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THE EOCENE APEX OF PANORPOID SCORPIONFLY FAMILY DIVERSITY

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ABSTRACT—The scorpionfly (Mecoptera) superfamily Panorpoidea underwent an Eocene radiation, replacing the extinct Mesozoic orthophlebiid grade and reaching its greatest family-level diversity: Panorpidae, Panorpodidae, Austropanorpidae, Holcorpidae, Dinopanorpidae, and a new family proposed here, the Eorpidae. Only the Panorpidae and Panorpodidae survived the Eocene and persist to the present day. This cluster of family extinctions is exceptional within Cenozoic insects. The Eorpidae includes at least one new genus and three new species described here from four localities of the early Eocene Okanagan Highlands of British Columbia, Canada, and Washington, U.S.A.: *Eorpa ypsipeda* n. gen. n. sp. (McAbee and possibly Falkland, BC, Canada; and Republic, WA, U.S.A.), *Eorpa elverumi* n. gen. n. sp. (Republic), and *Eorpa jurgeni* n. gen. n. sp. (Quilchena, BC). Some of the other fragmentary and poorly preserved specimens might represent further new species. We propose that the apex of Panorpoid family diversity ended by pressures from post-Eocene icehouse world climatic stress and the rise to ecological dominance of ants, some of which would have provided strong competition in scavenging for dead arthropods.

INTRODUCTION

INSECT FAMILIES accumulated in the Cenozoic with few, scattered losses—apart from a single, distinct exception of a cluster of family extinctions within the panorpoid Mecoptera. Why was this group different?

The mecopteran superfamily Panorpoidea (sensu Willmann, 1987) radiated to its greatest diversity of six families in the Eocene, but is today reduced to two. The great majority of the family Panorpidae, which now dominates the small order with over 400 species, has a mid-latitude, disjunct Holarctic distribution, with the remainder inhabiting lower latitudes of South and Southeast Asia into equatorial Indonesia (Byers and Penny, 1979; Cai et al., 2008). The other extant panorpoid family, the small Panorpodidae (about a dozen species), is restricted to the United States, Japan, China and Korea.

The earliest known panorpoids belonged to the paraphyletic stem group "Orthophlebiidae", which appeared in the late Triassic, diversified to numerous species in the Jurassic, and is last seen in decline in the early Cretaceous (Willmann, 1987; Hong and Zhang, 2007). The only other possible Mesozoic panorpoid is a single species of the early Jurassic Muchoriidae, represented by a single forewing specimen (Sukatsheva, 1985, Willmann, 1987). The phylogenetic analysis of Ren et al. (2009; supporting online material), however, creates considerable doubt as to whether this insect belongs in the Panorpoidea. The superfamily has not yet been found in the late Cretaceous and Paleocene.

The orthophlebiid grade was replaced in the Eocene by a set of new panorpoid families, the Austropanorpidae, Holcorpidae, Dinopanorpidae, Panorpidae, and Panorpodidae. Although the first three have been thought by some to represent the last remnants of the "Orthophlebiidae" (e.g., Willmann and Novokshonov, 1998; Novokshonov, 2002), these are now considered distinct (Willmann, 1987; Archibald 2005, 2010). The Dinopanorpidae is first seen in the early Eocene of the Okanagan Highlands deposits of far-western mid-latitude North America and the Eocene of Pacific coastal Russia (Archibald, 2005). Other recent discoveries show the Holcorpidae and Panorpidae were also present in the Okanagan Highlands, older than previously thought (Archibald, 2010, herein). The Panorpodidae and Austropanorpidae also appear in the Eocene, probably around Okanagan Highlands time (below). Here, we describe an assemblage of new early Eocene panorpoids from the Okanagan Highlands, which includes at least one new genus and three new species. We assign these to a new, sixth Eocene panorpoid family proposed here, the Eorpidae.

This Eocene flowering of the Panorpoidea appears primarily in temperate-climate, mid-latitude montane forests. Four of these families are gone by the Oligocene, leaving only the remnant two that persist in modern times.

THE FAMILY EORPIDAE

Fossils assigned here to the new family Eorpidae are preserved in lacustrine shales of four localities of the early Eocene Okanagan Highlands deposits in southern British Columbia, Canada, and northern Washington, U.S.A. (Archibald et al., 2011a, fig. 1, localities map). A montane forest covered this region with similarities to the modern mixed mesophytic eastern deciduous forests of North America, but with elements that are now extinct or persist only in East Asia or in low latitudes (Greenwood et al., 2005; Moss et al., 2005). Floristic proxies indicate a mesic climate with mild upper microthermal to lower mesothermal mean annual temperatures (MAT) with mild winters and few frost days, if any (Greenwood et al., 2005; Moss et al., 2005). These localities are: 1) McAbee, BC, Canada: an unnamed formation of Kamloops Group shale ~10 kilometers east of Cache Creek in south-central British Columbia, early Eocene 52.90 ± 0.83 Ma (Archibald et al., 2010). McAbee MAT is estimated as an upper microthermal ~10–13°C (Greenwood et al., 2005); 2) Falkland, BC, Canada: Kamloops Group sediments near the town of Falkland, BC, dated at 50.61 ± 0.16 Ma (Mortensen and Archibald, current research). MAT was lower mesothermal <15°C (Smith et al., 2012), upper microthermal ~9–12°C by leaf physiognomy (Smith et al., 2009), with nearest living relative analysis a few degrees warmer (Greenwood et al., 2005). Smith et al. (2009, 2010, 2012) discussed the Falkland forest and environment in detail; 3) Quilchena, BC, Canada: a small exposure of fossil-bearing shales and mudstones of the Coldwater Beds (Kamloops Group, Cockfield, 1948) along Quilchena Creek, radiometrically dated at 51.5 ± 0.4 Ma (Villeneuve and Mathewes, 2005). A diverse fossil flora has been known for over a century (Penhallow, 1908), recently supplemented by new collections of plants and insects (Archibald and Mathewes, 2000). Leaf margin analysis and nearest living relative analysis indicate that Quilchena was the warmest of the Okanagan Highlands localities, with MAT estimated as a lower mesothermal ~15°C (Greenwood et al., 2005); and 4) Republic, Washington, U.S.A.: outcrops of the early Eocene 49.4 ± 0.5 Ma (Wolf et al., 2003) Klondike Mountain Formation in and adjacent to the town of Republic, north-central Washington State: Thomas Burke Museum site UWBM B4131 in the town of Republic; SR locality S100 near Republic; Mount Elizabeth, east of Republic, UWBM locality B4213; and west of Republic in the Toroda Valley, SR locality S103. MAT estimates range from ~9–13°C (Greenwood et al., 2005).

Abbreviations of the names of institutions holding specimens described and discussed here are: CDM, Courtenay and District Museum (Courtenay, BC, Canada); RBCM, Royal British Columbia Museum (Victoria, BC, Canada); RTMP, Royal Tyrrell Museum of Palaeontology (Drumheller, Alberta, Canada); SFU, Simon Fraser University (Burnaby, BC, Canada); SR, Stonerose Interpretive Center (Republic, Washington, U.S.A.); TRU, Thompson Rivers University (Kamloops, BC, Canada); UWBM, Thomas Burke Museum (Seattle, Washington, U.S.A.). TRU accession numbers are cited without their UCCIPR L-18 prefix (which applies to all TRU specimens reported here) other than as listed in the Appendix, so as not to overburden the text.

Wings are figured in standard aspect (apex to the right, some images reversed). Venational terminology follows Carpenter (1992), except for branches of Sc, which are numbered from apical-most to basal-most. We follow Willmann's (1987) concept of the Panorpoidea, with the exception that we recognize the doubt concerning Muchoriidae's membership in this taxon shown by Ren et al. (2009). We use the terminology of Wolfe (1975) for mean annual temperature (MAT) categories: microthermal, ≤13°C; mesothermal, >13°C, <20°C; megathermal, ≥20°C.

SYSTEMATIC PALEONTOLOGY

Order MECOPTERA Packard, 1886
Superfamily PANORPOIDEA Latreille, 1805
Family EORPIDAE new family

Type genus.—*Eorpa* n. gen., by monotypy.

Diagnosis.—Most easily separated from other panorpoid families by 1) forewing with strong branch of Sc (Sc3) in mid-wing; further separated from all other panorpoid families except Holcorpidae, Dinopanorpidae by 2) media with five branches in both forewing and hind wing; further separated from Holcorpidae by 3) Rs3+4 longer than Rs1+2 (forewing and hind wing); by 4) abdomen not extended (male, female); from Dinopanorpidae by 5) R1 curves around pterostigma, immediately joining anterior margin as in Panorpidae, Holcorpidae.

Description.—Medium sized panorpoid Mecoptera with the following character states. Head capsule with prolonged downward extension, similar to that of Panorpidae. Thorax, generalized panorpoid morphology. Legs, with annulate pubescence. Forewing, subtriangular-ovate, widest point ~2/3 length. Humeral vein crossvein-like. Sc, forked to Sc1+2, Sc3 near mid-wing; Sc3 short, immediately joining C at oblique angle; Sc1+2 branching ~2/3 wing length; Sc2 short, joining C at right angle; Sc1 weak, curved toward, joining R1. R branched at ~1/4 length; R1 curved around pterostigma, terminating on C in "arrowhead" form as in Panorpidae. Rs with 6 to 7 branches; Rs1+2, Rs3+4 branching before mid-wing; Rs1+2 longer than Rs3+4; Rs2, Rs3, Rs4 simple; Rs1 with 3 to 4 branches. M with 5 branches, M1+2, M3+4 branching about mid-wing; base of Cu free; CuA joins margin at mid-wing; CuP mostly straight, sub-parallel to CuA. 1A mostly sub-parallel to CuP. 2A curved toward 1A basally, mostly straight to margin; 3A short, crossvein to posterior margin, then angled toward 2A, connected 2A by crossvein, then short to margin. Many weak crossveins detected between branches of Rs, M, particularly near apex; stronger crossveins in basal portion, posteriad M. Abdomen, external genitalia, similar gross morphology as Panorpidae (male) as known (external genitalia poorly preserved); (female) similar to that in Panorpidae.

Etymology.—The family name is formed from that of the type genus *Eorpa* and the suffix "-idae", as prescribed by the International Code of Zoological Nomenclature article 29 (International Trust for Zoological Nomenclature 1999).

Occurrence.—Southern portion of the early Eocene Okanagan Highlands mesic, upper microthermal to lower mesothermal montane forests of south-central British Columbia, Canada, and north-central Washington, U.S.A.

Remarks.—The apparent absence of Eorpidae from the northern Okanagan Highlands sites of Horsefly and Driftwood Canyon (Archibald et al., 2011a) is not readily explained; this is not likely an artifact of taphonomy or differential collecting intensity.

Genus EORPA new genus

Type species.—*Eorpa ypsipeda*, new species.

Other species.—*Eorpa elverumi*, new species; *Eorpa jurgeni*, new species.

Diagnosis.—Medium sized scorpionflies bearing 1) forewing with strong branch of Sc (Sc3) in mid-wing; 2) media with five branches in both forewing and hind wing; 3) Rs3+4 longer than Rs1+2 (forewing and hind wing); by 4) abdomen not extended (male, female); 5) R1 curves around pterostigma, immediately joining anterior margin.

Description.—Head capsule with prolonged downward extension, similar to that of Panorpidae. Thorax, generalized panorpoid morphology. Legs with annulate pubescence. Forewing subtriangular-ovate, widest point ~2/3 length. Humeral vein crossvein-like. Sc forked to Sc1+2, Sc3 near mid-wing; Sc3 short, immediately joining C at oblique angle; Sc1+2 branching ~2/3 wing length; Sc2 short, joining C at right angle; Sc1 weak, curved toward, joining R1. R branched at ~1/4 length; R1 curved around pterostigma, terminating on C in "arrowhead" form as in Panorpidae. Rs with 6 to 7 branches; Rs1+2, Rs3+4 branching before mid-wing; Rs1+2 longer than Rs3+4; Rs2, Rs3, Rs4 simple; Rs1 with 3 to 4 branches. M with 5 branches, M1+2, M3+4 branching about mid-wing; base of Cu free; CuA joins margin at mid-wing; CuP mostly straight, sub-parallel to CuA. 1A mostly sub-parallel to CuP. 2A curved toward 1A basally, mostly straight to margin; 3A short, crossvein to posterior margin, then angled toward 2A, connected 2A by crossvein, then short to margin. Many weak crossveins detected between branches of Rs, M, particularly near apex; stronger crossveins in basal portion, posteriad M. Abdomen, external genitalia: similar gross morphology as Panorpidae (male) as known (external genitalia poorly preserved); (female) similar to that in Panorpidae.

Etymology.—From the Greek *Eos* (goddess of the dawn), referring to the Eocene, and *–orpa*, a mecopteran genus suffix. Gender feminine.

Occurrence.—Southern Okanagan Highlands localities at Republic, Washington, U.S.A.; McAbee, Falkland, and Quilchena, BC, Canada; early Eocene.

EORPA YPSIPEDA new species
Figures 1–10

Diagnosis.—May be separated from other species of *Eorpa* by 1) forewing with Sc4, Sc5; 2) lacking stout crossveins connecting Rs3+4, M1+2 and connecting M3+4, CuA ("a" and "b" in Fig. 15);

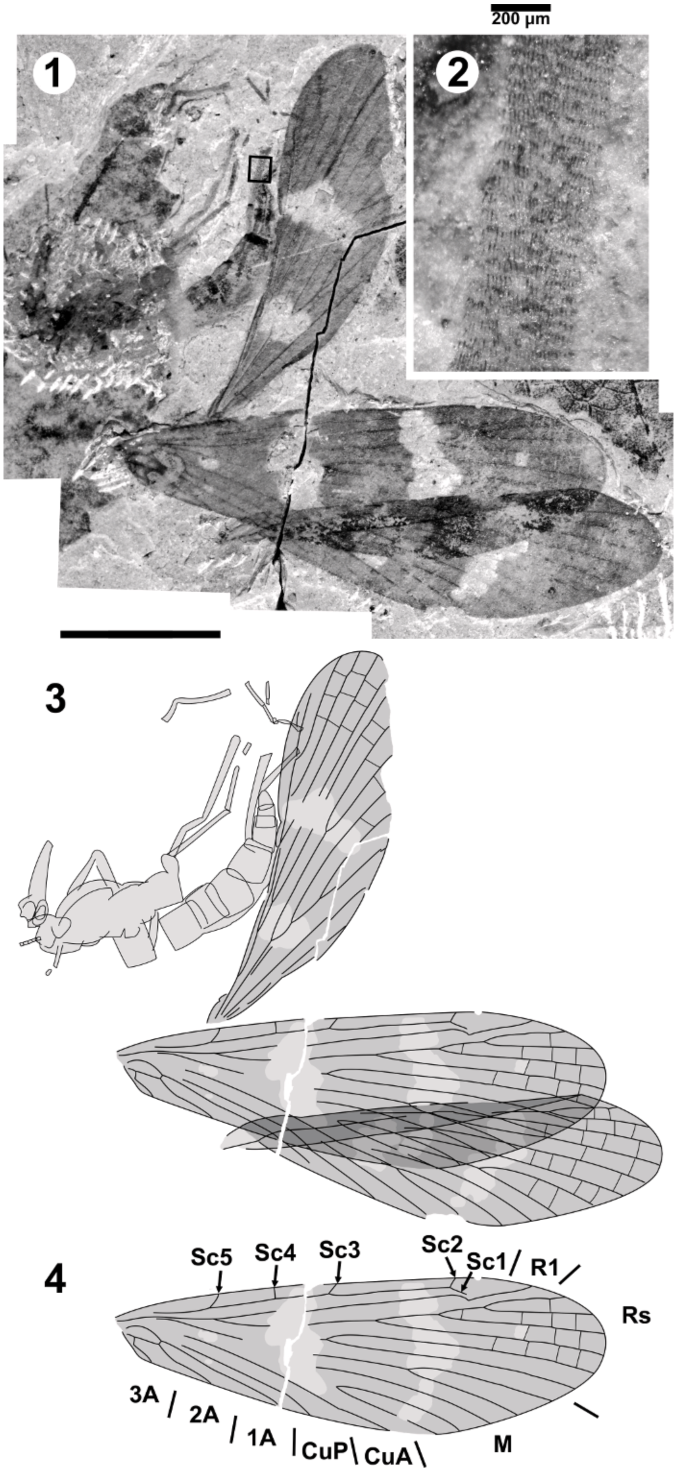

FIGURE 1—*Eorpa ypsipeda* n. gen. n. sp. F-1539, McAbee locality. *1*, photograph; *2*, closeup photograph of portion of the leg (area within square in *1*) showing annular pubescence, scale=200 µm; *3*, drawing of *1*; *4*, forewing drawing. Scale=5 mm except where noted.

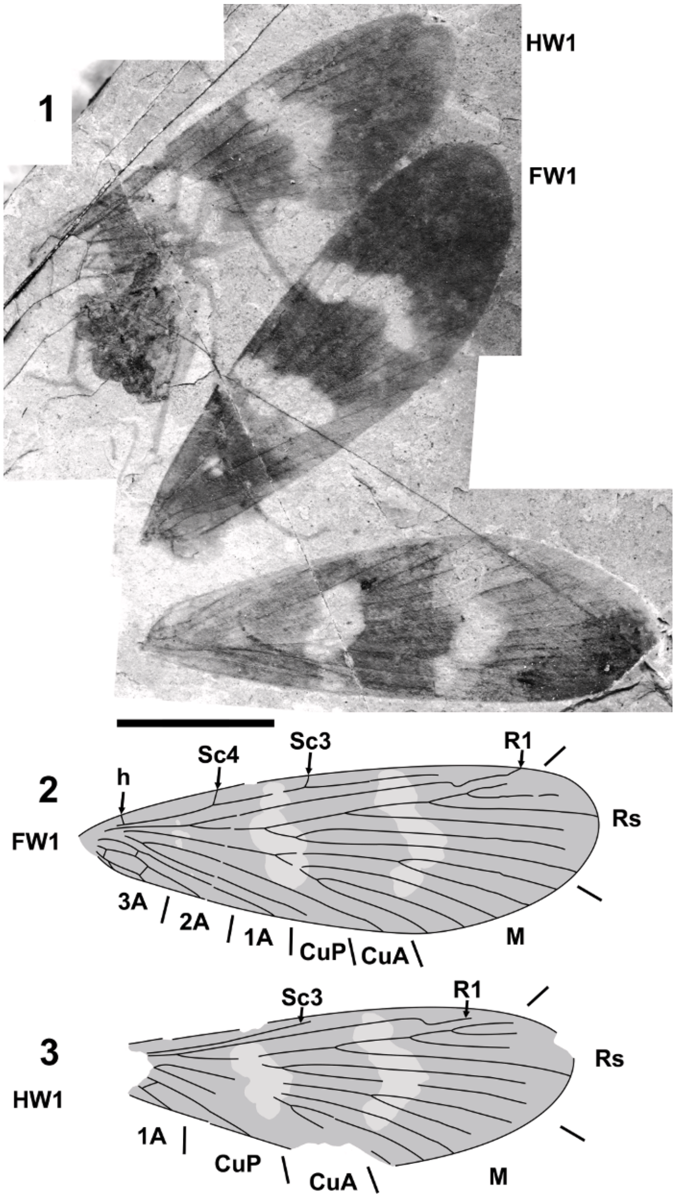

FIGURE 2—*Eorpa ypsipeda* n. gen. n. sp. F-1538, wings and body parts (McAbee): *1*, photograph of all four wings (two overlapping); *2*, drawing of forewing; *3*, drawing of hind wing. Scale=5 mm.

3) forewing and hind wing color pattern dark with distinct spots and fascia (see description); 4) shape, ratio of length/width ~3.

Description.—An *Eorpa* with the following: head capsule with prolonged downward extension, similar to that of Panorpidae. Thorax, generalized panorpoid morphology. Legs with annulate pubescence (Fig. 1.2). Forewing subtriangular-ovate, widest point ~2/3 length; length/width ~3; length ~15.5–16.5 mm, width ~5.0–6.0 mm; apex rounded; dark color patterning with two fasciae mid-wing, apical fascia larger, chevron-like, with point in wing centre facing apicad, basal fascia at times spot-like; in some specimens a small spot between basal fascia, wing base; spot between apical fascia, apex in some specimens. Sc with five branches: Sc1, Sc2 weak, short, fork in pterostigmal region; Sc1 oblique, joining R1, Sc2 straight, joins C perpendicular; Sc1+2, Sc3 branch about mid-wing, Sc3 strong, short, joins C oblique angle; Sc4, Sc5 weaker than Sc3, roughly evenly spaced between Sc3, humeral vein. Humeral vein short, crossvein-like near wing base. Hind wing as forewing, except average ~90 percent forewing size and slightly narrower at base. Color pattern as in forewing, except: sometimes with reduced basal fascia; without basal spot; apical spot variable (see remarks). Sc1+2 crossvein-like to join R1 to pterostigma, then (Sc2 or Sc1+2?) perpendicular to C; Sc3 joins C at low angle; Sc4, Sc5 usually weak (see remarks); CuA joins with, separates from M, CuP joins with, separates from 1A. Abdomen, external genitalia similar gross

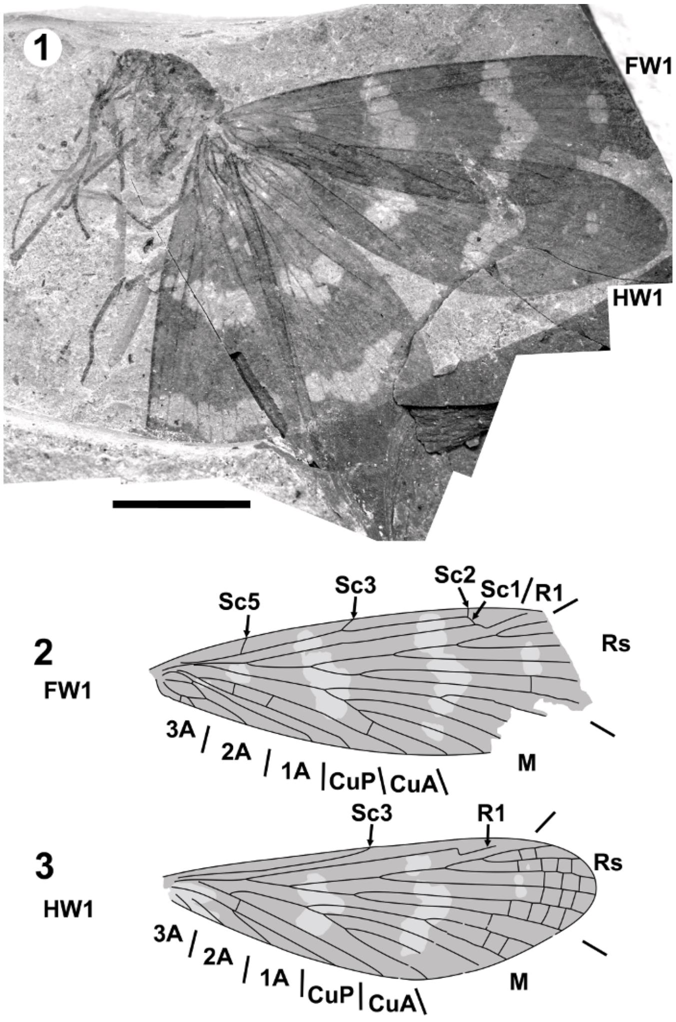

FIGURE 3—*Eorpa ypsipeda* n. gen. n. sp. F-1537, a mostly complete specimen (McAbee): *1*, photograph; *2*, forewing drawing; *3*, hind wing drawing. Scale=5 mm.

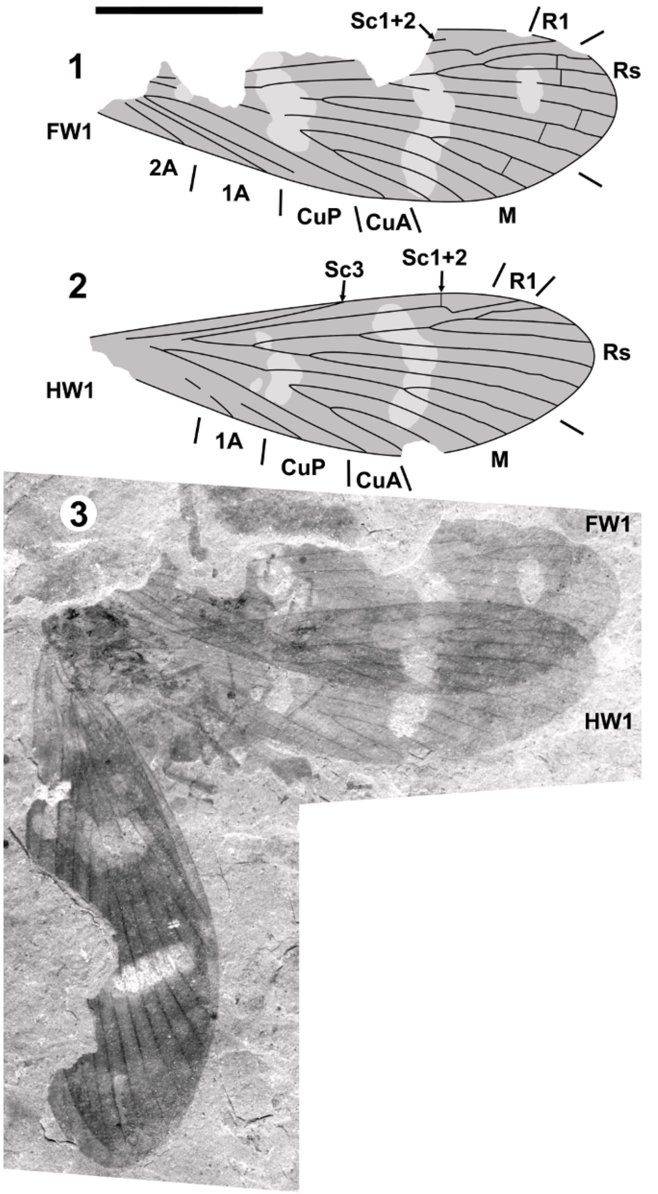

FIGURE 4—*Eorpa ypsipeda* n. gen. n. sp. 2003.2.3-CDM-027, a partially complete specimen (McAbee): *1*, photograph; *2*, forewing drawing; *3*, hind wing drawing. Scale=5 mm.

morphology as Panorpidae (male) as known (poorly preserved); (female) similar to that in Panorpidae.

Etymology.—The specific epithet is formed from the Greek *ypsipeda*, meaning "highlands", referring to the habitat of these insects.

Types.—Holotype 2003.2.6-CDM-030 (part, no counterpart): a forewing overlapping a hind wing with the second hind wing preserved nearby; McAbee locality; in the collection of CDM. Labeled HOLOTYPE *Eorpa ypsipeda* Archibald, Mathewes et Greenwood, 2013. Paratypes (all McAbee locality): 1) 2003.2.2-CDM-026 (part only), Figure 10.1, a partial forewing; CDM collection; 2) 2003.2.4-CDM-028 (part only), Figure 10.2, a mostly complete forewing; CDM collection; 3) TMP 83 39 1133 (part, counterpart), Figures 6, 10.19, an almost complete female missing one hind wing; RTMP collection; 4) 2003.2.8-CDM-032 (part, counterpart), Figure 10.16, a forewing overlaying a second wing; CDM collection; 5) 2003.2.9-CDM-033 (part only), Figure 10.4, a forewing; CDM collection; 6) F-986, 7 (part, counterpart), Figure 10.3, a forewing; TRU collection; 7) F-991 (part, counterpart), Figure 10.13, a forewing, two hind wings; TRU collection; 8) F-1024 (part only), Figures 8.1, 10.6, hind wing, forewing, and male terminalia; TRU collection; 9) F-984 (part only), Figure 10.5, a hind wing; TRU collection; 10) F-1536 (part only), Figure 10.7, hind wing; TRU collection; 11) F-1134, 5 (part, counterpart), Figure 10.8, a hind wing; TRU collection; 12) 2003.2.5-CDM-029 (part, counterpart), Figures 5, 10.9, a body missing the abdomen, forewing and hind wing; CDM collection; 13) 2003.2.3-CDM-027 (part only), Figures 4, 10.10, parts of the body and parts of four wings; CDM collection;14) F-1537 (part, counterpart), Figures 3, 10.11, partial body, three partial wings and a complete hind wing; TRU collection; 15) UWBM 78044 (part only), Figure 7, an almost complete male, with basal part of one forewing missing; UWBM collection; 16) F-1538 (part only), Figures 2, 10.12, four complete wings and body parts; TRU collection; 17) F-1539 (part only), Figures 1, 10.17, a complete, but disarticulated female missing one forewing; TRU collection; 18) F-1191 (part, counterpart), Figure 10.20, a forewing missing the basal portion, a mostly complete hind wing; TRU collection; collected by unknown person; 19) UWBM PB4075 (part only), Figures 9, 10.14, a well preserved forewing and hind wing; UWBM collection; 20) 2003.2.7-CDM-031 (part, counterpart), Figure 10.18, apical portions of two wings, CDM collection. All

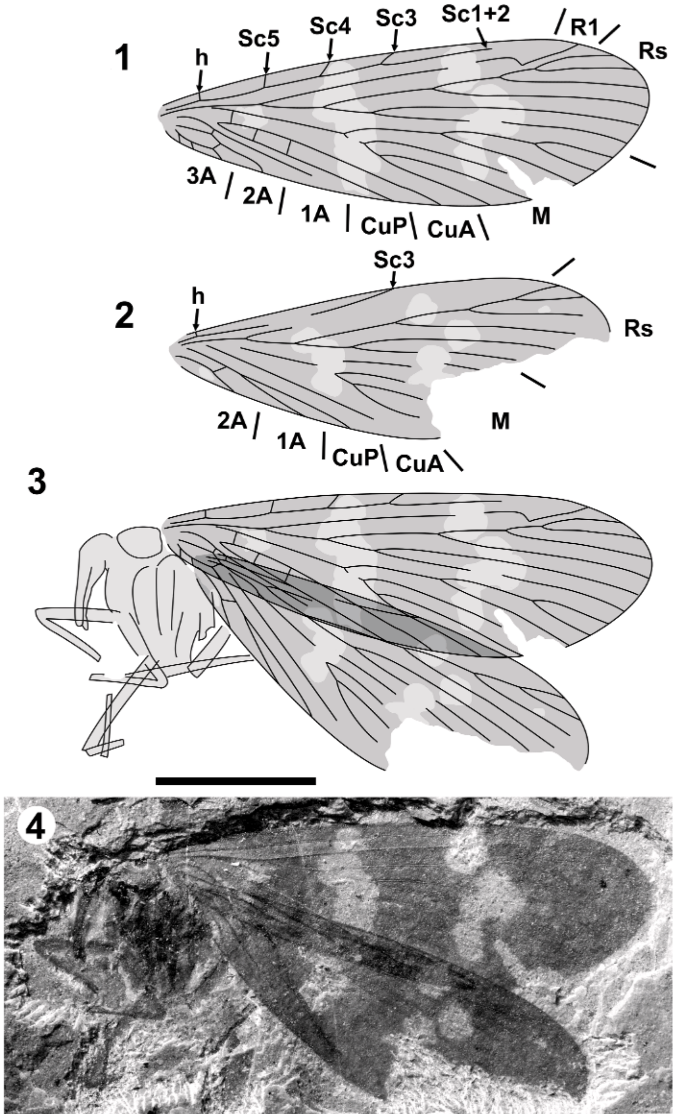

FIGURE 5—*Eorpa ypsipeda* n. gen. n. sp. 2003.2.5-CDM-029, a partially complete specimen (McAbee locality): *1*, forewing drawing; *2*, hind wing drawing; *3*, drawing; *4*, photograph. The branching of M1 in the forewing is considered adventitious, not seen in other specimens. Scale=5 mm.

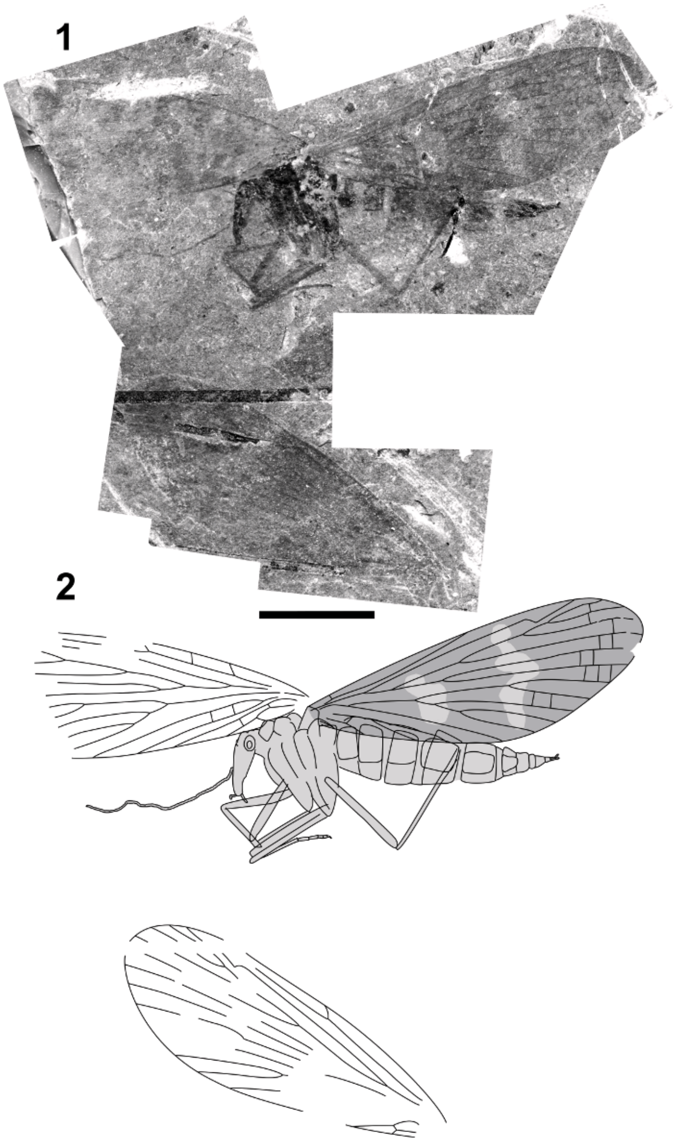

FIGURE 6—Female *Eorpa ypsipeda* n. gen. n. sp. TMP 83 39 1133, a complete specimen (McAbee): *1*, photograph; *2*, drawing (wing coloration omitted where vaguely preserved). Scale=5 mm.

labeled PARATYPE *Eorpa ypsipeda* Archibald, Mathewes et Greenwood, 2013. Further information is provided in Appendix.

Occurrence.—McAbee, and possibly Republic and Falkland; early Eocene.

Remarks.—Character state 1 readily distinguishes the forewings of *Eorpa ypsipeda* from those of *E. elverumi*, where branches Sc4 and Sc5 are absent. These species are further separated by character state 2, the lack of the stout crossveins listed as character states 4 and 5 in the diagnosis of *E. elverumi*. The hind wing of *E. ypsipeda* differs from that of *E. jurgeni* by its color pattern (character state 3) of spots and fasciae, while that of *E. jurgeni* is marbled; and by shape (character state 4), as the hind wing of *E. jurgeni* is broader.

While Sc4 and Sc5 are commonly seen in forewings of *E. ypsipeda*, they are rarely detected in hind wings of McAbee specimens (see Fig. 10.16: 2003.2.8-CDM-032; 10.20: F-1191; 10.21: UWBM 78044), quite possibly as an artifact of preservation (see Republic specimens, below).

If specimens from Republic and Falkland tentatively associated with this species (see below) do in fact belong to it, *E. ypsipeda* is the most widely distributed known insect species in the region. Multiple McAbee specimens alone make this the best represented of any insect species reported to date in the Okanagan Highlands (future work on the Bibionidae may change this), affording the greatest understanding of intraspecific variation in any from these deposits.

Variation in wing morphology (McAbee specimens, Fig. 10) include the following: 1) variation in size is well within the range reported by Ohm (1961) for modern species of *Panorpa*. Shape is consistent; 2) color patterning: the apical spot is present on forewings of six of sixteen insects (left and right wings do not differ in this regard, where known) where that region is preserved (Fig. 10). All are small, half very small. It is present on hind wings of two of fifteen insects, one very small; 3) branches of Rs: forewings of six insects have six branches of Rs, and three have seven. Hind wings have eleven with six branches, and four with seven. Where the fore- and hind wings of the same individual are preserved, there are equal numbers of branches on each. We find no correlation between wing size and number of branches; and 4) crossveins appear differentially preserved in known specimens, and so the

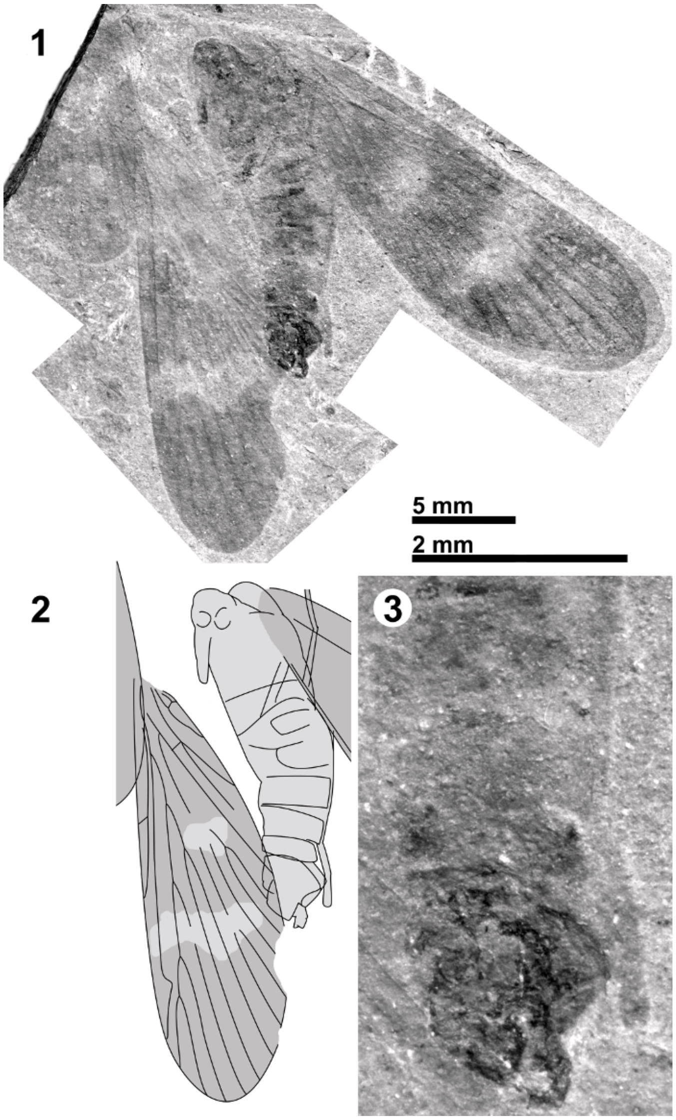

FIGURE 7—Male *Eorpa ypsipeda* n. gen. n. sp. UWBM 78044, a mostly complete specimen (McAbee locality): *1*, photograph; *2*, drawing (body, one hind wing, and portions of other wings drawn); *3*, close-up of male terminalia. Top scale=5 mm for *1*, *2*; bottom scale=2 mm for *3*.

extent of their variability is currently difficult to judge. The stout crossveins in part diagnostic of *E. elverumi*—character states 4 and 5 in its diagnosis—should, however, be visible in at least most of these if they were present, but were not detected in any specimen.

Other variation noted in these specimens appears to be adventitious in individuals, such as the sixth branch of M (M1 branched) in 2003.2.5-CDM-029 (Figs. 5, 10.9).

Eorpa ?ypsipeda
Figures 11–14, 16.6–16.14

1992 Ephemeroptera sp. indet.; Lewis, p. 17, pl. 1 fig. A. (UWBM 57198)

1993 Ephemeroptera sp. indet.; Lewis and Wehr, p. 36, fig. 2B. (UWBM 57198)

Material.—All specimens from Republic, details provided in the Appendix.

Exposure not known: 1) UWBM 57198, Figure 16.14. Exposure B4131: 2) SR 01-06-02, Figures 11, 16.6; 3) SR 08-35-04, Figures 12, 16.8, 22; 4) SR 08-35-07, Figure 16.11; 5) SR

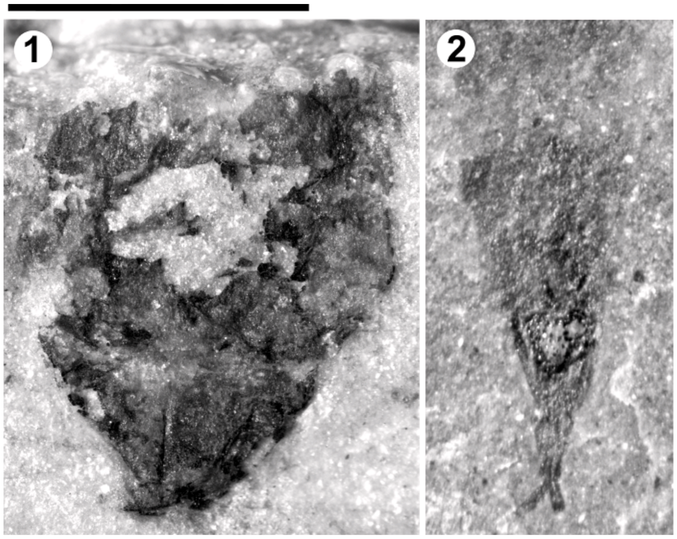

FIGURE 8—Male and female *Eorpa ypsipeda* terminalia (McAbee locality): *1*, male external genitalia (F-1024); *2*, female external genitalia (TMP 83 39 1133). Scale=2 mm.

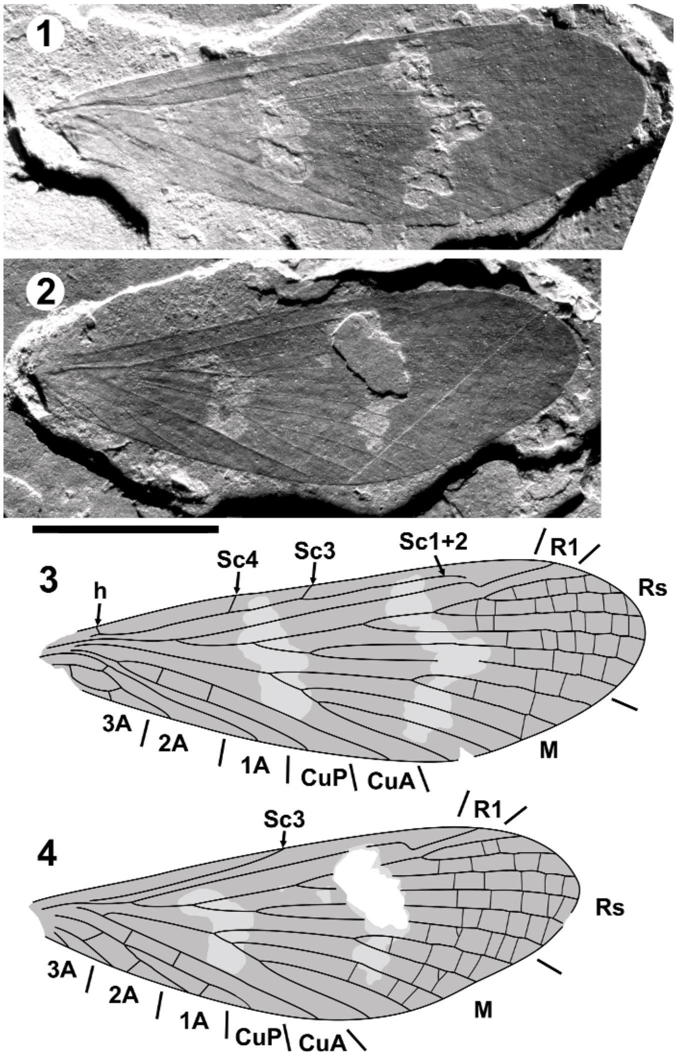

FIGURE 9—*Eorpa ypsipeda*, UWBM PB4075 (McAbee): *1*, photograph of a forewing; *2*, photograph of a hind wing; *3*, drawing of forewing in *1*; *4*, drawing of hind wing in *2*. Scale=5 mm.

09-11-01, Figures 14, 16.7; 6) SR 05-03-19, Figures 13, 16.9; 7) SR 10-02-04, Figure 16.12; 8) SR 12-004-002, Figure 16.10. Exposure S103: 9) SRUI 99-92-23, Figure 16.4.

Occurrence.—Klondike Mountain Formation localities B4131, S100, and S103 in the Republic region; early Eocene.

Remarks.—Although these Republic specimens bear resemblance to the *Eorpa ypsipeda* specimens from the McAbee locality upon which the species is based, we hesitate to firmly assign them to this species by their greater morphological variability than is displayed among the specimens of the more morphologically conservative McAbee assemblage. While it is possible that at least some of these may belong to *E. ypsipeda*, they might also represent one or more separate species (Fig. 16). Larger numbers of future specimens are needed to clarify this. The Republic forewing most similar to those of the McAbee *E. ypsipeda* (SR 01-06-02) has a prominent apical spot (Fig. 16.6), which is present in few forewings of the McAbee insects (above). The four hind wings with the apical region preserved all bear a prominent spot that is present in only two of fourteen McAbee *E. ypsipeda* hind wings. It's possible that this represents a color variant of *E. ypsipeda* that was more prevalent at Republic, either regionally (~290 kilometers separate them) or temporally (roughly a couple of million years later). The single forewing in this group has seven branches of Rs, as do three of five (determinable) hind wings. Sc4 and Sc5 are distinctly visible in most (six of seven) hind wings, unlike McAbee *E. ypsipeda* hind wings, where these are detected in few specimens (above); this, however, may be an artifact of differing diagenetic processes.

Eorpa elverumi new species
Figures 15, 16.1, 16.5

Diagnosis.—Forewing distinct by 1) lack of Sc4, Sc5; 2) mostly light coloration, darker in pterostigmal region, apparently a very light or hyaline fascia across mid-wing; 3) broad, length/width 2.2; 4) strong crossveins connecting Rs3+4, M1+2 ("a" in Fig. 15); 5) connecting M3+4, CuA ("b" in Fig. 15).

Description.—An *Eorpa* with character states as provided in the diagnosis.

Etymology.—The specific epithet is a patronym formed from the surname of Mr. John Elverum, who collected of the holotype, in recognition of this and his assistance in general collecting at Republic.

Types.—Holotype: SRUI 08-07-07a, b (part and counterpart); Figures 15, 16.5; a mostly well-preserved forewing; SR collection; labeled: HOLOTYPE *Eorpa elverumi* Archibald, Mathewes et Greenwood 2013. Paratype: SRUI 08-02-01a, b (part, counterpart); Figure 16.1; most of the basal portion of a forewing with some tearing around R1 (R1 present on part only); SR collection; Republic locality S100; labeled: PARATYPE *Eorpa elverumi* Archibald, Mathewes et Greenwood 2013.

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

Remarks.—Forewings of *Eorpa elverumi* are easily distinguished from those of *E. ypsipeda* by character state 1, their lack of Sc4 and Sc5; by their distinctive coloration (character state 2); by their broader shape (character state 3); and by character states 4 and 5, their strong crossveins connecting Rs3+4 and M1+2 and connecting M3+4, CuA. Although the hind wing of *E. elverumi* is unknown, its forewing indicates a distinct separation from *E. jurgeni* by character state 2, 4 or 5.

The absence of Sc4 and Sc5 is confident by the clearly preserved region of the holotype forewing where they would surely be seen if present. The robust crossveins mentioned in the diagnosis, distinctive coloration, and wider, notably stouter shape of the forewing also readily distinguish this species. This shape is unlikely an artifact of plastic distortion (see SRUI 99-92-23 from locality S103, below), as the paratype (SRUI 08-02-01) is also wide. Such distortion has never been noted in fossils from the extensively sampled B4131 locality.

In the holotype, veins in the basal region of the wing are highlighted by distinctive membrane coloration around them, further increasing their visibility, although this is not seen (preserved?) in the paratype. Further to the crossveins mentioned in the diagnosis ("a" and "b" in Fig. 15), other stout crossveins distal to those connect M and CuA in the holotype; some appear in roughly those positions in some specimens of *E. ypsipeda* (forewing: Fig. 10.1, 10.11) and Republic hind wings *E. ?ypsipeda* (Fig. 16.7, 16.8, 16.13). This is absent in all other forewings of Eorpidae reported here except in *E. ypsipeda* specimen 2003.2.2-CDM-026 (Fig. 10.1). Other, more distal crossveins connecting Rs and M (e.g., see Fig. 16.6) appear as the weaker crossveins that are generally detected scattered throughout the distal portions of wings that are well preserved.

The Republic hind wing, SR 95-10-03 (Fig. 16.13) presents a problem. It bears the diagnostic character states of the forewing of *E. elverumi* 2 through 5; however, Sc4 and Sc5 are clearly present, contrary to diagnostic character state 1. It's possible that the presence of these veins in both the fore- and hind wing was ancestral, and lost in the forewing only. We treat SR 95-10-03 as *Eorpa* incertae sedis until a future specimen with associated fore- and hind wings resolves this question.

Eorpa jurgeni new species
Figure 17

2000 Panorpidae sp. indet.; Archibald and Mathewes, p. 1449, fig. 8.

Diagnosis.—An *Eorpa* hind wing with 1) marbled coloration; 2) broad shape; 3) lacking strong crossveins connecting Rs3+4, M1+2 ("a" in Fig. 15); and 4) connecting M3+4, CuA ("b" in Fig. 15).

Description.—Hind wing length 16 mm preserved (complete estimated ~17–18 mm), width 8 mm; venation as in *E. ypsipeda* hind wing, except Rs branches from R_1 basally; 5 branches of Rs detected, but likely further missing apical portion; Cu apparently branching close to base (from CuA, CuP position, Cu basad of these branches not preserved), CuA joining with M and then separating (distance of joining not preserved), CuP joined with 1A, separating; 1A straight (basal portions not visibly preserved), 2A slightly curved, 3A short. Crossveins detected: 3 rs-m, 3 m2-m3, 2 m3-m4a, 2 cua-cup, likely more; 1 of 1a-2a.

Etymology.—The specific epithet is a patronym formed from the given name of Mr. Jurgen Mathewes, brother of R.W.M., in recognition of his many years of collecting plant and insect fossils at Quilchena and donating them to SFU.

Types.—Holotype: Q-0096, a hind wing missing the apical portion (part only); Figure 17; SFU collection; labeled HOLOTYPE *Eorpa jurgeni* Archibald, Mathewes et Greenwood, 2013.

Occurrence.—early Eocene; Quilchena.

Remarks.—The *Eorpa jurgeni* hind wing is distinct from that of *E. ypsipeda* by any of character states 1 through 4. Although the hind wing of *E. elverumi* is unknown, its forewing indicates a distinct separation from *E. jurgeni* by character state 1, 3 or 4.

This wing is large and broad. Q-0096 is 8 mm wide; all other hind wings in this collection are between 4.5 to a maximum of 5 mm. The broadest hind wing of E. *ypsipeda* has a length/width ratio of 2.8, while Q-0096 is broader yet at 2.2 (reconstructed whole). The marbled color pattern of Q-0096 is distinctive within the genus, easily distinguished from that of both the fore- and hind wings of *E. ypsipeda*, which vary as above. Color patterning is conservative between the fore- and hind wings of *E. ypsipeda*, which we reasonably presume to be consistent in the genus, readily separating the marbled hind wing of *E. jurgeni* from the

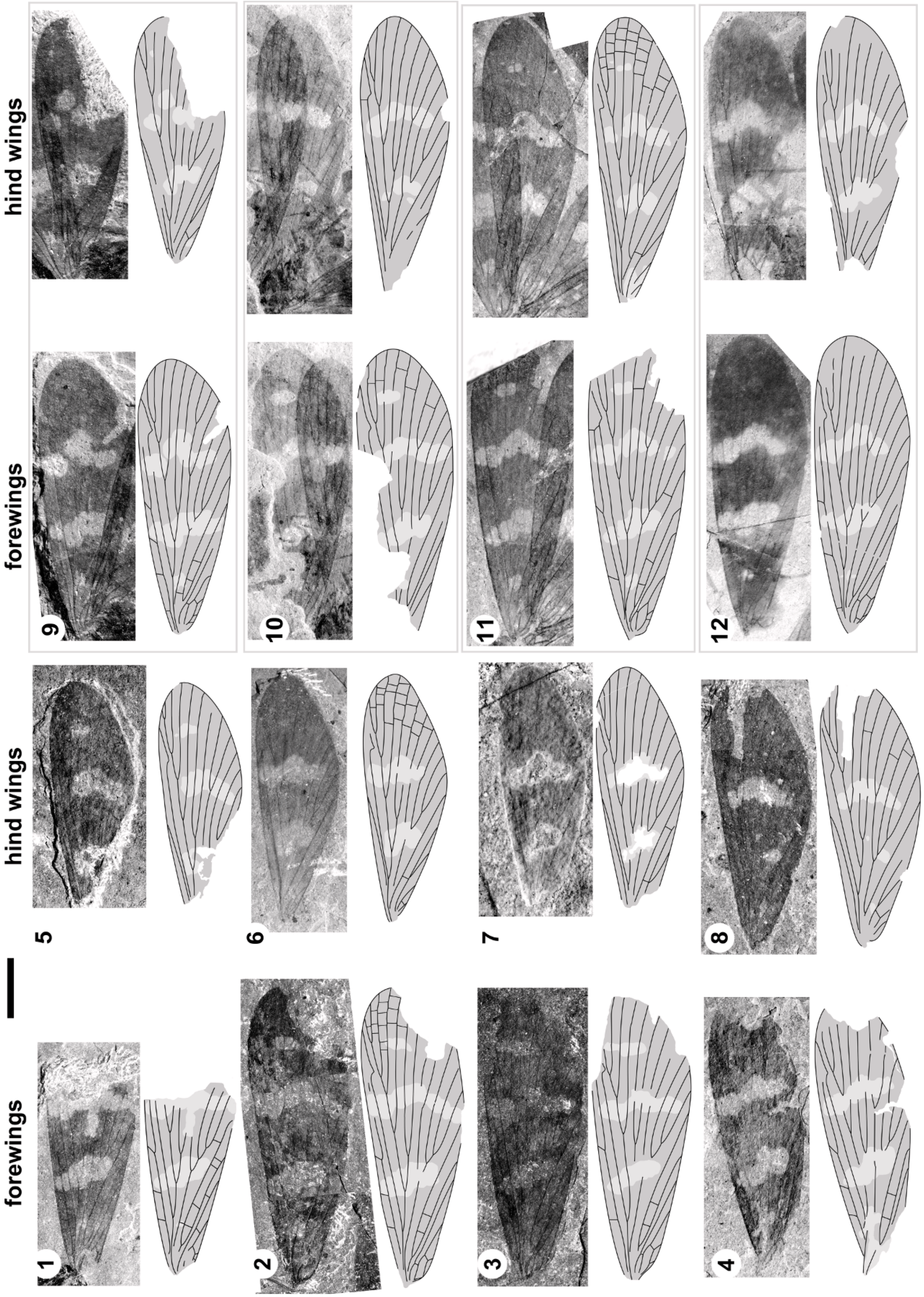

FIGURE *10*—Comparative *Eorpa ypsipeda* wings from the McAbee locality, photographs and drawings (photographs without drawings where overlapping wings obscure details of venation): *1*, 2003.2.2-CDM-026; *2*, 2003.2.4-CDM-028; *3*, F-986; *4*, 2003.2.9-CDM-033; *5*, F-984; *6*, F-1024; *7*, F-1536; *8*, F-1134-5; *9*, 2003.2.5-CDM-029; *10*, 2003.2.3-CDM-027; *11*, F-1537; *12*, F-1538; *13*, F-991; *14*, UWBM PB4075; *15*, 2003.2.6-CDM-030; *16*, 2003.2.8-CDM-032; *17*, F-1539; *18*, 2003.2.7-CDM-031; *19*, TMP 83 39 1133; *20*, F-1191; *21*, UWBM 78044. Forewings and hind wings as indicated. Scale=5 mm.

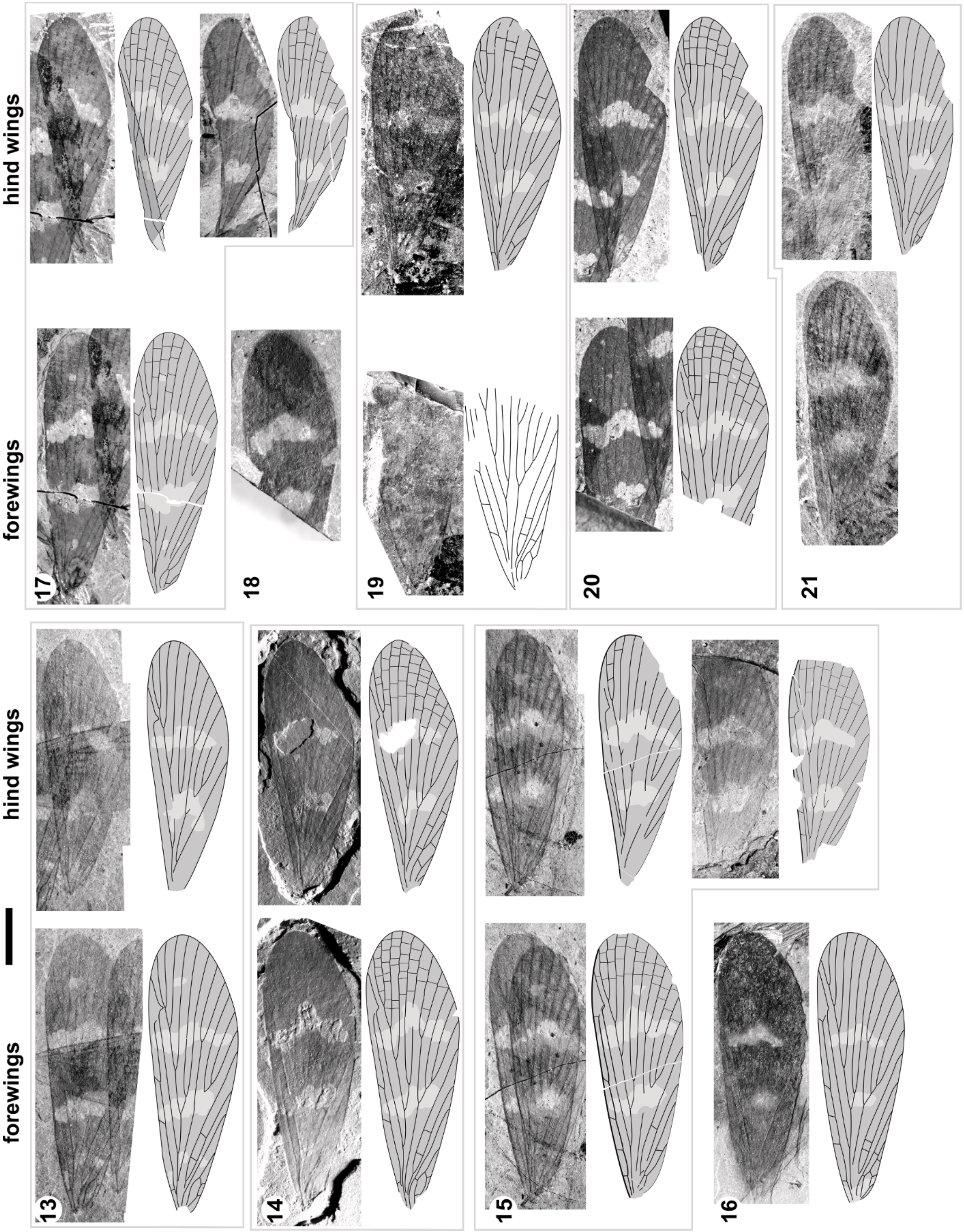

FIGURE *10*—Continued.

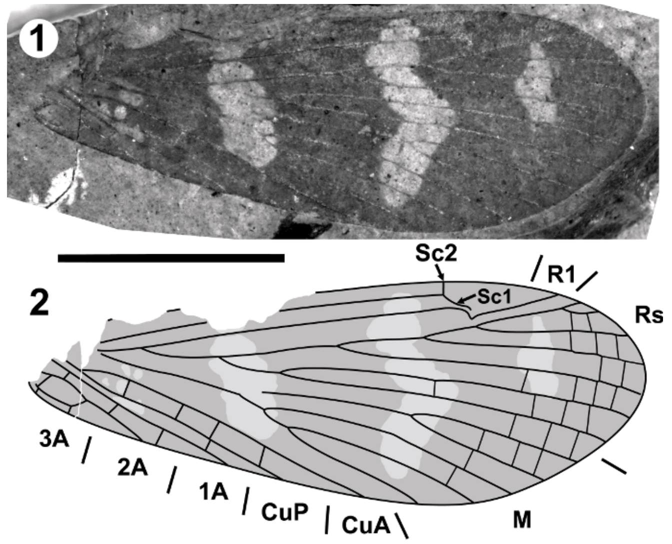

FIGURE 11—*Eorpa ?ypsipeda* SR 01-06-02, a forewing (Republic): *1*, photograph; *2*, drawing. Scale=5 mm.

forewing of *E. elverumi* with its simple, distinct patterning. The stout crossveins listed as character states 4 and 5 in the diagnosis of *E. elverumi* are absent in the holotype of *E. jurgeni*. It is unlikely that the Quilchena forewing Q-5032 is conspecific with Q-0096 by its coloration as preserved.

EORPA incertae sedis

Figures 16.3, 16.4, 16.13, 18, 19

Material.—SRUI 99-83-53 (Fig. 16.3) and SRUI 99-92-23 (Fig. 16.4); both forewings, broken, portions shifted; SR collection. SR 95-10-03 (Fig. 16.14); a broken hind wing; SR collection. Q-5032a, b (part and counterpart); a rather complete but damaged and partially stained forewing; SFU collection (Fig. 18). RBCM.EH2012.004.0001.001 (Fig. 19); a partial, very damaged forewing; RBCM collection.

Description.—Q-5032. Forewing: length ∼16 mm preserved (∼16.5 estimated whole), width 5.5 mm; color pattern: specimen deeply stained, but apparently mostly dark with single broad fascia mid-wing; venation: preserved portions apparently like *E. ypsipeda* except strong crossveins connecting Rs3+4, M1+2 (“a” in Fig. 18), connecting M4, CuA (“c” in Fig. 18); Rs with six branches.

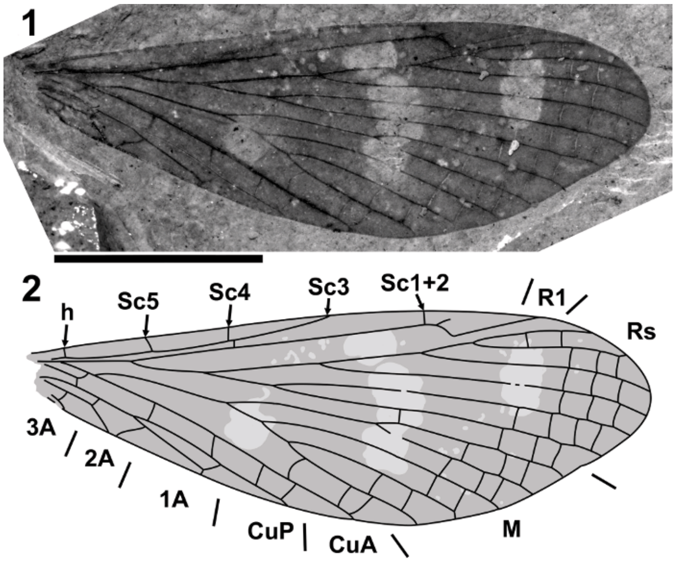

FIGURE 12—*Eorpa ?ypsipeda* SR 08-35-04, a hind wing (Republic): *1*, photograph; *2*, drawing. Scale=5 mm.

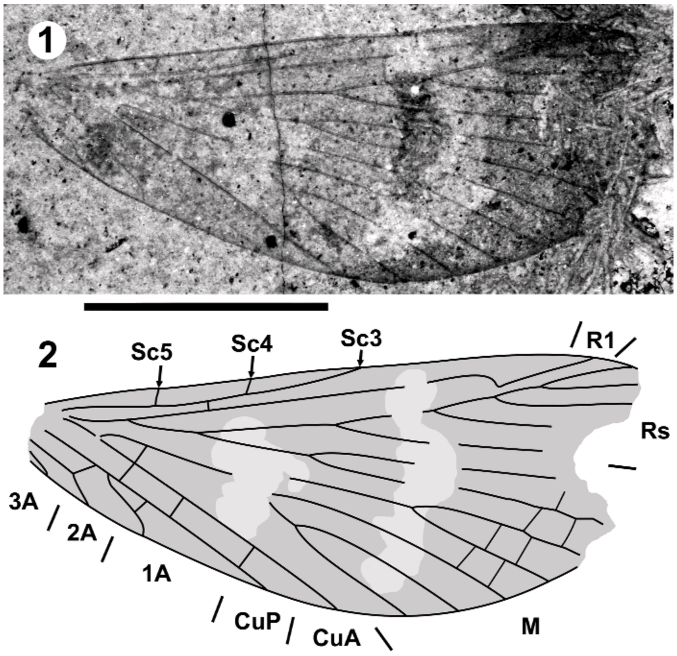

FIGURE 13—*Eorpa ?ypsipeda* SR 05-03-19, a hind wing (Republic): *1*, photograph; *2*, drawing. Scale=5 mm.

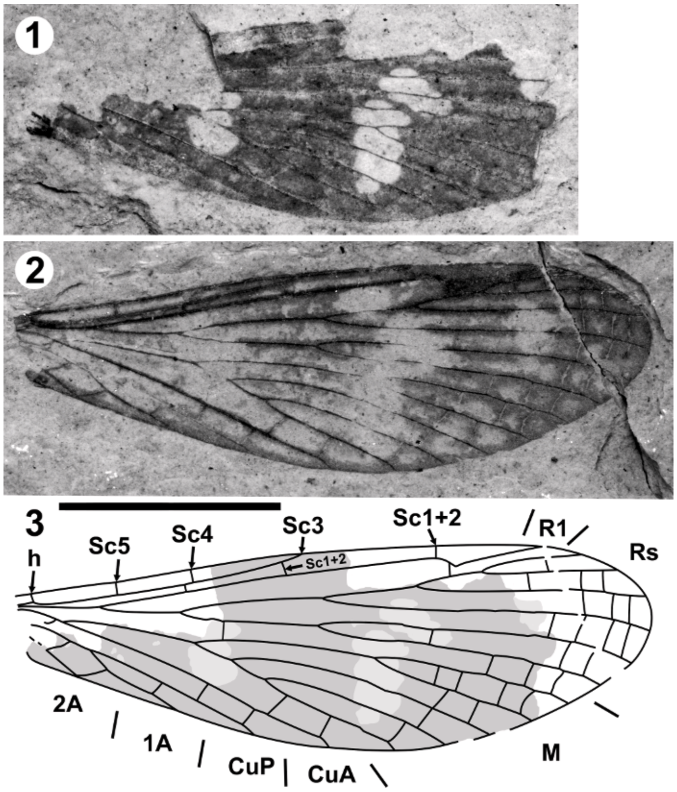

FIGURE 14—*Eorpa ?ypsipeda* SR 09-11-01, a hind wing (Republic): *1*, photograph of part (a side), showing color pattern; *2*, photograph of counterpart (b side); *3*, drawing. All to scale=5 mm.

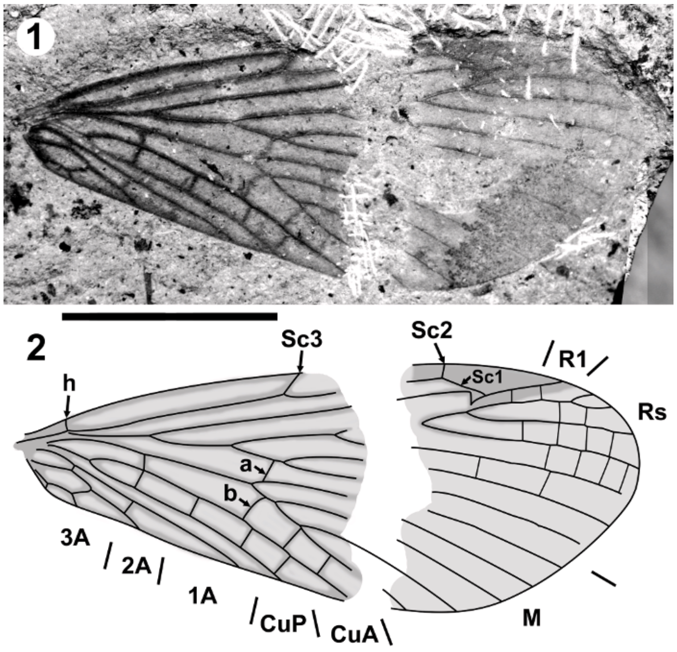

FIGURE *15*—Holotype forewing of *Eorpa elverumi* n. gen. n. sp. SRUI 08-07-07 (Republic): *1*, photograph; *2*, drawing. Strong crossveins labeled a-b are those connecting (a) Rs3+4 and M1+2; (b) M3+4 and Cua. Scale=5 mm.

Occurrence.—Q-5032: early Eocene; Quilchena. SRUI 99-83-53 and SRUI 99-92-23: early Eocene; Republic locality S103. SR 95-10-03: early Eocene; Republic locality B4131. RBCM.EH2012.004.0001.001: early Eocene; Falkland.

Remarks.—While we believe that these insects belong to *Eorpa*, they are too poorly preserved to assign to any species. SR 95-10-03 is discussed above (see *E. elverumi*).

Q-5032 is the only eorpid forewing known from Quilchena. The strong crossveins noted in the description seem distinct from those of *E. ypsipeda* (compare Figs. 15, 16.1 and 18). The distinct rs-m crossvein ("a" of Figs. 15, 18) is present in Q-5032, and a curved m-cu crossvein labeled "c" in Figure 18 appears placed in almost the same position as the similar crossvein labeled "b" in Figure 15. *Eorpa elverumi* also has a similar color patterning as preserved, with a single fascia mid-wing. The region where Sc4 and Sc5 would be positioned in *E. ypsipeda*—veins that are distinctly absent in *E. elverumi*—is missing in this specimen. Q-0532 is not as broad as *E. elverumi*, however, this is difficult to evaluate, and the wing is somewhat damaged. While it is possible that this specimen belongs to *E. elverumi*, we prefer to not even tentatively assign it to any species, awaiting new, less damaged specimens to clarify its position.

SRUI 99-83-53 and SRUI 99-92-23 are the only eorpids known from Republic locality S103. The plastic distortion apparent in SRUI 99-92-23 is consistent with compression/extension of fossil-bearing shale, extremely unusual in fossils from Okanagan Highlands localities. The lithology of S103 shale appears distinctly different from that of other sampled Klondike Mountain Formation sites, suggesting the possibility that this distortion might be peculiar to this locality.

RBCM.EH2012.004.0001.001 is the only known eorpid specimen from Falkland, establishing the presence of the family there.

EORPIDAE incertae sedis
Figures 16.2, 20

Material.—SR 93-14-05, a narrow forewing missing the apical third; SR collection.

Occurrence.—Early Eocene; Republic locality UWBM B4213.

Remarks.—Aside from shape, all preserved characters of SR 93-14-05 agree with those of *Eorpa ypsipeda*. Its long and narrow shape, however, is notably different from that of other known members of the family. While the preserved portion of this forewing indicates that the complete wing was within the length range of known *Eorpa* species, its width of three millimeters is considerably narrower. Insects from this site are little known, and so the likelihood of plastic distortion as seen in SR 99-92-23 from site S103 cannot be judged. While we suspect that this wing might belong to a different species, we refrain from proposing this pending confirmation of its morphology by new specimens.

THE EOCENE PANORPOID RADIATION AND EXTINCTIONS

Although much work remains to be done, a broad outline is emerging of the evolutionary trajectory of Cenozoic insects. The order level remained stable throughout. At the species level, however, high diversity that is today characteristic of low latitudes extended at least into higher mid-latitudes in the Eocene, indicating a subsequent net global decline (Archibald et al., 2010, 2013). Families continued to accumulate toward their modern complement of almost a thousand with a rate of loss near zero, suggesting extinction resistance at that level (Carpenter, 1992; Labandeira and Sepkoski, 1993; Labandeira, 1994, 2005; Jarzembowski and Ross, 1996; Dmitriev and Ponomarenko, 2002; Belayeva et al., 2002; Grimaldi and Engel, 2005). Our literature search finds fourteen extinct insect families within the Cenozoic. These are distantly related among each other, apart from the exceptional cluster of panorpoid family extinctions considered here (Table 1; Fig. 21).

The Mesozoic orthophlebiid grade is in part characterized by their wings, which all bear the distinctive combination of a media with five branches in the forewing (possessing M4b) and four branches in the hind wing (lacking M4b). Modifications to this pattern help define two groups of Cenozoic panorpoids (Penny, 1975; Willmann, 1987) (Fig. 22).

The first group consists of those that lost M4b in the forewing, resulting in four branches of the media in both pairs. These include the Austropanorpidae, Panorpidae, and the Panorpodidae. The Jurassic Muchoriidae also lost M4b in the forewing (hind wing not known), although Willmann (1987) considered this unlikely to indicate a close relationship with these. In fact, Muchoriidae may not belong to the Panorpoidea (Ren et al. 2009).

Austropanorpidae.—A single species of *Austropanorpa* is known by two specimens from the Redbank Plains Series at Dinmore, Queensland (Riek, 1952, 1967; Willmann, 1977). The Dinmore forest was humid, mesothermal to possibly megathermal (Greenwood and Christophel, 2005), apparently quite different from the forests of the Northern Hemisphere Eocene Panorpoidea. Willmann (1987) suggested that the loss of M4b in the forewing in *Austropanorpa* might be convergent with the Panorpidae+Panorpodidae. Volcanics overlying the Redbank Plains Series have been dated at 45 mya, indicating an age no younger than early Lutetian, and while it is possible that these sediments are as old as Paleocene, they are generally thought to be Eocene (Vickers-Rich and Molnar, 1996).

Panorpidae.—The oldest previously known panorpid fossils were from late Eocene Baltic amber (Carpenter, 1954, Krzeminski and Soszynska-Maj, 2012) (although some authors assign a slightly older age to Baltic amber, here, we follow the estimate of Perkovsky et al. [2007], as most reasonable). Here, we report their presence in the Okanagan Highlands (Republic, McAbee), extending their temporal range to the early Eocene (Fig. 23).

Panorpodidae.—The oldest confident panorpodid is from Baltic amber (Carpenter, 1954), but the recent discovery of a likely member of this family in the early Eocene (51.91 ± 0.22

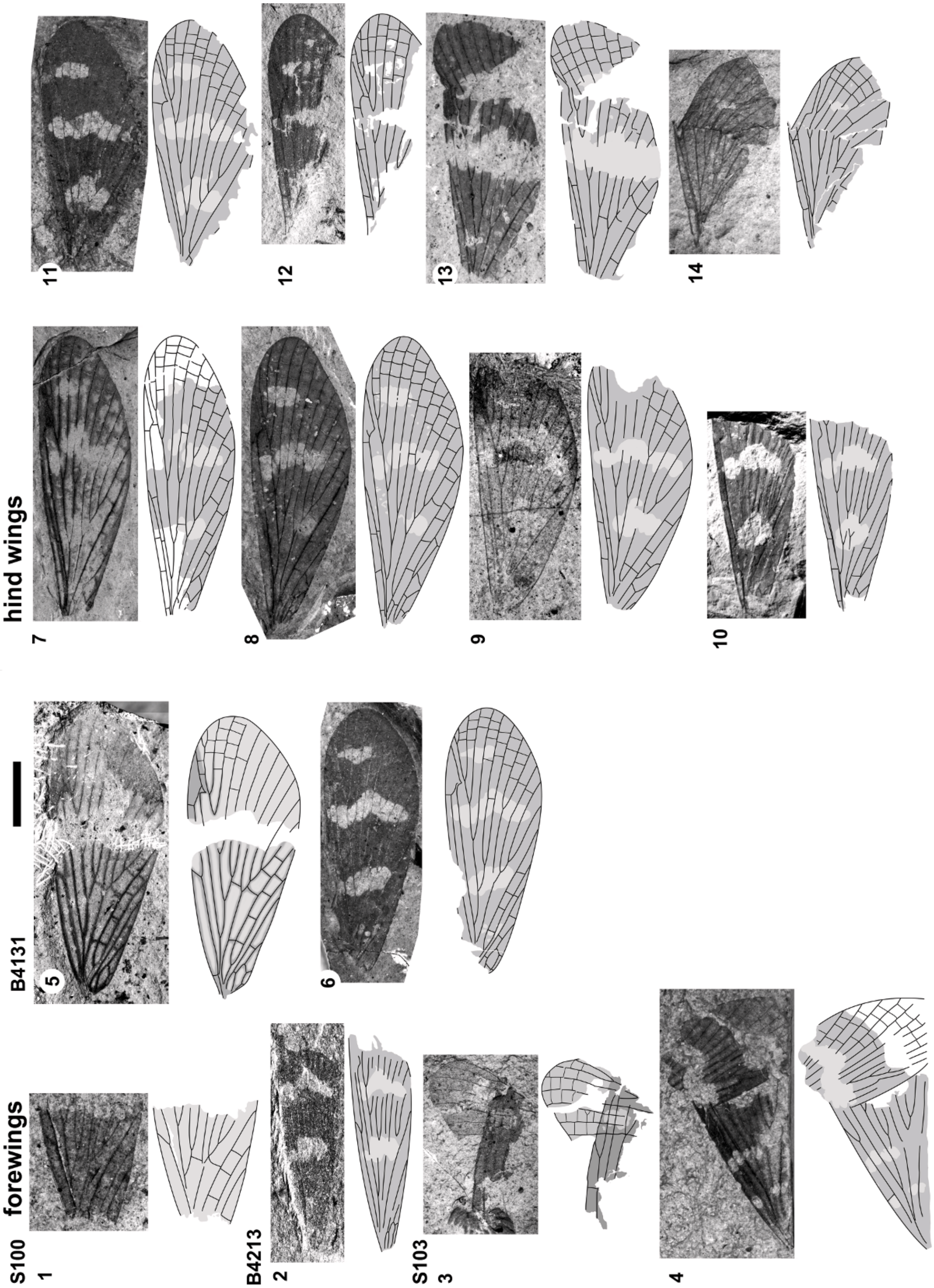

FIGURE *16*—Comparative wings of Eorpidae from the Klondike Mountain Formation in and near Republic. *1*, SRUI 08-02-01, exposure S100; *2*, SR 93-14-05, exposure B4213; *3*, SRUI 99-83-53, exposure S103; *4*, SRUI 99-92-23, exposure S103; *5–12*, exposure B4131: *5*, SRUI 08-07-07; *6*, SR 01-06-02; *7*, SR 09-11-01; *8*, SR 08-35-04; *9*, SR 05-03-19; *10*, SR 12-004-002; *11*, SR 08-35-07; *12*, SR 10-02-04; *13*, SR 95-10-03; *14*, UWBM 57198. Forewings, *1–6*; hind wings, *7–14*. All to scale=5 mm.

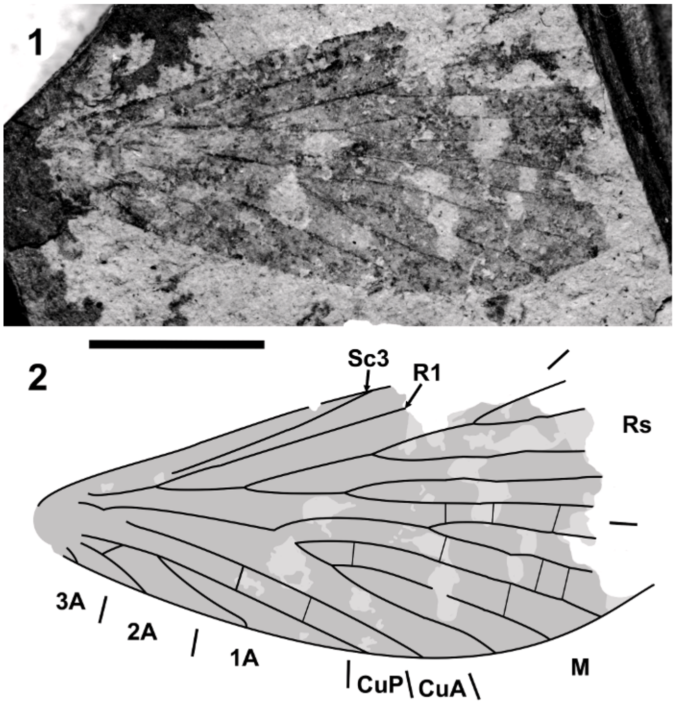

FIGURE 17—Holotype hind wing Q-0096, *Eorpa jurgeni* n. gen. n. sp. (Quilchena): *1*, photograph; *2*, drawing. Scale=5 mm.

Ma: Wilf et al., 2005a) of Laguna del Hunco, Patagonia, Argentina (Petrulevičius, 2009) provides support for its presence in Okanagan Highlands times as indicated by the occurrence there of its sister taxon, the Panorpidae. Laguna del Hunco was in a lowland setting with a mid-mesothermal MAT of 16.6 ± 1.3°C (Wilf et al., 2005a).

The second group consists of those families that possess M4b in the hind wing as well as the forewing, i.e., with five branches of the media in both wing pairs. These include the Dinopanorpidae, Holcorpidae, and Eorpidae—all of which are first seen at McAbee. This character state might well be homologous among them, suggesting that they constitute a monophyletic unit (Fig. 22). These are all known either from equable upper microthermal to lower mesothermal MAT uplands (Okanagan Highlands, Florissant), or sites that have not had detailed MAT analysis, but appear most likely to have had an equivalent climate by their similar elevation and/or flora set in the same latitude (Tadushi and Amgu: Archibald et al., 2005). None are known from the Eocene megathermal lowland localities with well-known, rich insect assemblages such as the Green River Formation in mid-continental United States or Messel, Germany (climates discussed and reviewed by Archibald et al., 2011b).

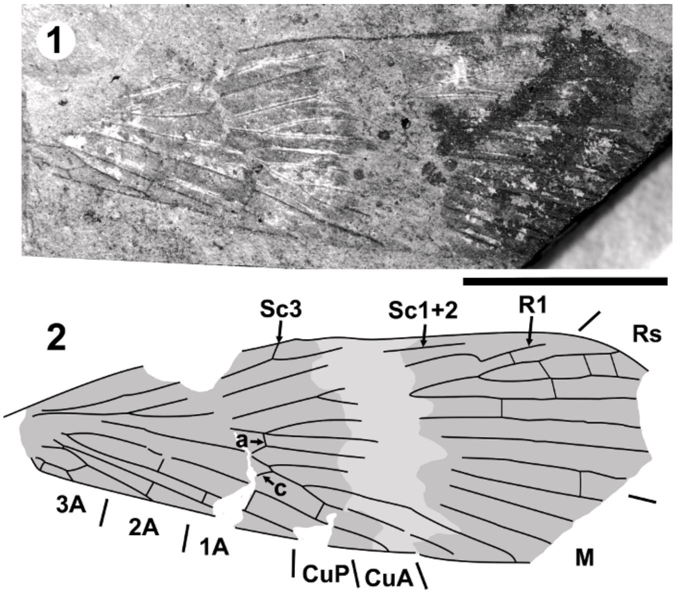

FIGURE 18—Forewing Q-5032 *Eorpa incertae sedis* from Quilchena: *1*, photograph; *2*, drawing (as others, drawn from both 'a' and 'b' sides). Crossvein labeled "a" as in Figure 15; crossvein labeled "c" connecting M4 and CuA, see text. Scale=5 mm.

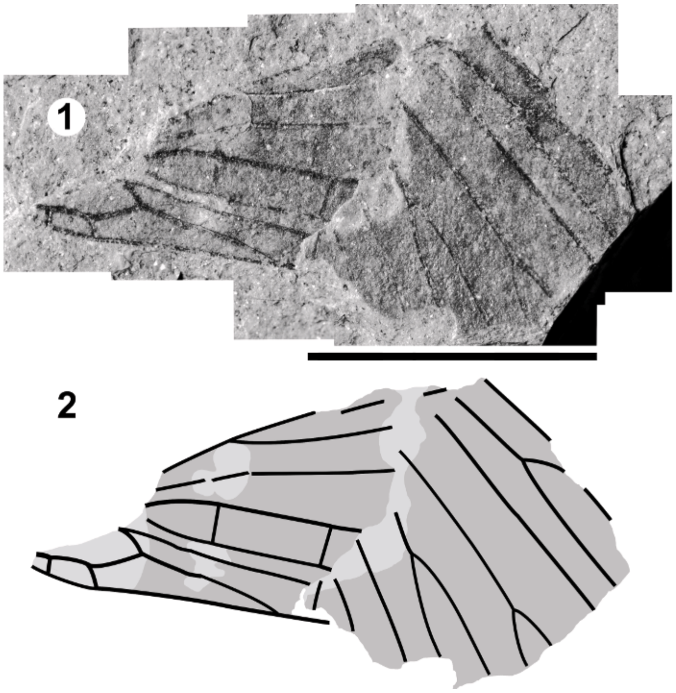

FIGURE 19—Forewing RBCM.EH2012.004.0001.001, *Eorpa incertae sedis* (Falkland): *1*, photograph, *2*, drawing. Scale=5 mm.

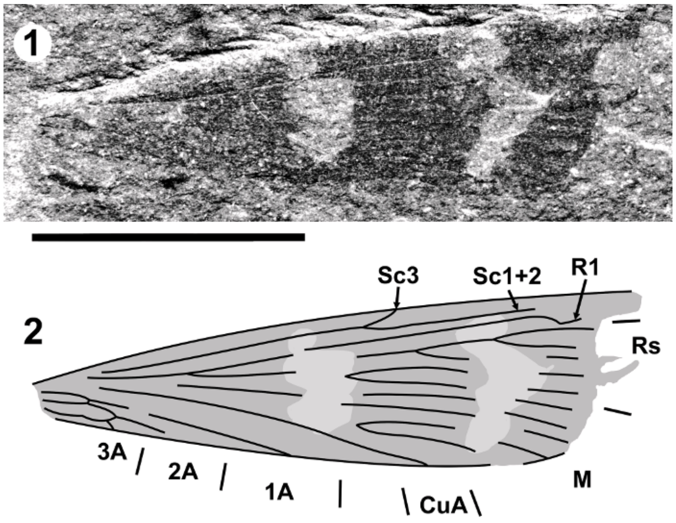

FIGURE 20—Forewing SRUI 93-14-05 (Republic exposure UWBM B4213): *1*, photograph; *2*, drawing. Scale=5 mm.

TABLE *1*—Extinct Cenozoic insect families. Others listed as extinct by Carpenter (1992) have been subsequently synonymized with living families. Some further enigmatic species known by incomplete specimens do not appear to fit any current family definition, e.g., the neuropteran *Oligogetes* (Makarkin, 1998).

Order	Suborder or Superfamily	Family
Odonata	Zygoptera	Sieblosiidae[1]
	Anisoptera	Palaeomacromiidae[2]
Blattodea		Cainoblattinidae[3]
Orthoptera	Caelifera	Promastacidae[4,5,6]
Hemiptera	Sternorrhyncha	Elektraphididae[5,6,7,8]
Strepsiptera		Mengeidae[5,7,9]
Mecoptera	Panorpoidea	Dinopanorpidae[5,10]
	Panorpoidea	Holcorpidae[12]
	Panorpoidea	Eorpidae[12]
	Panorpoidea	Austropanorpidae[13,14]
	Raptipeda	Cimbrophlebiidae[14,15]
Diptera	Brachycera	Eophlebomyiidae[5,6,16]
	Brachycera	Proneottiopilidae[5,6,16]
Hymenoptera	Symphyta	Electrotomidae[5,6,7,17]

[1] Jarzembowski and Ross (1996), [2] Petrulevicius and Nel (2002), [3] Nel et al (2005),[4] Kevan and Wighton (1981), [5] Carpenter (1992), [6] Labandeira (1994), [7] Grimaldi and Engel (2005), [8] Shcherbakov and Popov (2002), [9] Rasnitsyn (2002a), [10] Archibald (2005), [11] Archibald (2010), [12] this paper, [13] Riek (1952, 1967), [14] Willmann (1977), [15] Archibald (2009), [16] Blagoderov et al. (2002), [17] Rasnitsyn (2002b).

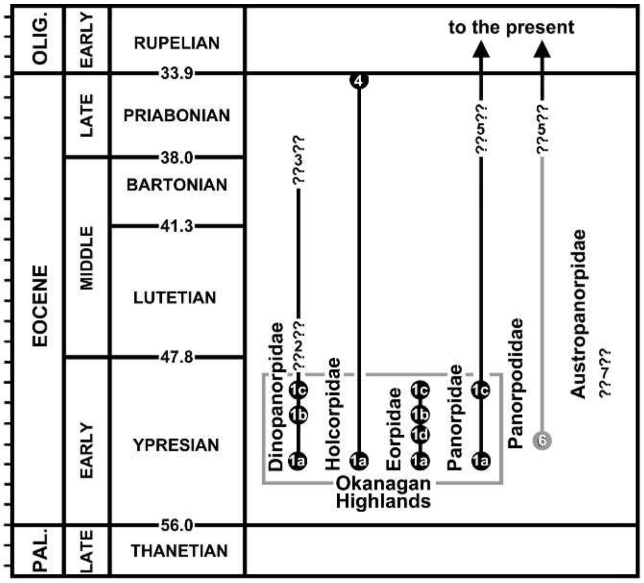

FIGURE *21*—Age and locality record of Panorpoidea in the Eocene. Localities: 1, Okanagan Highlands: 1a, McAbee, 1b, Falkland, 1c, Republic, 1d, Quilchena, (Dinopanorpidae is also known from the Okanagan Highlands locality at Horsefly River, BC, Canada, no radiometric age estimate); 2, Tadushi Formation, Primorye, Russia, age imprecisely known, might in part overlap Okanagan Highlands time; 3, Amgu locality, Primorye, Russia; 4, Florissant, Colorado, U.S.A.; 5, Baltic amber; 6, Laguna del Hunco, Patagonia, Argentina; 7, Redbank Plains Series, Queensland, Australia. Black dots indicate recent radiometric estimates of age; question marks indicate localities where the age is approximately estimated (Redbank Plains Series, Dinmore: see text); gray dot for Panorpodidae indicates that this family is provisionally established in the early Eocene (see text). Epoch/Age boundary dates from Gradstein et al. (2012).

Dinopanorpidae.—Originally known by single specimens from the Tadushi and Khutsin (at Amgu) Formations, both now considered Eocene (Otofuji et al., 1995; Popov and Grebennikov, 2001; M. Akhmetiev personal commun.). The family is most taxonomically diverse (six species) and abundant in the Okanagan Highlands (Archibald, 2005).

Holcorpidae.—*Holcorpa*, the single genus of the family, is known by two species: one with two specimens (Carpenter, 1931) from late Eocene Florissant, Colorado (34.07 ± 0.10 Ma: Evanoff et al., 2001) and a single specimen of a new species from McAbee (Archibald, 2010). Florissant and the Okanagan Highlands shared many common floral elements, e.g., as at McAbee, the most abundant leaves at Florissant belong to the Fagaceae (Manchester, 2001).

Eorpidae.—This family is only known by specimens reported here from the southern portion of the early Eocene Okanagan Highlands.

Origin and maintenance of Eocene panorpoid family diversity.—Modern panorpoid adults mostly inhabit the herbaceous understory of mesic and moist forests. Such forests in the seasonally equable early Eocene supported high levels of insect and plant diversities well into mid-latitudes (Archibald et al., 2010, 2013; Smith et al., 2012). By this time, incumbent advantage had been abandoned by extinct Mesozoic panorpoids, and increasingly complex angiosperm dominated forests had rebounded from K-Pg extinctions, creating rich, new conditions for the superfamily to flourish. Insect leaf herbivory ichnofossil data indicate destabilized food webs following the K/Pg extinction event, but recovery to diverse, balanced interactions by Okanagan Highlands times (Wilf and Labandeira, 1999; Labandeira, 2002; Labandeira et al., 2002; Wilf et al., 2003; Wilf and Johnson, 2004; Wilf et al., 2005a, 2005b; Wilf et al., 2006; Currano et al., 2008; Wappler et al., 2009; Wappler et al. 2012).

Their prolonged downward extension of the head capsule indicates that adult Eorpidae, Holcorpidae and Dinopanorpidae (the head of *Austropanorpa* is not known) fed much like modern Panorpidae, who are primarily scavengers of dead softer-bodied insects, mostly flies (Byers and Thornhill, 1983, Palmer, 2010) (Fig. 24). This distinctive head morphology is seen in "Orthophlebiidae" (e.g., see species figured by Willmann and Novokshonov, 1998), which is thought to be paraphyletic with regard to Cenozoic Panorpoidea (Willmann, 1987), indicating that it is plesiomorphic in them. Early Eocene forests such as those of the Okanagan Highlands would have provided ample opportunity for a variety of insect scavengers to coexist in the herbaceous understory.

Extinctions: possible climatic factors.—Large-scale patterns of climate change would have had a strong effect on panorpoids, as mostly mesothermal, globally equable greenhouse world climates over large parts of the globe gave way to the modern icehouse world of post-Eocene global MAT decline and increase in temperature seasonality outside of low latitudes (Zachos et al., 2008, Eldrett et al., 2009). Today, they mostly inhabit temperate-climate, mid-latitude regions of the Holarctic with cold winters; the ability to withstand these may have been a key adaptation helping facilitate the survival of Panorpodidae and Panorpidae in the modern world.

Panorpodidae is restricted to mid-latitude North America, Japan, China and Korea (Byers, 1988; Tan and Hua 2008; Penny, 2011; Zhong et al. 2011). Panorpidae is dominated by *Panorpa*, which inhabits mid-latitude mesic upper microthermal to mesothermal forests of the United States extending into Mexico (exclusively at middle and higher elevations), and in Europe, Russia, and China (Thornhill, 1980; Byers and Thornhill, 1983; Penny, 2011). The Chinese *Furcatopanorpa* and *Sinopanorpa* are known from cooler, mountainous regions (i.e., upper microthermal to mesothermal) where their habitats are reported (Cai et al., 2008; Ma and Hua, 2011). The remaining *Neopanorpa* and *Leptopanorpa* range in lower latitudes from India through equatorial regions in Java, Sumatra, and Borneo, almost entirely in cooler uplands forests with mild winters, like the Okanagan Highlands. All species of *Leptopanorpa* but one appear restricted to upper microthermal to mesothermal sub-montane and montane regions of Java and Sumatra (Leiftnick, 1936; Penny and Byers, 1979) and only two of thirteen Indonesian species of *Neopanorpa* are known to range down from mid and higher elevations into coastal lowlands (Chau and Byers, 1978). This pattern appears consistent in *Neopanorpa*

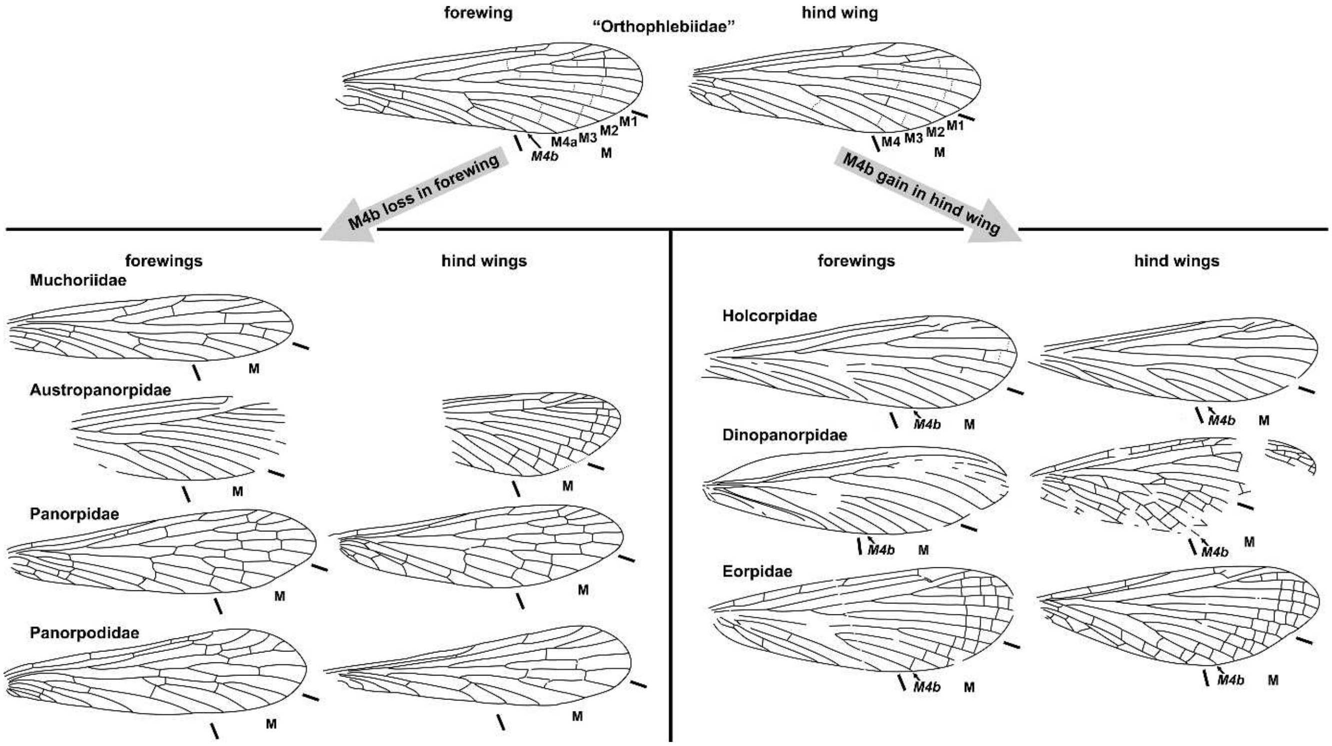

FIGURE *22*—The wings of Panorpoidea (although, note the uncertain status of Muchoriidae, see text), showing the media (M) in the orthophlebiid grade, branch M4b present in the forewing and absent in the hind wing; the loss of this branch in the forewings of Muchoriidae(?), Austropanorpidae, Panorpidae, and Panorpodidae; and the gain of this branch in Holcorpidae, Dinopanorpidae, and Eorpidae (Willmann, 1987). Muchoriidae: forewing, *Muchoria reducta*, redrawn from Sukatsheva (1985) (hind wing not known); Austropanorpidae: *Austropanorpa australis*, forewing redrawn from Riek (1952), hind wing redrawn from Riek (1967); Panorpidae: fore- and hind wings, *Furcatopanorpa longihypovalva*, redrawn from Ma and Hua (2011); Panorpodidiae: forewing *Brachypanorpa sacajawea*, redrawn from Byers (1990), hind wing *B. jeffersoni*, redrawn from Byers (1976); Holcorpidae: forewing and hind wing *H. maculosa*, redrawn from Archibald (2010); Dinopanorpidae: forewing *Dinokanaga dowsonae*, hind wing *Dinopanorpa megarche* both redrawn from Archibald (2005); Eorpidae: forewing 2003.2.6-CDM-030, hind wing SR 08-35-04. To no common scale for ease of comparison.

through Southeast Asia into the Indian subcontinent, where it inhabits upper microthermal to mesothermal uplands of the Western Ghats and Himalayan foothills (Byers, 1965, 1999; Rust and Byers, 1976; Webb and Penny, 1979; Chandra, 2004).

The decline of MAT in the post-Eocene icehouse world would have had a strong effect on all insect groups, and indeed, on all organisms. Perhaps more significantly here, however, the concomitant increase in seasonality outside of low latitudes, i.e., the onset of colder winters (e.g., Eldrett et al., 2009), would have created severe seasonal climatic stress in those taxa inhabiting these regions. Insects in equable, microthermal to mesothermal climates that could not withstand colder winters would have migrated to lower latitudes, evolved new groups with expanded climatic tolerance, or went extinct. As the latter outcome was exceedingly rare at the family level, something more must explain the exceptional cluster of extinctions in the Panorpoidea. This may have been pressure from change in habitat-related factors that differentially affected this group, and, when combined with climatic stress, created conditions where a variety of panorpoid families could no longer be supported.

Extinctions: possible biotic factors.—Despite declining post-Eocene extra-tropical species richness (Archibald et al., 2010), co-evolutionary relationships between diversifying angiosperms and phytophagous, predatory and parasitoid insect groups provided opportunities in new ecological roles, facilitating diversification above the species level (Farrell, 1998; review by Grimaldi and Engel, 2005). Generalist scavengers of dead insects, however, would have been largely unaffected by this expansion of opportunity. These factors may have been further exacerbated by the dramatic rise of a formidable competitor, placing further strong pressure on panorpoids.

Ants, long present as a minor community element in the Cretaceous, were among the groups undergoing a Paleogene increase in their taxa, roles, and abundance (Dlussky and Rasnitsyn, 2003). As the modern assemblage emerged after the Eocene, they rose to greater ecological importance, which included diversification of major groups such as the Mymicinae (Dlussky and Rasnitsyn, 2003; Wilson and Hölldobler, 2005). Thornhill (1980) suggested that intense scavenging competition from ants might at least in part preclude *Panorpa* from the modern tropics. Insect carrion persists there only minutes before being consumed by ants, which possess the advantage of large numbers of foraging workers to constantly monitor large areas and quickly mass-recruit nest mates to recover food items (Carroll and Janzen, 1973, Thornhill, 1980). Today, ants comprise at least a third of global insect biomass—in the Amazon of Brazil, about four times that of terrestrial vertebrates (Wilson and Hölldobler, 2005). Their ascendancy to such great community impact would have had a particularly strong effect on any competing insect groups.

Conclusions.—The apex of panorpoid family-level diversity occurred during a time when the dominant Mesozoic analogue group was gone, but before the ecological dominance of scavenging ants. This elevated diversity occurred in mesic and moist angiosperm-dominated forest habitats that were increasing in ecological complexity following recovery from the K-Pg extinction. These forests supported high diversity angiosperm and insect communities into upper microthermal to mid-mesothermal, mid-latitude uplands; and in regions with climates as cool as

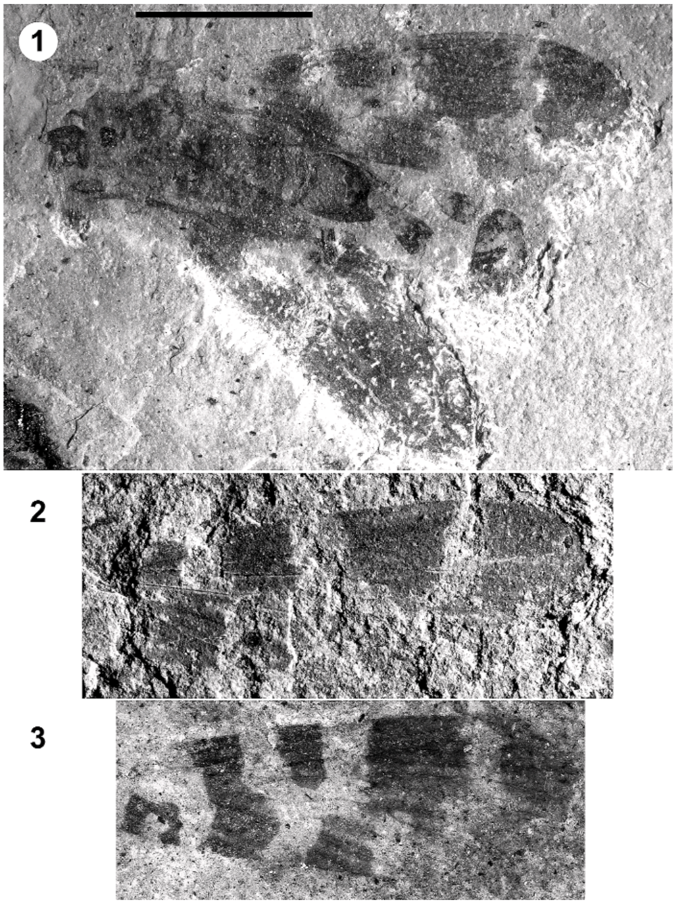

FIGURE 23—New, undescribed Panorpidae from the early Eocene: *1*, complete specimen from McAbee (2003.2.8-CDM-034), and two wings from Republic; *2*, (DMNH 1. 2130), wings from Republic; and *3*, SR 96-11-28. All to scale=5 mm.

upper microthermal, which sustained mild winters with few, if any, frost days (above references).

Such conditions that we suggest were suitable to support a variety of Panorpoidea may have ended after the Eocene when insect and plant diversities declined outside of low latitudes, lessening community potential to support a variety of families that forage for dead insects in the herb stratum; foraging competition from ants increased with their continued ascendance to their great modern ecological impact; and harsh winters developed in the mid-latitudes preferred by the majority of Panorpoidea. While the factors that we propose as favorable to high panorpoid family diversity might be expressed individually in various regions, we know of no place where they are combined today.

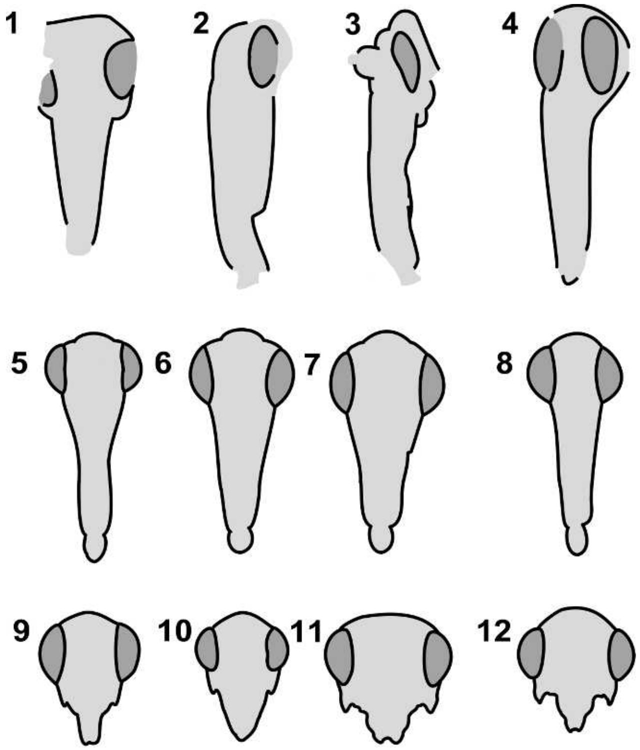

FIGURE 24—Head morphologies of Eocene and modern Panorpoidea. Antennae and mouthparts excluded (mouthparts mostly indistinct in fossils); all in frontal aspect except fossils *2–4*, preserved in lateral aspect. The prolonged downward extension of the head capsule seen in modern Panorpidae and Eocene Panorpoidea is associated with carrion feeding in modern Mecoptera; the short head capsule seen in Panorpodidae is associated (where known) with phytophagy (Palmer 2010). *1–4*, Eocene Panorpoidea: *1*, Panorpidae (specimen from Fig. 23.1); *2*, Eorpidae (*E. ypsipeda*, TMP 83 39 1133); *3*, Dinopanorpidae (*Dinokanaga hillsi*, redrawn from Archibald 2005); *4*, Holcorpidae (*Holcorpa maculosa*, redrawn from Archibald 2010); *5–12*, modern Panorpidae (*Panorpa*), redrawn from Palmer (2010): *5*, *P. americana*; *6*, *P. cornigera*; *7*, *P. fluvicauda*; *8*, *P. japonica; 9–12*, modern Panorpodidae (*Panorpodes* and *Brachypanorpa*): *9*, *P. brachypodus*; *10*, *P. colei*; *11*, *B. carlinensis*; *12*, *B. sacajawea*. None to scale; sizes roughly equalized for comparison.

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APPENDIX

Specimens

McAbee

Eorpa ypsipeda Holotype, labeled: HOLOTYPE *Eorpa ypsipeda* Archibald, Mathewes *et* Greenwood 2012:

1) 2003.2.6-CDM-030 (part only), Figs. 10.7, 21, a forewing, two hind wings; CDM collection; collected by S.B.A., summer 2000.

Eorpa ypsipeda Paratypes: all labeled: PARATYPE *Eorpa ypsipeda* Archibald, Mathewes *et* Greenwood 2012:

2) 2003.2.2-CDM-026 (part only), Fig. 10.1, a partial forewing; CDM collection; collected by unknown person, before 2000.
3) 2003.2.4-CDM-028 (part only), Fig. 10.2, a mostly complete forewing; CDM collection; collected by S.B.A., June 2000.
4) TMP 83 39 1133 (part, counterpart), Figs. 6, 10.19, an almost complete female missing one hind wing; RTMP collection, collected by Len Hills, Maureen Hills and Katherine Higgins, July-August 1985.
5) 2003.2.8-CDM-032 (part, counterpart), Fig. 10.16, a forewing overlaying a second wing; CDM collection; collected by S.B.A., July 2000.

6) 2003.2.9-CDM-033 (part only), Fig. 10.4, a forewing; CDM collection; collected by S.B.A., before 1999.
7) UCCIPR L-18 F-986, 7 (part, counterpart), Fig. 10.3, a forewing; TRU collection; collected by unknown person.
8) UCCIPR L-18 F-991 (part, counterpart), Fig. 10.13, a forewing, two hind wings; TRU collection; collected by unknown person.
9) UCCIPR L-18 F-1024 (part only), Figs. 8.1, 10.6, hind wing, forewing, and male terminalia; TRU collection; collected by unknown person;
10) UCCIPR L-18 F-984 (part only), Fig. 10.5, a hind wing; TRU collection; collected by unknown person.
11) UCCIPR L-18 F-1536 (part only), Fig. 10.7, hind wing; TRU collection; collected by John Leahy.
12) UCCIPR L-18 F-1134, 5 (part, counterpart), Fig. 10.8, a hind wing; TRU collection; collected by unknown person.
13) 2003.2.5-CDM-029 (part, counterpart), Figs. 5, 10.9, a body missing the abdomen, forewing and hind wing; CDM collection; collected by S.B.A., July 2000.
14) 2003.2.3-CDM-027 (part only), Figs. 4, 10.10, parts of the body and parts of four wings; CDM collection; collected by S.B.A., June 2000.
15) UCCIPR L-18 F-1537 (part, counterpart), Figs. 3, 10.11, partial body, three partial wings and a complete hind wing; TRU collection, collected by John Leahy;
16) UWBM 78044 (part only), Fig. 7, an almost complete male, with basal part of one forewing missing; UWBM collection; collected by Wes Wehr and Peter Dunthorne in 1992.
17) UCCIPR L-18 F-1538 (part only), Figs. 2, 10.12, four complete wings and body parts; TRU collection, collected by John Leahy.
18) UCCIPR L-18 F-1539 (part only), Figs. 1, 10.17, a complete, but disarticulated female missing one forewing; TRU collection, collected by John Leahy.
19) UCCIPR L-18 F-1191 (part, counterpart), Fig. 10.20, a forewing missing the basal portion, a mostly complete hind wing; TRU collection; collected by unknown person.
20) UWBM PB4075 (part only), Figs. 9, 10.14, a well preserved forewing and hind wing; UWBM collection; collected by unknown person.
21) 2003.2.7-CDM-031 (part, counterpart), Fig. 10.18, apical portions of two wings, CDM collection, collected by S.B.A., July 2000.

Republic

Eorpa elverumi Holotype, labeled: HOLOTYPE *Eorpa elverumi* Archibald, Mathewes *et* Greenwood 2012:

Exposure B4131

22) SRUI 08-07-07 a, b (part, counterpart); Figs. 15, 16.5, a forewing; SR collection; collected by John Elverum, April 2007.

Eorpa elverumi Paratype, labeled: PARATYPE *Eorpa elverumi* Archibald, Mathewes *et* Greenwood 2012:

Exposure S100

23) SRUI 08-02-01 (part only); Fig.16.1 most of the basal portion of a forewing with some tearing around R1 (R1 present on part only); SR collection; collected by Karl Volkman, July 2007.

Eorpa sp. Hypotypes, labeled: HYPOTYPE *Eorpa* sp. Archibald, Mathewes *et* Greenwood 2012:

Exposure B4131

24) SR 01-06-02 (part only), Figs. 11, 16.6, a nearly complete wing; SR collection; collected by Katheryn Kelsey, date unknown.
25) SR 08-35-04 (part only), Figs. 12, 16.8, 22, a complete hind wing; SR collection; collected by Tom Rafoth, May 2008.
26) SR 08-35-07a, b (part, counterpart), Fig. 16.11, a hind wing; SR collection; collected by Warne Roubideaux, May 2008.
27) SR 09-11-01 (part only), Figs. 14, 16.7, a complete, mostly well-preserved hind wing; SR collection; collected by Katrina Pruett, June 2008.
28) SR 05-03-19 (part only), Fig. 16.9, a hind wing missing the apical portion; SR collection; collected by Gregg Wilson, May 2005.
29) SR 95-10-03 (part only), Fig. 16.13, a broken hind wing; SR collection; collected by Brian Saulsman, date unknown.
30) SR 10-02-04 (part only), Fig. 16.12, a broken hind wing; SR collection; collected by Brian Hutchinson, July 2009.
31) SR 12-004-002 (part only), Fig. 16.10, a broken and somewhat crumpled hind wing; SR collection; collected by Harriet Crumb, June 2012.

Exposure S103

32) SRUI 99-92-23a, b (part, counterpart), Fig. 16.4, a basal portion of a forewing and distal portion of a wing; SR collection; collected by Nils Larsen, July 2009.
33) SRUI 99-83-53 (part only), Fig. 16.3, a broken partial forewing; SR collection; collected by Karl Volkman, June 2009.

Exposure not recorded

34) UWBM 57198 (part only), Fig. 16.14, a broken hind wing; UWBM collection, collected by unknown person before 1992; figured by Lewis (1992) and Lewis and Wehr (1993).

Eorpidae *incertae sedis* Hypotype, labeled: HYPOTYPE Eorpidae *incertae sedis*. Archibald, Mathewes *et* Greenwood 2012:

Exposure B4213

35) SR 93-14-05 (part only), Figs. 16.2, 20, a forewing; SR collection; collected by Lisa Barksdale, date unknown.

Quilchena

Eorpa jurgeni Holotype, labeled: HOLOTYPE *Eorpa jurgeni* Archibald, Mathewes *et* Greenwood 2012:

36) Q-0096 (part only), Fig. 17, a hind wing; SFU collection; collected by R.W.M. in the 1990's.

Eorpa sp. Hypotype, labeled: HYPOTYPE *Eorpa* sp. Archibald, Mathewes *et* Greenwood 2012:

37) Q-5032 (part only), Fig. 18, a forewing; SFU collection; collected by R.W.M. in the 1990's.

Falkland

Eorpa sp. Hypotype, labeled: HYPOTYPE *Eorpa* sp. Archibald, Mathewes *et* Greenwood 2012:

38) RBCM.EH2012.004.0001.001 (part only), Fig. 19, a very damaged forewing; RBCM collection; collected by Robin Smith, June 2007.