with two branches and 2A not preserved; holotype is indistinct in this region). 3A not preserved. Three gradate series of crossveins (series 2–4 of Oswald 1993a) posterior to R1. Series 1 inferred to have been present but not preserved. Second series represented by 3 crossveins: 2r-m, 2m-cu, 2cua-cup, other possible crossveins not preserved; third series with 6 crossveins (from 3ir1 to 3m-cu); fourth series with 9 crossveins (from 4ir1 to 4m-cu). Crossveins between branches of CuA not detected, apparently absent. Wing patterning (darkened areas): third and fourth gradate series, bases of ORBs, CuA around crossveins 2m-cu and 2cua-cup, and wing margin posterior to apex.

Locality and age

The holotype is from the Quilchena locality, about 200 km northwest of Republic, Washington, United States of America. This is an exposure of Coldwater Formation shale in the Merritt basin on Quilchena Creek, about 3 km south of the town of Quilchena in south-central British Columbia, Canada.

Recent ^{40}Ar – ^{39}Ar dating of sanidine from Quilchena tephra suggests an Early Eocene age of approximately 51.5 Ma (R Mathewes and M Villeneuve, personal communication), making this among or possibly the oldest locality of the series. Eocene sedimentary rocks of the Merritt basin have been recently correlated with the Princeton Group, indicating a closer relation of Quilchena to insect-bearing sites <100 km to the south (Similkameen, Tulameen, Blakeburn Mine, Hospital Hill, Whipsaw Creek) than to those of the Kamloops Group (Tranquille, McAbee, Hat Creek), about equidistant to the north (Read 2000). Coal deposits associated with lacustrine shales in the Merritt basin indicate regional swamp as well as open-lake environments. The flora of Quilchena is described and reviewed in Mathewes and Brooke (1971).

Discussion

The vein M appears fused basally with R for some distance, but this may be a preservational artifact. In all extant Hemerobiidae in which the basal relationships of M and R are closely examined, these veins are either clearly separated or closely approximated to each other at their bases for some distance and (because they frequently overlap vertically) may appear fused in dorsal view; drawings apparently depicting fusion may be due to the difficulties of graphically representing this relationship between veins rather than to actual morphology. Because of the closely approximated basal association of these veins, it is often hard to determine conclusively if, or where, fusion actually occurs in fossils. Here, the wing base in *W. mathewesi* is poorly preserved and basal M–R fusion cannot be distinguished from the alternative that M and R are free. Although the possibility of actual fusion cannot be excluded, it is reasonable here to assume that close association of the basalmost preserved portions of M and R is suggestive of apparent, not actual, fusion.

Although crossveins in the subcostal space are quite poorly preserved, at least five were detected with certainty (Fig. 1b). The presence of only a single (basal) crossvein in the prestigmal subcostal space was considered plesiomorphic for the Hemerobiidae by Oswald (1993a). In some hemerobiid taxa there is an additional “intermediate” crossvein of fairly characteristic position (*i.e.*, in the subfamilies Psychobiellinae, Notiobiellinae, Drepanacrinae, some Drepanopteryginae, Megalomiinae, and the genus *Noiuis* Navás in Micromiinae), the presence of which has been interpreted to be apomorphic (Oswald 1993a). Although the polarity of this transformation appears plausible, it is interesting to note that the oldest known (here undoubted) hemerobiids (the Jurassic genus *Promegalomus* Panfilov in Dolin *et al.* (1980) and Early Cretaceous genus *Cretomerobius* Ponomarenko) have one or two intermediate crossveins in similar positions. This suggests an early origin for this trait, and, in the continued absence of early fossil hemerobiids with only a single basal sc–r crossvein, could cast doubt on the polarity suggested by Oswald’s analysis of extant taxa. Extant *Megalomus ricoi* Monserrat from Brazil may possess three intermediate crossveins (Monserrat 1997), and in some extant species of Drepanopteryginae (*e.g.*, *Drepanopteryx punctata* Okamoto, *Drepanopteryx algida* Erichson) there are several (up to at least four seen, but likely more adventitiously). The living *Berotherobius reticulatus* Monserrat and Deretsky, recently described from Chile, has up to 11 crossveins between Sc and R1 (Monserrat and Deretsky 1999). Thus, the condition of more than one post-basal subcostal crossvein does occur uncommonly in extant hemerobiids, though in such cases the number of these crossveins is frequently unstable, and the condition can generally be regarded as derived. It may be reasonably assumed that the presence of numerous intermediate crossveins in *W. mathewesi* is, likewise, a derived state. Occasional occurrence of several “intermediate” crossveins in species of those genera that usually have two prestigmal crossveins (*e.g.*, genera *Megalomus* and *Drepanopteryx*) suggests that

this character, when it occurs, is either a species-level apomorphy or an occasional adventitious condition.

The arrangement of the third and fourth gradate series of crossveins found in *W. mathewesi* is most similar to that of those few species of the genus *Hemerobius* where these series are subparallel and both reach CuA (*i.e.*, crossveins 3m-cu and 4m-cu are both present). Among the genus *Hemerobius*, this arrangement of crossveins is currently known to be highly characteristic only of the extant East Asian species *H. tristriatus* Kuwayama (both 3m-cu and 4m-cu present in 77% of 171 examined wings) and in the Miocene *H. incertus* Makarkin (Makarkin 1991, Fig. 3). In the majority of the other species of this genus (as well as nearly all species of the genus *Wesmaelius*), these series tend to converge toward the hind margin of the wing and have only one m-cu crossvein present. *Wesmaelius mathewesi* is the first known species of the genus *Wesmaelius* to exhibit the arrangement seen in *H. tristriatus*. Lacking reliable phylogenies of the genera *Hemerobius* and *Wesmaelius*, it is not currently possible to determine whether this trait is plesiomorphic or apomorphic.

Wesmaelius mathewesi may be confidently placed in the subfamily Hemerobiinae based on forewing venation. Based on the analysis of Oswald (1993b, p 369, Fig. 13), the change from 1 to 2 forewing ORBs is a synapomorphy of the Hemerobiinae, and the change from 2 to 3 ORBs is a synapomorphy of non-*Biramus* hemerobiines. *Wesmaelius mathewesi* clearly possesses the 3-ORB condition typical of non-*Biramus* hemerobiines. In addition, the configurations of the M and CuA, and the arrangement of crossveins posterior to R1, are consistent with the Hemerobiinae, and differ substantially from all other subfamilies.

The extant Hemerobiinae comprised five genera. The genera *Hemerobius* and *Wesmaelius* are both widely distributed (particularly in the Holarctic) and contain numerous species; another three genera, all with few species or monotypic, are restricted to the Hawaiian Islands (*Nesobiella* Kimmins) or the northern neotropics (*Hemerobiella* Kimmins and *Biramus* Oswald) (Oswald 1993a, 1993b). Of the exclusively extinct genera described to date, none may be referred with certainty to this subfamily. The venation of the new species is clearly similar to that of both the genera *Wesmaelius* and *Hemerobius*, which have similar forewing venation. The primary venational difference between these genera is the position of crossvein 2r-m, which is almost always located distal to the fork of M in the genus *Wesmaelius*, but almost always far proximal to this fork (or absent) in the genus *Hemerobius* (rarely located slightly distal, *e.g.*, in the extant Japanese *Hemerobius kobayashii* Nakahara). Based on this character, the new species may be interpreted as (i) a species of the genus *Hemerobius* in which crossvein 2r-m is shifted farther distally than is known in any extant species (less likely) or (ii) a species of the genus *Wesmaelius* in which the third and fourth gradate crossvein series are arranged as in some *Hemerobius* species (hitherto unknown for the genus *Wesmaelius*). The new species is associated here, although somewhat tentatively, with the genus *Wesmaelius* because of the position of crossvein 2r-m. Also supporting this interpretation is the location of crossvein 2m-cu. In the new species, this crossvein is located not more than its own length distal to the medial fork (as in the extant genus *Wesmaelius*), resulting in cell c2m-cu broad distally. In all extant *Hemerobius* species, this crossvein is located more distally, resulting in cell c2m-cu narrowed apically. Of the other venational characters, there are none that would clearly exclude the taxon from the genus *Wesmaelius*.

Given the character and taxonomic uncertainties discussed above, we have considered the appropriateness of describing *mathewesi* in a new genus placed near the genera *Hemerobius* and *Wesmaelius*; however, because we have been unable to identify any characters that, in our opinion, would constitute reliable and defensible apomorphies for the differentiation of such a genus from other hemerobiine hemerobiid genera

(particularly the genera *Hemerobius* and *Wesmaelius*), we have chosen here the more taxonomically conservative option of describing *mathewesi* as a new species in the genus *Wesmaelius*, where we believe it is best placed at the current time.

Fossils of Hemerobiinae were previously known only from the Miocene of Stavropol, which can be assigned to the genus *Hemerobius* with certainty (Makarkin 1991), and of Miocene Dominican amber, which can be referred to a species "apparently near *Hemerobius* or *Wesmaelius*" (Oswald 1999, p 297). If our determination of the genus is correct, this species is the only described fossil *Wesmaelius* and the oldest representative of the Hemerobiinae known to date.

Paleoecology

The vast majority of the approximately 60 extant species of the genus *Wesmaelius* are distributed in the northern temperate regions, with approximately 50 species distributed widely throughout the Nearctic and Palearctic regions from their southern boundaries into the Arctic. In the southern parts of the Nearctic and Palearctic, *Wesmaelius* species are often restricted to higher elevation montane sites. Six species are known from the Ethiopian region (including Madagascar), one from the northern Neotropical region (Guatemala), and one from the southern Oriental region (Philippines). The genus *Wesmaelius* is not known from the Australian region, except for the clear introduction of one species into New Zealand (Tjeder 1961; Klimaszewski and Kevan 1987; Monserrat 1990, 2000; Makarkin 1995, 1996; Monserrat and Deretzky 1999).

Almost all occurrences of the genus *Wesmaelius* within the tropics are of species found in cool mountainous regions: Uganda at 3210 m (*W. majusculus* Kimmins), Guatemala above 2134 m (*W. magnus* Kimmins), and Kenya at 3000 m (Kimmins 1928, 1959; Monserrat and Deretsky 1999). Nothing is known of the habitat of three species described from only single specimens: *W. praenubilus* Fraser from Madagascar (Fraser 1951), *W. davidicus* Navás from the Philippines (Navás 1910) (doubtful record: incomplete description, not illustrated), and *W. obscuratus* Navás from Kenya (Navás 1936). Probably only one species is truly capable of life in the tropical heat (*i.e.*, *W. nubilus*), which is discontinuously distributed from South Africa to the southern Arabian Peninsula, including Namibia, Angola, Zambia, Cameroon, and Kenya (Monserrat and Deretsky 1999). The record of this species at high altitude in Kenya (2500 m), however, indicates that perhaps *W. nubilus* is eurythermic rather than thermophilic.

Many Eocene sites in middle and high latitudes contain biotic assemblages associated with both tropical and temperate regions today; this has been hypothesized as a consequence of increased climatic equability (decreased temperature seasonality) in the early Tertiary. Presumably milder winters in Eocene regions of intermediate to low mean annual temperatures (determined by taxon-free leaf margin analysis), allowed thermophilic biota that today would be excluded from such temperate regions by their intolerance to associated low cold-month temperatures to be found in assemblage with those whose nearest living relatives are associated with the temperate region (Wing and Greenwood 1993; Greenwood and Wing 1995; Archibald and Farrell 2003). There are many such examples of thermophilic biota occurring in the fossil record of the microthermal – low mesothermal Okanagan Highlands (*e.g.*, a diplopterine cockroach at Quilchena that is restricted today to low latitudes (Archibald and Mathewes 2000; Archibald and Farrell 2003)).

The modern distribution of the genus *Wesmaelius* lends support for considering *W. mathewesi* as a temperate-associated element of the Quilchena assemblage; however, forewing morphology suggests that this species is somewhat removed from the extant members of this genus. Therefore, the autecological parameters of modern species in this case are only suggestive.

Subfamily *incertae sedis*

Genus *Cretomerobius* Ponomarenko, 1992

Included species

Two species: *Cretomerobius disjunctus* Ponomarenko, 1992 (type species; designated as “*C. distinctus* (*sic*) Ponomarenko, sp. nov.” (*lapsus calami*): Ponomarenko 1992, p 105), early Cretaceous of Bon-Tsagan, Mongolia; *Cretomerobius wehri* **sp. nov.**, early Eocene of Republic, Washington. One undescribed incomplete forewing in the Paleontological Institute (Moscow) collection from the Paleocene of the Zerkalnaya River, Sithote-Alin Mountains, Russian Far East (see map in Makarkin 1998), may also belong to this genus.

Discussion

See Discussion under *Cretomerobius wehri* **sp. nov.** below.

Cretomerobius wehri **sp. nov.**

(Figs. 3–4)

Type material

Holotype: UWBM77543 (part; no counterpart). Labeled: (back) “77543”; “07B” (portion, original lettering damaged, presumably referring to locality number A0307B); (front) “HOLOTYPE: *Cretomerobius wehri* Makarkin, Archibald & Oswald”. Deposited in the Thomas Burke Memorial Washington State Museum (University of Washington, Seattle, Washington, United States of America). A well-preserved incomplete left forewing collected by Wesley Wehr in 1993.

Etymology

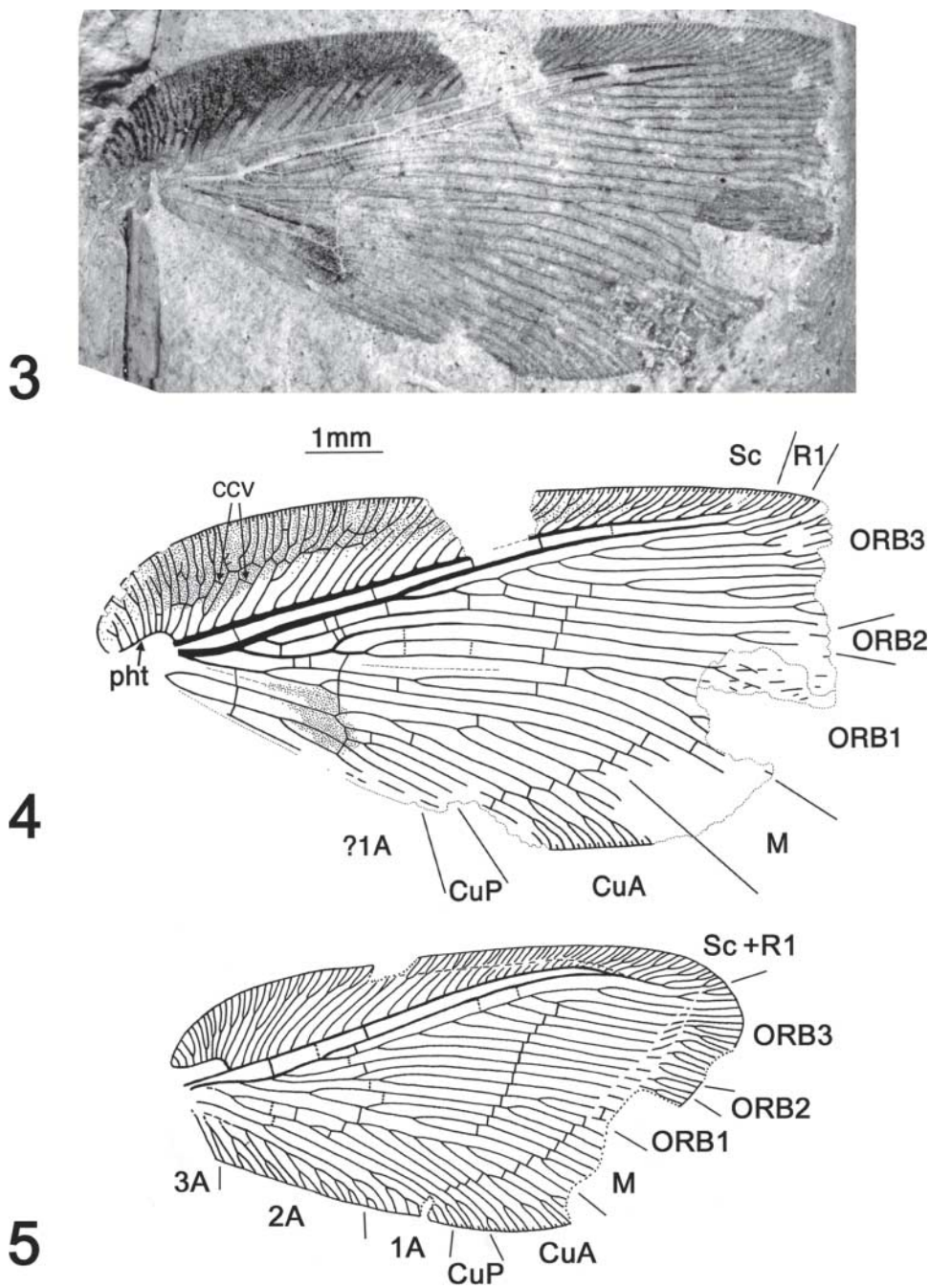
The specific name is from the surname of Wesley C Wehr, in recognition of his work at and support of paleontology at Republic.

Diagnosis

Cretomerobius wehri can be distinguished from *C. disjunctus* by any of the following forewing characters (characters of *C. disjunctus* given in brackets): (i) proximal portion of costal space with a longitudinal series of crossveins joining subcostal veinlets [crossvein series absent]; (ii) subcosta not fused with anterior radial trace (R1) in pterostigmal region [fused]; (iii) third gradate series (crossing medial and cubital spaces near middle of wing) irregular [long and regular].

Description

Forewing (Figs. 3, 4) moderately broad, approximately 9 mm long (estimated), 4.0 mm wide. Wing patterning represented by distinct shading in costal space, around origin of most proximal branch of CuP, and by poorly visible small areas of shading throughout the wing, especially in distal half. Radiomedial and mediocubital flexion lines well developed. Trichosors prominent along entire (preserved) wing margin. Costal space expanded basally, narrowed apically. All subcostal veinlets branched, proximally sometimes 2 or 3 times, ending on costa. Humeral veinlet (most proximal subcostal veinlet) with about nine branches, proximal humeral trace strongly recurrent.



FIGURES 3-5. *Cretomerobius* Ponomarenko. 3 and 4, *C. wehri* holotype UWBM77543: 3, forewing; 4, forewing drawing (both converted to standard right dorsal view). 5, *C. disjunctus* holotype PIN 3559/2710: forewing. ccv, costal crossvein; other abbreviations as in Figure 2. All have the same scale.

Humeral cell long and rather narrow. Costal series of gradate crossveins present, extended at most to midpoint of space, rather irregular and possibly incomplete, approximately a dozen crossveins detected. Subcosta not fused distally with R1. Subcostal space moderately expanded for entire length (except basally), towards apex somewhat narrowed; three well-visible crossveins in proximal half of space; crossveins in distal half of space not detected (poor preservation?) (perhaps more than depicted in Fig. 4). R1 space narrow, as wide as width of subcostal space in distal half. Radius bearing 3 ORBs. ORB1 (basalmost) and ORB2 located close to wing base and to each other, whereas origin of ORB3 is shifted far distally. ORB1 running as a straight line, giving off short series of two anteriorly directed pectinate branches proximally, posteriorly directed pectinate branches distally. ORB2 not forked, except for end-twigging, bent parallel to most proximal branch of ORB1. ORB3 with six to seven pectinate branches, sometimes forked. M appears fused with R1 only for short distance at wing base (possible only closely approximated in life), and with four dichotomous branches occupying large area. Cu divided into CuA and CuP close to wing base. CuA pectinately branched in oblique manner, with rather long branches, of these, proximal one forked 2 times close to its origin (five long branches total). CuP either deeply forked once, or has two pectinate branches (partially and poorly preserved here). If former, then 1A partly preserved (most likely); if latter, then proximal branch of CuP located close to origin of CuP, anal veins not preserved. Crossveins posterior to R1 in basal half of wing irregular. First (basalmost) series extends from ORB2 to 1A, second extends from ORB1 to CuP. Third and fourth series of crossveins more regular, but poorly preserved. Several intermediate crossveins between series.

Locality and age

The holotype is from one of the much-studied shale exposures of the Tom Thumb Tuff Member of the Klondike Mountain Formation at Republic, Washington (Burke Museum site A0307B, the type locality of many of the plant species from Republic described in Wolfe and Wehr 1987). Throughout the last century, this site has been assigned to the Miocene, Paleocene, and then Middle Eocene (see review in Wolfe and Wehr 1987). In 1992, ^{40}Ar - ^{39}Ar dating of igneous rocks above and below the Klondike Mountain formation placed the fossil-bearing shale between 49 and 50 Ma, or late Early Eocene (personal communication with B Berger cited in Wehr and Hopkins 1994). The Republic flora has been characterized as a low montane – mixed coniferous forest (Wolfe 1979), with a cool climate (mean annual temperature determined by foliar physiognomy is 12–13°C (Wolfe and Wehr 1987)). This flora has received much attention (*e.g.*, see above references and Wehr and Manchester 1996).

Discussion

The new species *wehri* is placed here in the genus *Cretomerobius*. A comparison of the wings of the two species now placed in this genus shows their remarkable similarity (*cf.* Figs. 4 and 5). The following traits are particularly notable. In both species the anterior radial trace has 3 ORBs. ORB1 and ORB2 are located close to the base of the wing and to each other, and the base of ORB3 is located more distally, after a somewhat larger gap (though it is still nearer the wing base than the most distal ORB is in most other hemerobiids). The anterior trace of ORB3 is pectinately branched posteriorly. The posterior trace of ORB1 has a short series of branches pectinate anteriorly (see character A below). The media has several deep branches and occupies a fairly broad sector of the wing, particularly near the wing margin (see character B below). The posterior cubitus is deeply forked (see character C below).

Two features that might argue against considering *disjunctus* and *wehri* as congeneric species are the distally fused Sc and R1 in *disjunctus* (not fused in *wehri*) and the large temporal disjunction between the known occurrences of the two species (early Cretaceous for *disjunctus* and early Eocene for *wehri*). Because distal fusion of the Sc and R1 occurs rarely in the Hemerobiidae, and is probably apomorphic when it does occur (based on the phylogenetic analyses of Oswald 1993a, 1993b, 1994), we here consider this feature to be an autapomorphy of *disjunctus* and expand the generic concept of the genus *Cretomerobius* to include species without this trait. The wide temporal disjunction between *wehri* and *disjunctus* can be viewed as problematic, particularly as it implies the persistence of the genus *Cretomerobius* across the severe end-Mesozoic extinction event. The majority of the intrinsic characters exhibited by the available material, however, appears to support the hypothesis that these species are congeneric as treated here.

Character A (proximal branching of forewing ORB1). The genus *Cretomerobius* is characterized by an ORB1 with multiple (>1) anteriorly directed pectinate branches. This character, which incorporates the twin notions of deep basal branching of the ORB1 and the presence of multiple anteriorly pectinate branches along the posterior ORB1 trace, occurs in all extant genera of the subfamilies Drepanacrinae (genera *Conchopterella* Handschin, *Austromegalomus* Esben-Petersen, *Drepanacra* Tillyard), Megalominae (several New World species of the genera *Megalomus* and *Navasiella* Gonzalez-Olazo), and Drepanepteryginae (some species of the genus *Neuronema*) (Oswald 1993a; Monserrat 1997). All fossil hemerobiid species from the Jurassic to the Early Eocene also possess this ORB1 configuration, including the Late Jurassic genus *Promegalomus*, which is the oldest known representative of the family (Panfilov 1980, Fig. 91). Tertiary fossil species that possess this character have usually been referred (often tentatively) to the extant genus *Megalomus* (Henriksen 1922; Illies 1941; Makarkin 1991). The presence of a deeply forked ORB1 was considered plesiomorphic by Oswald (1993a, p 176, character 34) in his cladistic analysis of extant hemerobiid genera, which is consistent with the polarity for this character suggested by known hemerobiid fossils. The functional significance of anteriorly directed ORB1 pectinations is probably related to wing flexion in broad-winged species — as wing width increases, the restriction of ORB1 pectinations to the “anterior” side of this vein may act to preserve the linearity of the R–M wing space and its imbedded flexion line. Similar one-sided pectinations occur in a number of other neuropteran groups (e.g., the anteriorly pectinate MP vein in Mesozoic kalligrammatids).

Character B (proximal branching of forewing M). In most extant hemerobiids, M has a single near-basal fork whose simple branches run more-or-less parallel for some distance before twiggling more distally near the wing margin. Based on its wide distribution within the family (see illustrations in Oswald 1993a, 1993b, 1994), including all genera in the several most basal family lineages, this state is probably plesiomorphic within the family relative to the multiply branched basal M condition found in some extant genera in the subfamilies Drepanepteryginae (genus *Drepanepteryx* and some species of the genus *Neuronema*), Drepanacrinae (e.g., genus *Conchopterella*), and Megalominae (several New World species of the genera *Megalomus* and *Navasiella*). This polarity is supported by the presence of a single near-basal M fork in the genus *Promegalomus*, which is the oldest known fossil hemerobiid, and supports the interpretation of the multiply branched basal M condition and comparatively broad medial area found in the genus *Cretomerobius* as apomorphic. It seems likely that some fundamental relationship exists between wing size (particularly width) and the number of M (and ORB) branches present in the wing, although to our knowledge this question has never been examined in detail.

Character C (proximal branching of forewing CuP). The genus *Cretomerobius* character state “CuP deeply forked” occurs in all genera of the subfamilies Drepanopteryginae, Drepanacrinae, and Megalominiinae, in the genus *Notiobiella* of the subfamily Notiobiellinae, and rarely in Microminiinae. In other extant hemerobiids the CuP is normally simple (*i.e.*, not branched before its typical marginal end-twigging). A deeply forked CuP was considered apomorphic and a shallowly forked CuP plesiomorphic by Oswald (1993a, p 179, character 48). This polarity is supported by the presence of a shallowly forked CuP in all genera belonging to the four basalmost extant hemerobiid lineages, corresponding to the subfamilies Adelphohemerobiinae, Hemerobiinae, Sympherobiinae, and Psychobiellinae (Oswald 1993a, 1994). This polarity, however, is not currently corroborated by the majority of known hemerobiid fossils, most of which, like the genus *Cretomerobius*, possess a deeply forked CuP.

Subfamily placement of the genus *Cretomerobius*

The genus *Cretomerobius* cannot be placed with confidence in any of the 11 currently recognized subfamilies of extant hemerobiids (Oswald 1993a, 1993b, 1994; Monserrat and Deretsky 1999). Most of these subfamilies (Adelphohemerobiinae, Berothimerobiinae, Carobiinae, Notiobiellinae, Sympherobiinae, Psychobiellinae, Hemerobiinae, and Microminiinae), however, can be excluded from consideration because their venation differs too greatly from that of the genus *Cretomerobius*.

In general phenotype, the forewing venation of the genus *Cretomerobius* most strongly resembles that of the extant genera *Conchopterella*, *Drepanacra*, *Austromegalomus* (all Drepanacrinae) and, particularly, *Neuronema* (Drepanopteryginae). Each of these genera has several of the following general points in common with the genus *Cretomerobius*: (i) crossvein 2sc-r present, (ii) longitudinal veins in the radial area relatively numerous and dense, (iii) humeral lobe of costal space well developed, (iv) proximal humeral trace prominently recurved and pectinately branched, (v) radius with 3 or more ORBs, (vi) posterior trace of ORB1 with several anteriorly pectinate branches, (vii) media with multiple deep forks (*i.e.*, >1 fork basad of distal half of anterior or posterior medial traces), and (viii) cubitus posterior deeply forked (*i.e.*, CuP stem shorter than posterior CuP trace beyond deepest fork).

Based on the phylogenetic analysis of Oswald (1993a, pp 192–3, Fig. 23), the presence of crossvein 2sc-r (even if perhaps not uniquely differentiable from other post 1sc-r crossveins in the subcostal area), a deeply forked CuP, and only 3 ORBs suggests that the genus *Cretomerobius* may represent a separate departure (*i.e.*, not belonging to any currently named subfamily) from the “main axis” of hemerobiid evolution somewhere along lineage 14, at the base of the poorly resolved Drepanacrinae–Megalominiinae–Drepanopteryginae subfamily grade. The presence of a broad humeral lobe and a well-developed, pectinately branched, humeral veinlet clearly excludes the genus *Cretomerobius* from the “terminal” subfamily Microminiinae. The presence of 3 [not 2] ORBs and a well-developed fourth gradate series (visible in at least the medial and cubital areas of both species of the genus *Cretomerobius*) [not absent] clearly excludes the genus *Cretomerobius* from the subfamily Notiobiellinae, the sister group to the clade Drepanacrinae + Megalominiinae + Drepanopteryginae + Microminiinae.

A more definitive statement about the phylogenetic relationships of the genus *Cretomerobius* must await the discovery of additional material that will permit assessment of intra- and inter-specific variation and more detailed investigation of the venation in the wing regions lacking in the known specimens.

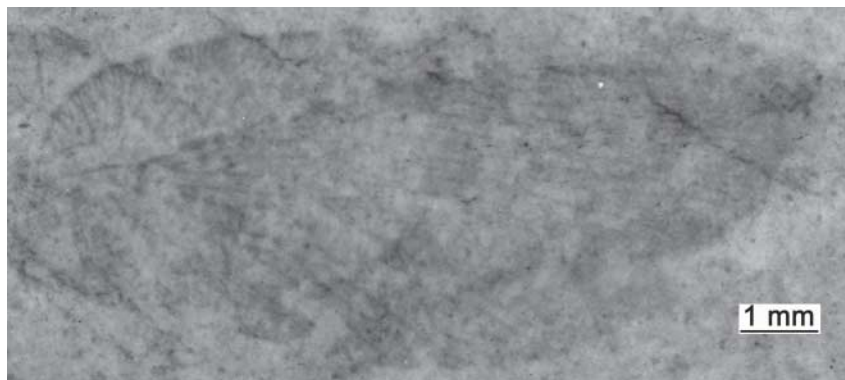


FIGURE 6. *Neuroptera incertae sedis*, Hemerobiidae? Specimen SBA1165, forewing.

***Neuroptera incertae sedis*, Hemerobiidae?**

(Fig. 6)

Material

SBA1165 (part; no counterpart), to be deposited with BC Parks (British Columbia Ministry of Water, Land, and Air Protection; Smithers, British Columbia, Canada). A poorly preserved incomplete forewing and possibly portions of another overlaid wing collected by SBA in August 2002.

Description

Forewing moderately broad, approximately 11 mm long, approximately 5 mm wide (true measurements uncertain owing to poor preservation), with some faint banding (possibly representing regions of crumpled or overlapping wings or membrane patterning). Costal space broad basally, narrowed distally, lacking distinguishable crossveins. Trichosores apparently present (at least) along humeral margin. Preserved subcostal veinlets mostly (all?) branched. Humeral veinlet well developed; proximal humeral trace strongly recurrent and with seven to eight pectinate branches. Subcostal space poorly preserved, lacking distinct crossveins. Radial and medial areas with numerous, poorly preserved, parallel branches; 2 or more gradate crossvein series tenuously visible. Venation of cubital and anal areas fragmentary and indistinct.

Locality and age

The single specimen is from an outcrop of lacustrine shale of the Eocene Ootsa Lake Group along Driftwood Creek in Driftwood Canyon Provincial Park in west-central British Columbia, about 700 km northwest of Quilchena. Palynological analysis (White 1977) of localities within the Ootsa Lake Group indicate that the Group is latest Paleocene to Late Eocene from one locality and probably Eocene (or possibly younger) for another locality (the Driftwood site was not specifically sampled). Recent ^{40}Ar - ^{39}Ar and U-Pb dating of Ootsa Lake Group volcanics (Grainger *et al.* 2001) indicate a 53.2–47.6 Ma (Early to Middle Eocene) age for magmatism within this group, although the stratigraphic position of the Driftwood Canyon shale is not clear in relationship to these igneous rocks. The Driftwood Canyon locality has been described as early Middle (Lutetian) Eocene (*e.g.*, Wilson 1977a, 1977b), based on correlation of the flora and fauna with those of other Okanagan Highlands localities. In the past decade, however, the presumed ages of several of these localities (*e.g.*, Quilchena, Republic) have been

reexamined and are now considered Early Eocene (Ypresian). Until precise U–Pb dating of ash layers intercalated between shale beds can be completed (ongoing research by SBA), the precise position of the Driftwood Canyon beds within the Eocene (Ypresian or Lutetian) will remain unclear. The fossil fauna of the Driftwood Canyon is discussed by Wilson (1977*a* (fish); 1977*b* (insects)).

Discussion

Because of the poor condition of this specimen it has not been possible to assign it with confidence to any neuropteran family. But based on its general size and shape, and the general configuration of its venation (*e.g.*, well-developed humeral area, prominent recurrent humeral vein, parallel remigial veins, trichosores, branched subcostal veinlets, relatively few crossveins, and these apparently grouped into gradate series), it seems likely that this specimen belongs to the family Hemerobiidae. It is not definitely assigned to this family here because the preservation of the anterior radial trace is insufficient to clearly show multiple oblique radial branches; the primary venational synapomorphy for the Hemerobiidae (present in all known species except *Adelphohemerobius enigmaramus* Oswald, the putative extant sister-species of the remainder of this family (Oswald 1994)).

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