Ecology and Distribution of Cenozoic Eomeropidae (Mecoptera), and a New Species of *Eomerope* Cockerell from the Early Eocene McAbee Locality, British Columbia, Canada

S. BRUCE ARCHIBALD,[1] ALEXANDR P. RASNITSYN,[2] AND MIKHAIL A. AKHMETIEV[3]

Ann. Entomol. Soc. Am. 98(4): 503–514 (2005)

ABSTRACT *Eomerope macabeensis* sp. nov. (Mecoptera: Eomeropidae) is described from the Early Eocene (Ypresian) McAbee locality in British Columbia, Canada. This is the first record of the family Eomeropidae in the Okanagan Highlands fossil deposits of British Columbia (Canada) and Washington state (United States). Previously known Cenozoic occurrences of the family include *Eomerope tortriciformis* Cockerell 1909 from the Eocene of Florissant, CO; *Eomerope pacifica* Ponomarenko & Rasnitsyn 1974 from the Paleocene Tadushi Formation., and *Eomerope asiatica* Ponomarenko & Rasnitsyn 1974 from the Eocene or Oligocene Amgu River of far-eastern Russia; and the extant *Notiothauma reedi* MacLachlan, 1877, from southern Chile. The new species seems to be closely related to *E. asiatica*. Where environmental parameters are known, these occurrences are mostly from highlands, with upper microthermal to mid-mesothermal climates and mild winters. *N. reedi* is phytophagous or saprophagous. Although Cenozoic Eomeropidae are associated with *Fagus*, *Nothofagus*, or *Fagopsis*-dominated forests in the Western Hemisphere, the Fagaceae and Nothofagaceae are minor elements or not known in the Russian localities. Intercontinental dispersal by either Gondwanan or Beringian routes is possible.

KEY WORDS *Notiothauma reedi*, fossil insects, Okanagan Highlands, Paleogene, biogeography

THE SOLE EXTANT SPECIES OF the family Eomeropidae, *Notiothauma reedi* MacLachlan, 1877, occurs in the southern beech forests of southern Chile (Peña 1968, Penny 1975). The known fossil record of the family is small. The Triassic fossils described by Ponomarenko and Rasnitsyn (1974) from Madygen, Kirghizia, and later placed into Eomeropidae (Willmann 1978, 1981) are now found to form the separate family Thaumatomeropidae, distant from Eomeropidae (Novokshonov 1977, 2002). A new eomeropid has been found from the Middle Jurassic of Daohugou, Inner Mongolia, China (collection of the Nanjing Institute of Geology and Palaeontology, CAS, Nanjing, China) (Zhang Junfeng, personal communication). At present, this is the only Mesozoic record of the family.

The described Cenozoic fossil taxa of this family includes three species in the genus *Eomerope* Cockerell 1909: *Eomerope asiatica* Ponomarenko & Rasnitsyn 1974, of the Late Paleocene Yushangou locality of the Tadushi Formation in Primorye (Maritime Province), Pacific-coastal Siberia; *Eomerope pacifica* Ponomarenko & Rasnitsyn 1974, from the Late Eocene/Early Oligocene Khutsin Formation Amgu River locality (also in Primorye); and *Eomerope tortriciformis* Cockerell 1909, from the Late Eocene (Evanoff et al. 2001) Florissant Formation of Florissant, CO.

Cockerell (1909) (p. 383) called *E. tortriciformis:* “one of the most puzzling fossil insects that I have had the occasion to describe.” He found the outwardly bowed costa of the forewing, with numerous cells in the broad costal area, to be particularly peculiar, but most similar to the extant eastern American genus *Merope* Neuman 1838. He therefore erected the new subfamily Eomeropinae for this species within the family Meropeidae.

Carpenter (1972) disagreed with this assignment, finding this fossil insect most similar to the extant *N. reedi*, the only species of the family Notiothaumidae, assuming that Cockerell was simply unaware of this insect, which was obscure in his time. *Notiothauma* shares with *Eomerope* the broadened costal area with rows of cells and a similar branching of Rs and R1 (Rs continues in a straight line from R, with R1 diverging anteriorly), character states not found in Meropeidae. More importantly, in males of both *Eomerope* and *Notiothauma,* the genital bulb is not greatly expanded and the claspers extended as in Meropeidae. Ponomarenko and Rasnitsyn (1974) noted that as the family Notiothaumidae was not established by Ebsen-Pe-

---

[1] Department of Organismic and Evolutionary Biology, Harvard University, Museum of Comparative Zoology, 26 Oxford St., Cambridge, MA 02138 (e-mail: barchibald@oeb.harvard.edu).

[2] Palaeontological Institute RAS, Moscow 117868, Russia and Natural History Museum, Cromwell Rd., London SW7 5BD, United Kingdom (e-mail: rasna@online.ru)

[3] Geological Institute RAS, Moscow 119017, Russia (e-mail: akhmetiev@ginras.ru).

0013-8746/05/0503–0514$04.00/0

tersen until 1915; Eomeropinae thus predated it and therefore they placed *Notiothauma* and *Eomerope* in the Eomeropidae, nom. trans. ex Eomeropinae.

We describe a new species of *Eomerope* from the Early Eocene (Ypresian) McAbee beds, Okanagan Highlands, British Columbia, Canada. The Okanagan Highlands (British Columbia, Canada; Washington state) series of Early and early Middle Eocene fossil deposits, rich in fossil insects, is summarized in Greenwood et al. (2005). We examine biotic and abiotic environmental factors potentially determining the distribution of the family in the Cenozoic and consider possible dispersal routes.

Materials and Methods

The single fossil of the new species described here is preserved in fine-grained, thinly bedded shale, which, as is usual at the McAbee locality, split cleanly. Therefore, this specimen required no preparation. However, portions of (possibly) another wing are visible on a small exposure of a layer slightly below the surface plane, but the preparation required to expose it would destroy at least part of the forewing, and so was not done.

In drawings, dotted lines indicate faintly observed structures; dashed lines indicate the boundaries of broken or obscured regions of the fossil. There is no representation in drawings of hypothesized missing morphology.

Venational terminology follows Willmann (1989); abbreviations used are as follow: C, costa; Sc, subcosta; R, radius; Rs, radial sector; M, media; Cu, cubitus; Cu1 (=CuA), anterior branch of the cubitus; Cu2 (=CuP), posterior branch of the cubitus; A, anal vein. Institution abbreviations are: MCZ, Museum of Comparative Zoology (Cambridge, MA); PIN, Paleontological Institute, Russian Academy of Sciences (Moscow, Russia); UCC, University College of the Cariboo (Kamloops, British Columbia, Canada); YPM, Yale Peabody Museum (New Haven, CT). Climate abbreviation: MAT, mean annual temperature; CMMT, coldest month mean temperature; CLAMP, Climate-Leaf Analysis Multivariate Program. Because the terms "temperate" and "tropical" are associated with both MAT values and geographic areas in the modern world, and not necessarily in the Paleogene, the MAT categories of Wolfe (1979) are here used: microthermal, MAT <13°C; mesothermal, 13–24°C; and megathermal, >24°C.

Family Eomeropidae Cockerell, 1909
Genus *Eomerope* Cockerell, 1909
Eomerope macabeensis sp. nov.
(Figs. 1 and 2)

Diagnosis. Forewings may be distinguished from other *Eomerope* by a combination of: no more than two rows of cells formed by crossveins between C and anterior branch of Sc; A2, A3 strongly zig-zagged by crossveins.

Female. Body length 17.0 mm preserved (slightly extended, but likely close to life length). *Head.* Antenna with at least basal flagellomeres hardly elongate, eyes elongate (Figs. 1 and 4C), distant from upper head margin, rostrum moderately long (but shorter than in *Notiothauma:* Figs. 1 and 4C), with side margins not concave. *Legs.* More stout than in *Notiothauma,* particularly fore pair; tibiae, to much lesser extent; tarsi, with many thick, long hairs (in contrast to *Notiothauma,* no stiff setae found on femora). *Thorax.* Deformed and difficult to interpret. *Abdomen.* Tapering caudad, terga leaving exposed membranous pleura laterad in dorsal view, tergum 9 narrow, distal portion of gonocoxite 8 (sensu Mickoleit 1976, Willmann 1989) narrow, extending slightly beyond hind margin of segment 9, dark spots interpreted as laterotergites 9 (below) evident on A9, tergum 10 truncated, with only apical sclerotization, cerci three-segmented, segments comparatively long, with basal segments fused basally with each other as well as with rudimentary tergum 11 (cercifer), probably as in *Notiothauma* (Willmann 1989, Fig. 56). *Forewing.* Length 18.0 mm, width 6.5 mm, broad (width:length 1:2.7), expanded costal space; veins thickened in basal approximately three-fourths, then narrower; no coloration detected; C bowed outward basally, then rather straight from about distance of Rs branching to about termination of Rs branches; costal space with regular double cell row ending before three apical branches of Sc1; Sc with two branches, forking ≈one-eighths wing length; R forks at basal one-fourths, beyond forking of Sc; R1 rather straight (but somewhat zig-zagged by crossveins) to anterior margin with three distinct apical branchlets; Rs (including MA sensu Ponomarenko and Rasnitsyn 1974) with at least eight dichotomously forking branches (indistinctly preserved near apex); base of M very close to R, straight or only slightly bent posteriad through region of forking of R1, Rs; dividing into three main branches just distad of first branching of Rs, desclerotized at trichotomy, further irregularly branched into approximately nine branches; Cu branched immediately before branching of Sc; both Cu1 and Cu2 apparently simple, Cu1 strongly zig-zagged by crossveins, bent sharply posteriad approximately two-thirds length (at branching of M); Cu2 not sharply bent, rather straight (but zig-zagged) to hind margin; three anal veins, 1A somewhat zig-zagged, 2A, 3A strongly zig-zagged (anal region strongly cellularized); jugal flap small, apparently veinless (preserved folded back against wing blade with its hind margin apparently crossing anal veins); crossveins numerous, forming two rows of cells in most of costal space; many between branches of Rs, M, stronger basally, not preserved apically (but evident by zig-zag of branches of Rs, M); creating irregular cells between branches of Cu, A.

Type Material. UCCIPRL-18F-826 (part only) (Figs. 1 and 2), deposited in the UCC collection. A well-preserved female, with body, portions of six legs and one forewing, which is rotated out of life position. A possible portion of another wing is visible on exposure of a plane slightly below the surface plane. Col-

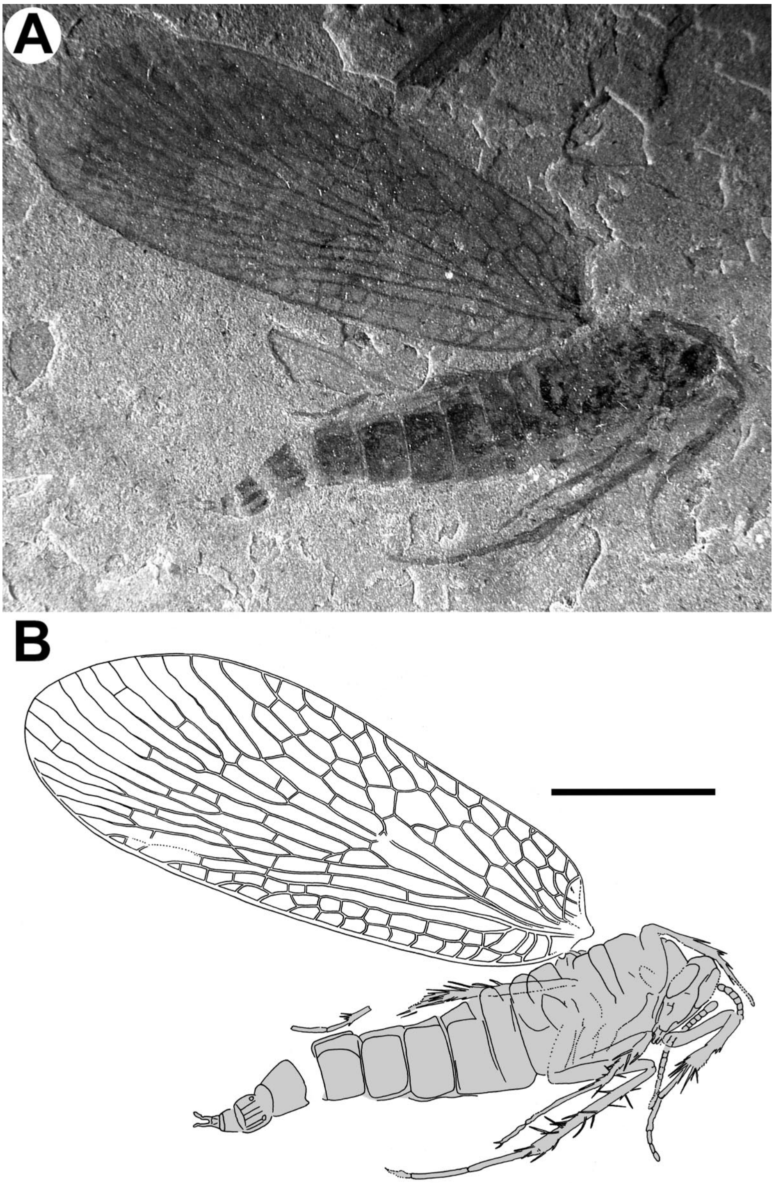

Fig. 1. Habitus of the holotype of *E. macabeensis* sp. nov. (UCCIPRL-18 F-826). (A) Photograph. (B) Drawing. Both to scale; bar, 5 mm.

lected by unknown person at McAbee in 2002, donated to the UCC collection by David Langevin.

Locality and Age. McAbee locality of the Okanagan Highlands series of Eocene deposits (Greenwood et al. 2005), unnamed formation of the Kamloops Group near Cache Creek, British Columbia, Canada; Early Eocene (≈51 Ma).

Etymology. The specific epithet *macabeensis* refers to the McAbee locality (The name "McAbee" is derived from the surname of a local pioneering family. It is spelled "*mac-*" not "*mc-*" in accordance with ICZN Grammar appendices, Appendix D III, Article 21a; International Trust for Zoological Nomenclature 1985).

Discussion

Within *Eomerope*, the forewing morphology of *E. macabeensis* is most similar to that of *E. asiatica.* Like *E. asiatica, E. macabeensis* bears only two rows of cells in the costal space (although *E. asiatica* paratype PIN 3364/2372 bears two cells between these two rows; Ponomarenko and Rasnitsyn (1974), Fig. 7e), whereas in all other *Eomerope* there are three to four rows in

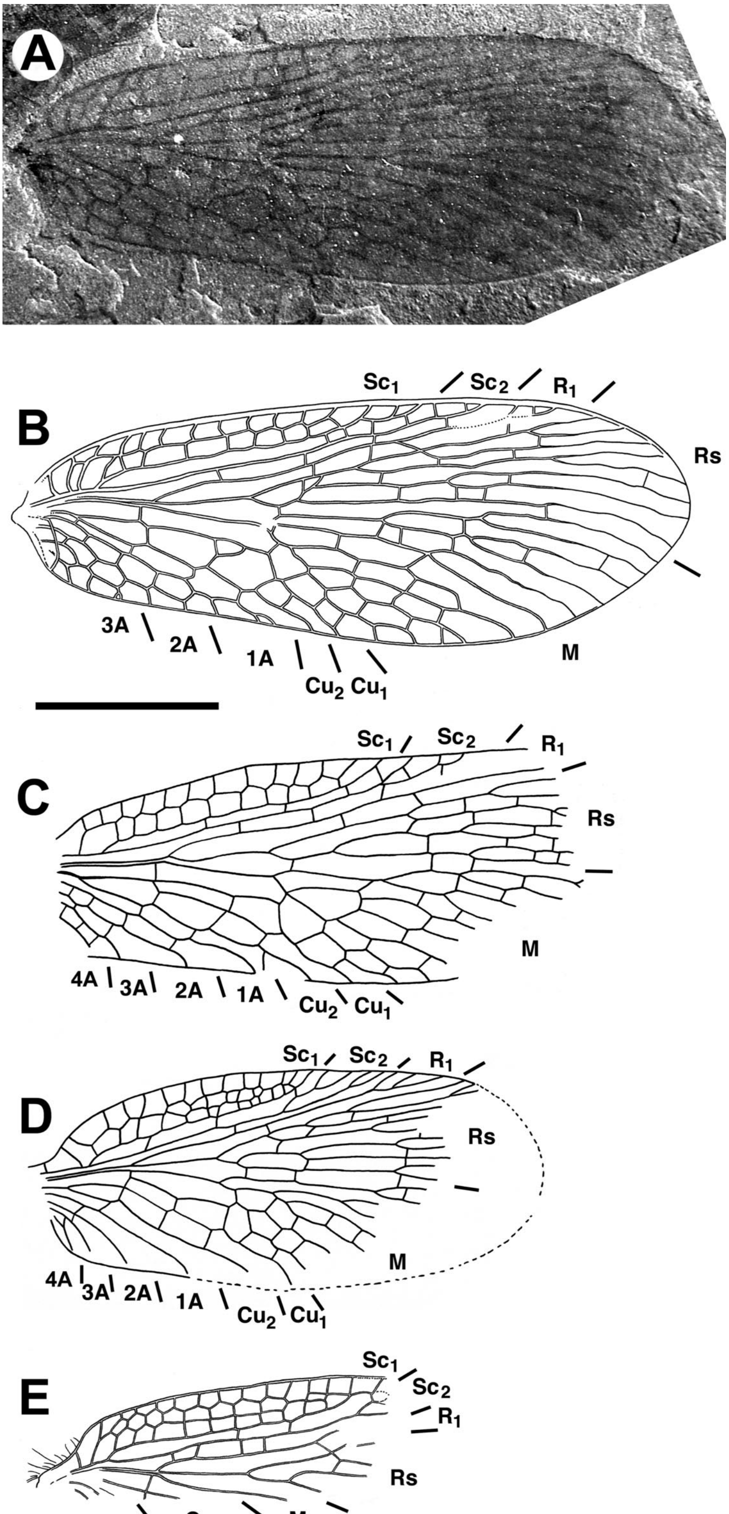

Fig. 2. Forewings of *Eomerope* (abbreviations as in *Materials and Methods*). (A) *E. macabeensis*: photograph of forewing. (B) *E. macabeensis*: drawing of forewing. (C) *E. asiatica*: drawing of forewing (holotype PIN 3364/2381) (redrawn from Ponomarenko and Rasnitsyn 1974). (D) *E. pacifica*: drawing of forewing (holotype PIN 2961/1) (redrawn from Ponomarenko and Rasnitsyn 1974). (E) Drawing of forewing of *E. tortriciformis* (holotype YPM-26176). All to scale; scale bar, 5 mm.

at least part of this space. Both have similarly shaped forewings: those of *E. asiatica* are 2.5–3 times longer than wide; the sole specimen of *E. macabeensis* is 2.7 times longer than wide (*E. pacifica* 2.25; *E. tortriciformis* not known, as wings are incomplete). There is also a great similarity in much of the forewing cell shape, notably that of the polygonal cell (adjacent, distad to the sharp bend of Cu1), which is about as long as wide, diagnostic for *E. asiatica* (differently shaped in other *E. pacifica* and *E. tortriciformis*). *Eomerope asiatica,* has ≈10 branches of Rs, and *E. macabeensis* 8 (*E. pacifica* has 14, *E. tortriciformis* not known due to incomplete wings).

However, *E. macabeensis* may be separated from *E. asiatica* by the following characteristics: 1) cells in costal space: in *E. asiatica,* this series almost reaches the apex of Sc branch, such that the last crossvein ends in a penultimate Sc1 branchlet, whereas in *E. macabeensis,* there are three free apical branchlets; 2) M begins branching dichotomously in *E. asiatica,* whereas the first branching of M is in a trident fashion in *E. macabeensis* (although the exact point of branching is not preserved or not sclerotized); 3) anal veins: in *E. asiatica* there are four distinct anal veins, and these are rather straight, whereas in *E. macabeensis,* they are most probably only three, and these are strongly bent by crossveins (anal area cellularized, 2A, 3A, strongly zig-zagged); and 4) the longitudinal veins are almost the same thickness to the wing apex in *E. asiatica* but seem to thin in the apical region of *E. macabeensis.*

Ponomarenko and Rasnitsyn (1974) noted extensive variability in the wing venation of *E. asiatica,* as in the extant *N. reedi.* For example, the 12 specimens examined display differing numbers of branches of Rs and M, sometimes pectinately, sometimes dichotomously branched. The characters listed for *E. macabeensis* above, however, are outside of this variance.

E. asiatica and *E. macabeensis* also differ in age: the former is Late Paleocene, possibly Thanesian (55.8–58.7 Ma) (Rasnitsyn and Zherikhin 2002), the latter is Early Eocene (≈51 Ma: Ewing 1981). This, however, could indicate only about a 5–8 Ma difference between Yushangou and McAbee times.

Useful comparison of the body of the new species can only be made with that of *N. reedi;* other *Eomerope* are either known by wings only, or (*E. tortriciformis,* Fig. 3) the body morphology is for the most part indistinctly preserved and difficult to decipher (thoracic morphology and head: the possible outline of the head seen in Fig. 3 is difficult to confirm), or incomparable (male versus female abdomen). An exception is the leg morphology of *E. macabeensis* (particularly seen in the hind), which is similar to that of *Notiothauma* in the general form and spinosity of the tibiae, but apparently not femora, although they are stouter in the new species (Figs. 1, 4A and B). Furthermore, the dark spots evident on A9 are interpreted as laterotergites, as in *N. reedi* (Mickoleit 1976, Fig. 15; Willmann 1983, Fig. 6; although these correspond with the position of structures that Artigas 1999, Fig. 2 interprets as spiracles on *N. reedi*).

In comparison with *Notiothauma,* the body structure of the present fossil is generally similar; however, the flagellomeres are shorter and thicker, the head is wider and rostrum shorter, the eyes are slightly shorter, and the legs are more robust and apparently with no femoral stiff setae. Furthermore, some aspects of the abdomen of *E. macabeensis* seem particularly different: it is tapered caudad, with reduced sclerotization of terga 9 and 10, and with unusually long cerci. Until further specimens of *Eomerope* are studied for their body structure, it is unknown if the above-mentioned differences are of specific or generic value.

Distribution and Ecology of Cenozoic Eomeropidae

Cenozoic Eomeropidae occur in widely separated regions: Pacific coastal Siberia (Primorye, Russia); British Columbia (Canada) and Colorado (United States); and southern Chile (Fig. 5). Various explanatory dispersal scenarios based on tectonic intercontinental connections and hypothetical environmental and biotic niche factors discussed below may be considered.

Range. The seemingly disjunct distribution of *Eomerope* between western North America and the Russian Far East was apparently not so in the Paleocene/Early Eocene, because these regions were connected by the Bering Land Bridge at that time (Budantsev 1983, Hamilton 1983, Tiffney and Manchester 2001) at paleolatitude of ≈70° N the Early Eocene (Andrews 1985). Tectonically, Beringia, including eastern Siberia east of the Cherskiy Range, is part of the North American plate. Temperature would not have been a limiting factor in Eocene Beringia: forests grew even farther north at 75–80° N, in a climate with an estimated MAT of 12–15°C in the Canadian arctic, with winters mild enough to allow the presence of frost-intolerant vertebrates and plants (McKenna 1980, Estes and Hutchinson 1980, Basinger et al. 1994). Extensive intercontinental interchange of both floral and mammal taxa occurred across Beringia in the Paleocene/Eocene (Graham 1972, Tiffney 1985, Beard and Dawson 1999, Manchester 1999, Bowen et al. 2002).

The only known Mesozoic occurrence of the family is in the Jurassic of East Asia (above). Furthermore, as the oldest reported occurrence of the genus *Eomerope* is at the Yushangou locality (Primorye) in the Late Paleocene, it may be thought that the genus originated in Asia, entering North America via Beringia before Early Eocene McAbee time (≈51 Ma). The paucity of Paleocene insect localities in North America, however, precludes any supposition as to their absence there predating Yushangou time. Origination of *Eomerope* in, and migration from, either continent is not indicated by these occurrences.

The genus *Notiothauma,* the nearest living relative and sister-taxon of *Eomerope* (and only extant eomeropid), has a known range of its single species (*N. reedi*) in western portions of southern Chilean Valdivian *Nothofagus* (southern beech) forests between 37 and

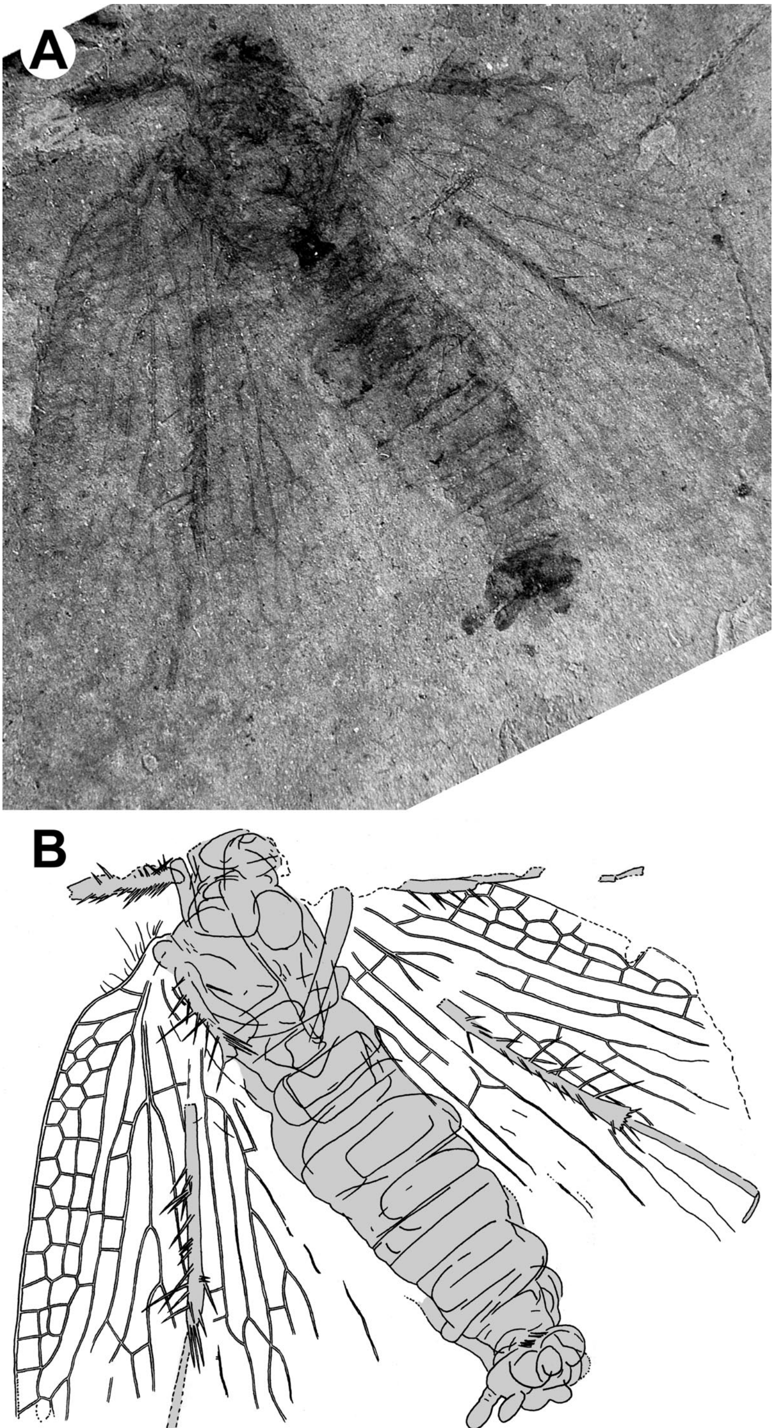

Fig. 3. Holotype of *E. tortriciformis* YPM-26176. (**A**) Habitus photograph. (**B**) Habitus drawing. The possible outline of the head may be an artifact. Both to scale; scale bar, 5 mm.

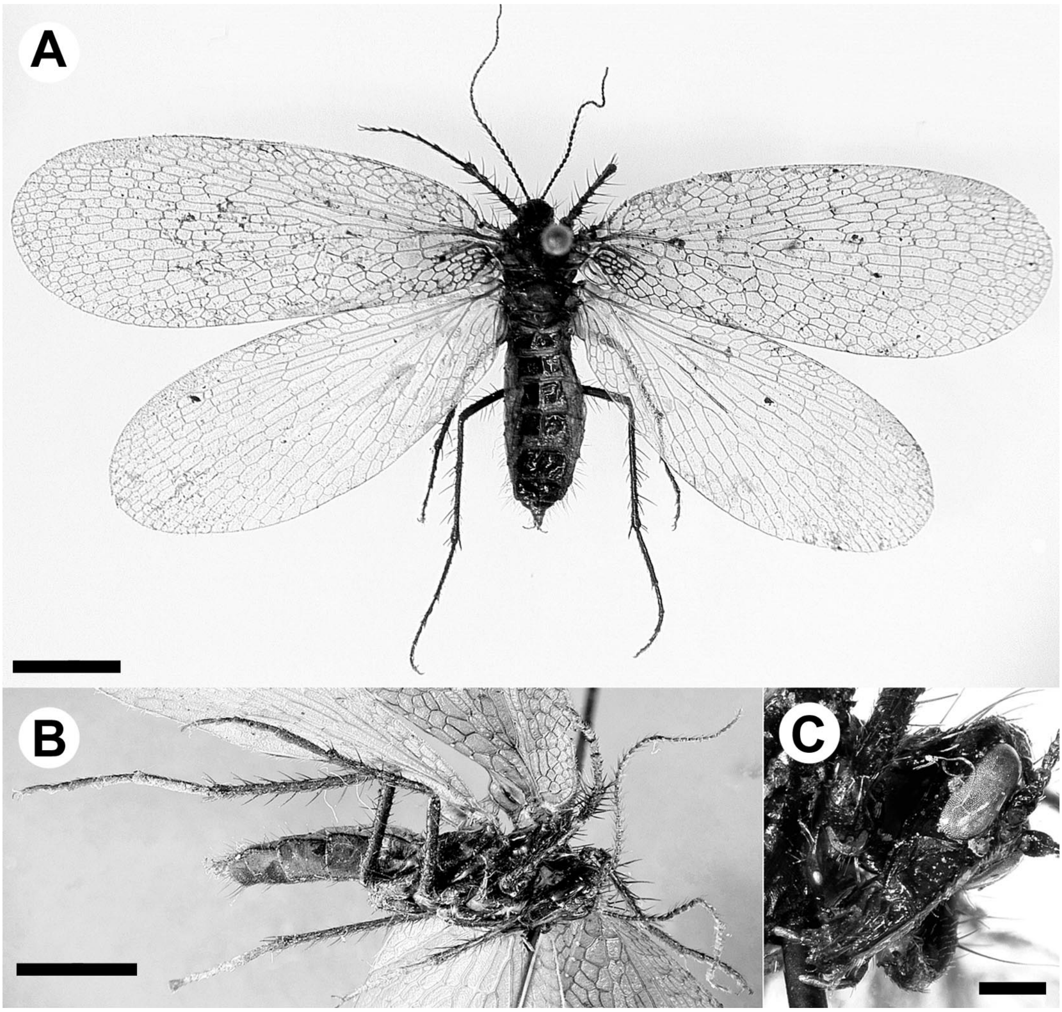

Fig. 4. *N. reedi*, female pinned specimen from MCZ collections. (A) dorsal habitus. (B) Lateral aspect, body and legs. (C) Head. Scale bars, 5 mm (A and B) and 1 mm (C).

41° S latitude (list of localities in Rebolledo et al. 1990). *Notiothauma* has no known fossil record.

Life Habit. *Notiothauma* lives a nocturnal cockroach-like existence on the *Nothofagus* forest floor. The dense venation, heavy veins, and increased sclerotization of their wings presumably protect them from damage as they crawl through leaf litter and under logs and rocks (Peña 1968, Penny 1975). Their spined, cursorial legs, flattened body with wings folded flat incumbent, and castaneous coloration of body and wing veins are also distinctively blattoid rather than mecopteroid.

Members of the mecopteran family Meropeidae share this distinctive morphology and life habit with *Notiothauma* (Penny 1975). This striking correlation between extant mecopterans of these two families suggests a similar life habit for *Eomerope*, which shares this morphology with them (flattened body and coloration not determinable).

Adult *Notiothauma* are phytophagous or saprophagous: their gut contents consist of plant material (plant organ not determinable) and they exhibit distinctive mandibular morphology characteristic of phytophagous Mecoptera (Byers 1965, Peña 1968, Byers and Thornhill 1983, Hepburn 1969) (the mandibles are not clearly preserved in any *Eomerope* specimen). The diet of the larvae is not known (Rebolledo et al. 1990).

Floral Association. Willmann (1981) discussed the zoogeographic history of Eomeropidae. Given the association of *Notiothauma* with *Nothofagus*, he considered the possibility that the common ancestor of *Eomerope* and *Notiothauma* originated in the Northern Hemisphere along with *Nothofagus* (noting its phylogenetic closeness to the Northern Hemisphere beech genus, *Fagus*) and spread to South America with it.

Plant host associations of insects are often highly conservative; phylogenetic studies have shown coevolutionary relationships between insects and plants dating back to the Mesozoic (Mitter et al. 1991, Farrell 1998, Sequeira et al. 2000). Such persistent associations explaining disjunct distributions have been recently demonstrated: *Araucaria* feeding of scolytine

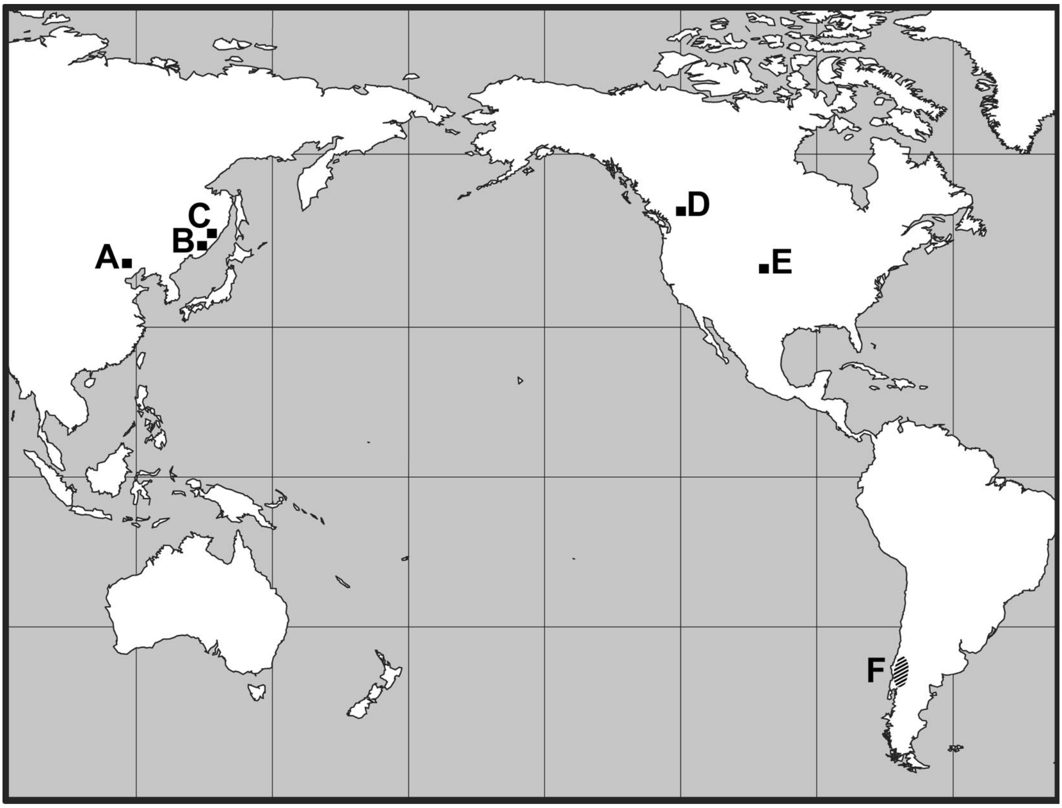

Fig. 5. Occurrences of Eomeropidae. (A) Daohugou, Inner Mongolia, China (Middle Jurassic). (B) *E. pacifica*: Amgu River, Primorye, Russia (Late Eocene or Early Oligocene). (C) *E. asiatica*: Yushanguo River (Tadushi Formation: Paleocene), Primorye, Russia. (D) *E. macabeensis*: McAbee locality, British Columbia, Canada (Early Eocene). (E) *E. tortriciformis*: Florissant, CO (Late Eocene). (F) *N. reedi*, the Valdivian *Nothofagus* forest region (part), Chile (extant).

bark beetles (Coleoptera: Curculionidae) seems to have been conservative because the Late Cretaceous, predating the breakup of Gondwana and persisting today in South America and Australia (Sequeira and Farrell 2001). Cross-Beringial dispersal before the Middle Eocene of insect taxa tracking host plants is indicated in the aphid subfamily Melaphidina (Hemiptera: Aphididae), which feeds on *Rhus*, in both North America and in Asia (Moran 1989).

Nothofagus has a pollen record dating to the Maastrichtian in parts of southern South America, Australia, and New Zealand (Raven and Axelrod 1974). *Nothofagus*-dominated floras are common in the Eocene of Antarctica, in an upper microthermal climate at determined localities (Hunt and Poole 2003).

Nothofagus is the only genus of the family Nothofagaceae, placed basally within the Fagales by molecular phylogeny, with Fagaceae the sister-taxon to the remainder (Savolainen et al. 2000). Extant Fagaceae are widespread in the Northern Hemisphere, in both tropical and temperate regions; *Fagus* is found in temperate regions of eastern North America, Europe, and East Asia. *Nothofagus* is present exclusively in the Southern Hemisphere: southern Australia, New Guinea, New Zealand, and southern portions of South America and Africa.

The place of origin and route of dispersal of Fagales has generated considerable discussion. A Middle Cretaceous Laurasian origin has been proposed, with *Nothofagus* migrating south into Gondwana (Raven and Axelrod 1974). Its origin has been placed in North America but also in East Asia (Jones 1986, and references therein). Alternatively, it has been proposed that the ancestral group originated in warm regions of western Gondwana, radiating poleward: *Nothofagus* into more southern latitudes, Fagaceae (and portions of the other Fagales) into the north (Romero 1986).

Flowers of Fagaceae are known as far back as the Santonian in North America (Taylor 1990, Manchester 1999). *Fagus* occurs in the North American Eocene, including Early Eocene Okanagan Highlands localities (Gray 1960, Wehr 1998, Gandolfo 1996, Pigg and Wehr 2002, Denk 2004, Dillhoff et al. 2005, Greenwood et al. 2005, Moss et al. 2005) and in East Asia in the Oligocene (Early Oligocene, Tanai 1995; Late Oligocene, Tanai 1974, Manchester 1999). The genus *Fagopsis* is reported from the early Middle Eocene of Japan (Tanai 1995), Rarytkin Ridge (North East Russia) (Akhmetiev and Samsonenko 1997), and the Middle Eocene-Oligocene Sikhote-Alin (Akhmetiev 1988), but Manchester and Crane (1983) restrict this genus to those fossils leaves with diagnostic infructescences attached, only known from the Eocene of western North America. The position of *Fagopsis* within Fagaceae is unclear: pollen structure may indicate a closer affinity to *Quercus* than *Fagus* (Manchester and Crane 1983). Fagaceae is reported from the Eocene of Japan: *Dryophyllum* from the early Middle Eocene and *Quercus* from the late Middle Eocene (Tanai 1995).

The flora of McAbee includes *Fagus;* its leaves are the dominant floral element at this locality (Wehr 1998, Pigg and Wehr 2002, Manchester and Dillhoff 2004, Dillhoff et al. 2005, Greenwood et al. 2005). Like the *Nothofagus* forests of Chile, the McAbee floral assemblage includes conifers of the families Cupressaceae and "Taxodiaceae" (now placed within the Cupressaceae). At Florissant, *Fagopsis longifolia* contributes the most abundant leaves in the flora (Cupressaceae and "Taxodiaceae" also present) (Manchester 2001).

Fagaceae has not, however, been reported from the Paleocene Yushangou site (Bersenev et al. 1969). The family, including *Fagus,* is present at the Late Eocene or Early Oligocene Amgu locality (Kryshtofovich 1921, Akhmetiev 1988), although only as a minor element there, 0.2% of the flora (Akhmetiev 1988). The co-occurrence of Cenozoic Eomeropidae with *Fagus*/*Fagopsis*/*Nothofagus*-dominated forests in the Western Hemisphere is not, therefore, reflected in the Primorye localities.

If Cenozoic Eomeropidae are host-dependent at the family level on a plant taxon or related taxa, one consideration is that they may feed specifically on *Fagus*/*Fagopsis*/*Nothofagus* leaf litter in the Western Hemisphere, with a host shift to a taxon providing their key dietary factor in Primorye (or vice versa, depending on place of origin), or they may depend on a nonfagaceous plant that is itself dependent on any of these forest types. Alternatively, they also may require a set of climatic or other (unknown, e.g., the dynamics of a common forest structure) requirements that are shared with each of these particular forests, requiring no host shift across Beringia. *Pinus* is the only genus known to be in common between the four fossil localities; a number of genera are common to three localities. No tree genus is shared between reported occurrences at the fossil localities (above-mentioned references) and those listed by Veblen et al. (1996) as common in the Chilean Valdevian *Nothofagus* forest. It would seem that the floral associations of Eomeropidae in the Cenozoic are more complex than dependency on the dominance of particular Fagales in their respective forests. Any such floral association(s) also may be distinct only at a lower taxonomic level.

Climatic Parameters. The Early Eocene was the warmest time of the Cenozoic (Zachos et al. 2001). Wolfe (1994) reports Early Eocene MAT for low altitude localities in far-western North America of an upper mesothermal ≈19°C for coastal Kulthieth, AK, and a megathermal >27°C at Susanville, CA. Between these localities, upland McAbee had an upper microthermal MAT of ≈10°C by leaf physiognomy (both CLAMP and leaf margin analysis) and ≈13°C by nearest living relative of flora analysis, with mild winters as indicated by the presence of palms (pollen) limited to CMMT >5°C (Greenwood and Wing 1995, Greenwood et al. 2005, Moss et al. 2005). MAT estimates at Late Eocene upland Florissant (cooler worldwide than the Early Eocene, Zachos et al. 2001) indicate a lower mesothermal ≈13–14°C by leaf physiognomy (Gregory and McIntosh 1996), to a mid-mesothermal MAT of ≈17°C by the nearest living relative of flora method, with few, if any frost days also indicated by the presence of palms (Leopold and Clay-Poole 2001). Preliminary analysis by leaf physiognomy (CLAMP) gives an upper microthermal 10–12°C MAT for Amgu, and CMMT of 4–6°C (M.A.A., unpublished data). The climatic parameters of the Yushangou locality have not been determined.

Notiothauma has been collected near the coastal town of Picatrihue (MAT 15°C) and from localities into the cooler highlands (no elevation data given): Cordillera de Nahuelbuta (13°C MAT); Cerrol Nielol National Monument (12°C MAT). Although the modern Chilean *Nothofagus* forests may receive snowfall, and even snow lie, the ground never freezes (D. R. Greenwood, personal communication). Temperature at the sea level city of Concepción (37° S), in the Valdevian *Nothofagus* forest, varies between a CMMT of ≈9°C and a summer high of ≈17°C (Veblen et al. 1996).

The Eocene is characterized as having increased equability (lower temperature seasonality) extending into mid- and high latitudes, with support from plant, vertebrate, and insect fossils (above; Wing and Greenwood 1993, Markwick 1994, Greenwood and Wing 1995, Archibald and Farrell 2003).

From these data, where climatic parameters have been determined, Cenozoic Eomeropidae is known to range in regions of climates with upper microthermal to mid-mesothermal MAT, and mild winters with few, if any, freezing days.

This model of climatic tolerance, however, leaves the problem of dispersal between the Northern and Southern Hemispheres across megathermal low latitudes. Raven and Axelrod (1974) speculate on the similar problem of migration of *Nothofagus* into the Gondwanan region from a hypothesized Laurasian origin, discussing the possibility of sufficiently high montane regions across Africa-India in the mid-Cretaceous. There is a conspicuous absence of *Nothofagus* pollen in the fossil record of these continents, however, and although this is negative evidence, the lack of detection in Africa and India of its abundant and well-known fossil pollen is thought to be significant (Hill and Dettmann 1996).

Mountainous regions today extend through Central America, ending close to the northern Andes. The possibility may be considered that Eomeropidae entered South America relatively recently, after the late Neogene connection of Central and South America. By the Pleistocene, significant uplands had developed through this region, and cool temperate North American taxa such as *Quercus* (Fagaceae) and *Alnus* (Betulaceae) occurin the Andes at this time (Hooghiemstra and Ran 1994, Graham 2003).

A possible earlier dispersal route is through the proto-Antilles. This island group is currently modeled as forming in the Jurassic, roughly in the region occupied by the Isthmus of Panama today, although not (significantly) emergent to form a terrestrial corridor until the Middle Eocene (Iturralde-Vincent and MacPhee 1999, Graham 2003). The period of maximal land exposure was in the Late Eocene–Early Oligocene; during this time, positioned significantly eastward by plate movement, interrupted highlands regions had formed along its almost continuously emergent length, connected at its southern end to South America (Iturralde-Vincent and MacPhee 1999).

Although the climatic regimes and taxa differ, a similar problem arises with the disjunct distribution of flora between the Sonoran-Chihuahuan deserts of the southwestern United States and the Monte region of Argentina (Solbrig 1972).

Regional Topography. *Eomerope macabeensis, E. asiatica,* and *E. tortriciformis* are all found in Eocene montane regions. The McAbee locality is one of the Okanagan Highlands series of fossil localities, which extends through ≈1,000 km of southern British Columbia (Canada) into northeastern Washington state. This region is regarded as an Eocene upland from geological indicators (Ewing 1981, Tribe 2005), and through comparison of both the composition and the derived MAT of the Okanagan Highlands floras with those of coeval coastal lowland formations in British Columbia and Washington state (Rouse et al. 1971, Wolfe and Wehr 1987). Although he did not include McAbee specifically in his analyses, Wolfe (1994) determined a paleoaltitude above 2,000 m for Okanagan Highlands localities to the north and south of it (Wolfe 1994, Wolfe et al. 1998). Tribe (2005) determines a paleoaltitude for McAbee of ≈500–800 m. Paleoelevation estimates for Florissant (summarized by Meyer 2001) indicate similar to much higher (maximum 4,133 m: Wolfe 1994) elevations than those hypothesized for the Okanagan Highlands. Akhmetiev (1973) assumed paleoaltitude of at least 1,000 m for the Tadushi Fm (including Yushangou); Zherikhin (1978) also considered these sites to be montane. Paleoelevation of the Amgu locality has not been established, although the microthermal MAT value estimated for Amgu (see above) indicates montane topography.

Notiothauma is recorded from both lowland coastal and montane regions (see above).

Conclusions. The extant realized niche of Eomeropidae, expressed in a geographically restricted portion of Southern Chile, consists of that combination of particular environmental and biotic factors necessary for the family, which may constitute a relict subset of those expressed more widely in parts of western North America and far-eastern Asia in the early Paleogene. They are known from forested regions, in particular those dominated by Fagaceae or Nothofagaceae in the Western Hemisphere. It is also possible (in East Asia as well) that they require communities structurally similar to those forest types, or which contain an unknown subordinate and common key floral taxon. They are known almost exclusively from uplands, and, where climatic parameters are known, are always found in upper microthermal to mid-mesothermal MAT that lack freezing days in the winter.

None of these hypothetical requirements exclude dispersal models of Cenozoic Eomerope between Asia and North America via Beringia (*Eomerope* in particular), or from a possibly ancestral Asia through Antarctica to Chile. By these criteria, dispersal through the low latitudes between the northern and southern hemispheres, however, remains unclear. Possibilities include migration through uplifted regions of the Isthmus of Panama after the later Neogene, or via highlands of the proto-Antilles in the latest Eocene to earliest Oligocene.

Acknowledgments

We thank Ken Klein (UCC) for loan of the specimen; David Langevin for donation of the specimen to the UCC collection; Stephen Fisher; David Greenwood (Brandon University), Brian Farrell (MCZ), Andrew Knoll (MCZ), Vladimir Makarkin (Institute of Biology and Soil Sciences, RAS), Bruce Tiffney (University of California, Santa Barbara), Roger Vila (MCZ), and Rainer Willmann (Georg-August University) for discussion of aspects of this research and for proving literature and translation; Zhang Junfeng (Nanjing Institute of Geology and Palaeontology, CAS, Nanjing, China) for information about the new eomeropid from Daohugou; and Jen Fogarty (MCZ) for photography. We thank two anonymous reviewers for helpful comments. Funding (to S.B.A.) was provided in part by a Natural Science and Engineering Research Council scholarship and a Putnam Expeditionary Grant.

References Cited

Akhmetiev, M. A. 1973. Miocene flora of Sichote-Alin (Botchi River). Akad Nauk USSR, Geol. Inst. Moscow Trans. 247: 1–104.

Akhmetiev, M. A. 1988. Kainozoiskie flory vostochnogo Sikhote-Alinya [The Cenozoic floras of eastern Sikhote-Alin]. Geol. Inst. Moscow.

Akhmetiev, M. A., and V. L. Samsonenko. 1997. New species of the Eocene plants from the Rarytkin Ridge (North Korjakia). Paleont. J. 2: 94–102.

Andrews, J. A. 1985. True polar wandering: an analysis of Cenozoic and Mesozoic paleomagnetic poles. J. Geophys. Res. B. 90: 7737–7750.

Archibald, S. B., and B. D. Farrell. 2003. Wheeler's dilemma, pp. 17–23. *In* E. Krzeminska and W. Krzeminski [eds.], Proceedings of the Second Congress on Paleoentomology "Fossil Insects", Kraków, Poland, 5–9 September 2001. Acta Zool. Cracov. 46 (supplement).

Artigas, J. N. 1999. Morfologia de las partes duras en la genitalia de la hembra de *Notiothauma reedi* MacLachlan (Mecoptera-Eomeropidae). Bol. Soc. Biol. Concepción Chile 70: 45–54.

Basinger, J. F., D. R. Greenwood, and T. Sweda. 1994. Early Tertiary vegetation of Arctic Canada and its relevance to palaeoclimatic interpretation, pp. 176–198. *In* M. C. Boulter and H. C. Fisher [eds.], Cenozoic plants and climates of the Arctic. NATO ASI Series, 27, I. Springer, Berlin, Gremany.

Beard, K. C., and M. R. Dawson. 1999. Intercontinental dispersal of Holarctic land mammals near the Paleocene/

Eocene boundary: paleogeographic, paleoclimatic and biostratigraphic implications. Bull. Soc. Géol. Fr. 170: 697–706.

Bersenev, I. I., Y. B. Ustinovskaya, I. Buryanova, S. I. Nevolina, and V. V. Medvedev. 1969. Paleogenovaya systema, pp. 317–344. *In* Geologia SSSR. Tom 32. Primorskii Krai. Chast' 1. Geologicheskie opisaniya. Nedra Press, Moscow, Russia.

Bowen, J. B., W. C. Clyde, P. L. Koch, S. Ting, J. Alroy, T. Tsubamoto, Y. Wang, and Y. Wang. 2002. Mammal dispersal at the Paleocene/Eocene boundary. Science (Wash. DC) 295: 2062–2065.

Budantsev, L. Y. 1983. The Arctic flora history of Early Cenophytic. Nauka, Leningrad.

Byers, G. W. 1965. New and uncommon Neotropical Mecoptera. J. Kans. Entomol. Soc. 38: 135–144.

Byers, G. W., and R. Thornhill. 1983. The biology of Mecoptera. Annu. Rev. Entomol. 28: 203–228.

Carpenter, P. M. 1972. The affinities of *Eomerope* and *Dinopanorpa.* Psyche 19: 79–87.

Cockerell, T.D.A. 1909. Description of Tertiary insects, VI. Am. J. Sci. 27: 381–387.

Denk, T. 2004. Revision of *Fagus* from the Cenozoic of Europe and southwestern Asia and its phylogenetic implications. Doc. Natur. 150: 1–72.

Dillhoff, R. M., E. B. Leopold, and S. R. Manchester. 2005. The McAbee Flora and its relation to the early middle Eocene Okanagan Highlands flora of the Pacific Northwest. Can. J. Earth Sci. 42: 151–166.

Estes, R., and J. H. Hutchinson. 1980. Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago. Palaeogeogr. Palaeoclimatol. Palaeoecol. 30: 325–347.

Evanoff, E., W. C. McIntosh, and P. C. Murphey. 2001. Stratigraphic summary and 40Ar/39Ar geochronology of the Florissant Formation, Colorado. Proc. Denver Mus. Nat. Sci. Ser. 4: 1–16.

Ewing, T. E. 1981. Regional stratigraphy and structural setting of the Kamloops group, south-central British Columbia. Can. J. Earth Sci. 18: 1464–1477.

Farrell, B. D. 1998. "Inordinate fondness" explained: why are there so many beetles? Science (Wash. DC) 281: 555–559.

Gandolfo, M. 1996. The presence of Fagaceae (oak family) in sediments of the Klondike Mountain Formation (Middle Eocene), Republic, Washington. Wash. Geol. 24: 20–21.

Gray, J. 1960. Temperate pollen genera in the Eocene (Claiborne) flora, Alabama. Science (Wash. DC) 132: 808–810.

Graham, A. 1972. Outline of the origin and historical recognition of floristic affinities between Asia and eastern North America, pp. 1–18. *In* A. Graham [ed.], Floristics and paleofloristics of Asia and eastern North America. Elsevier, Amsterdam, The Netherlands.

Graham, A. 2003. Geohistory models and Cenozoic paleoenvironments of the Caribbean region. Syst. Bot. 28: 376–386.

Greenwood, D. R., S. B. Archibald, R. W. Mathewes, and P. T. Moss. 2005. Fossil biotas from the Okanagan Highlands, southern British Columbia and northeastern Washington State: climates and ecosystems across an Eocene landscape. Can. J. Earth Sci. 42: 167–185.

Greenwood, D. R., and S. L. Wing. 1995. Eocene continental climates and latitudinal gradients. Geology 23: 1040–1048.

Gregory, K. M., and W. C. McIntosh. 1996. Paleoclimate and paleoelevation of the Oligocene pitch-pinnacle flora: Sawatch Range, Colorado. Geol. Soc. Am. Bull. 108: 545–561.

Hamilton, W. 1983. Cretaceous and Cenozoic history of the northern continents. Ann. Mo. Bot. Gard. 70: 440–458.

Hepburn, H. R. 1969. The proventriculus of Mecoptera. J. Ga. Entomol. Soc. 4: 159–167.

Hill, R. S., and M. E. Dettmann. 1996. Origin and diversification of the genus *Nothofagus,* pp. 293–353. *In* T. T. Verblen, R. S. Hill, and J. Read [eds.], The ecology and biogeography of *Nothofagus* forests. Yale University Press, New Haven, CT.

Hooghiemstra, E., and E.T.H. Ran. 1994. Late Pliocene-Pleistocene high resolution pollen sequence of Columbia: an overview of climatic change. Quat. Int. 21: 63–80.

Hunt, R. J., and I. Poole. 2003. Paleogene West Arctic climate and vegetation history in light of new data from King George Island. Geol. Soc. Am. Special Paper 369: 395–412.

International Trust for Zoological Nomenclature. 1985. International code of zoological nomenclature. 3rd ed. International Trust for Zoological Nomenclature, London, United Kingdom.

Iturralde-Vincent, M. A., and R.D.E. MacPhee. 1999. Paleogeography of the Caribbean region: implications for Cenozoic biogeography. Bull. Am. Mus. Nat. Hist. 238: 1–95.

Jones, J. H. 1986. Evolution of the Fagaceae: the implications of foliar features. Ann. Mo. Bot. Gard. 73: 228–275.

Kryshtofovich, A. N. 1921. Tertiary plants of the Amgu River of the Primorye Region Collected by A. G. Kurznetsov. Mater. Geol. Min. Res. Far East No. 15: 1–15.

Leopold, E. B., and S. T. Clay-Poole. 2001. Florissant leaf and pollen floras of Colorado compared: climatic implications, pp. 17–70. *In* E. Evanoff, K. Gregory-Wodzicki, and K. Johnson [eds.], Fossil flora and stratigraphy of the Florissant Formation, Colorado. Proc. Denver Mus. Nat. Sci. Ser. 4, no. 1.

Manchester, S. R. 1999. Biogeographical relationships of North American Tertiary floras. Ann. Mo. Bot. Gard. 86: 472–522.

Manchester, S. R. 2001. Update on the Megafossil Flora of Florissant, Colorado, pp. 137–162. *In* E. Evanoff, K. Gregory-Wodzicki, and K. Johnson [eds.], Fossil flora and stratigraphy of the Florissant Formation, Colorado. Proc. Denver Mus. Nat. Sci. Ser. 4, no. 1.

Manchester, S. R., and P. R. Crane. 1983. Attached leaves, inflorescences, and fruits of *Fagopsis,* an extinct genus of fagaceous affinity from the Oligocene Florissant flora of Colorado, U.S.A. Am. J. Bot. 70: 1147–1164.

Manchester, S. R., and R. M. Dillhoff. 2004. *Fagus* (Fagaceae) fruits, foliage, and pollen from the Middle Eocene of Pacific Northwestern North America. Can. J. Bot. 82: 1509–1517.

Markwick, P. J. 1994. "Equability," continentality, and Tertiary "climate": the crocodilian perspective. Geology 22: 613–616.

Meyer, H. W. 2001. A review of paleoelevation estimates from the Florissant flora, Colorado, pp. 205–216. *In* E. Evanoff, K. Gregory-Wodzicki, and K. Johnson [eds.], Fossil flora and stratigraphy of the Florissant Formation, Colorado. Proc. Denver Mus. Nat. Sci. Ser. 4, no. 1.

McKenna, M. C. 1980. Eocene paleolatitude, climate, and mammals of Ellsmere Island. Palaeogeogr. Palaeoclimatol. Palaeoecol. 30: 349–362.

Mickoleit, G. 1976. Die Genital- und Postgenitalsegmente der Mecoptera-Weibchen (Insecta, Holometabola). II. Das Dach der Genitalkammer. Zoomorphol. 85: 133–156.

Mitter, C., B. D. Farrell, and D. J. Futuyma. 1991. Phylogenetic studies of insect-plant interactions: insights into the genesis of diversity. Trends Ecol. Evol. 6: 290–293.

Moran, N. A. 1989. A 48-million-year-old aphid-host plant association and complex life cycle: biogeographic evidence. Science (Wash. DC) 245: 173–175.

Moss, P. T., D. R. Greenwood, and S. B. Archibald. 2005. Regional and Local Vegetation Community Dynamics of the Eocene Okanagan Highlands (British Columbia/ Washington State) from Palynology. Can. J. Earth Sci. 42: 187–204.

Novokshonov, V. G. 1977. Rannyaya evolyutsiya skorpionnits [Early evolution of scorpionflies (Insecta: Panorpida)]. Nauka, Moscow, Russia.

Novokshonov, V. G. 2002. Order Panorpida Latreille, 1802. The scorpionflies, pp. 194–199. *In* A. P. Rasnitsyn and D.L.J. Quicke [eds.], History of insects, Kluwer Academic, Dordrecht, The Netherlands.

Pigg, K. B., and W. C. Wehr. 2002. Tertiary flowers, fruits, and seeds of Washington State and adjacent areas—part III. Wash. Geol. 30: 3–16.

Peña, L. E. 1968 Natural History Notes on *Notiothauma.* Discovery (Yale University) 4: 42–44.

Penny, N. D. 1975. Evolution of the extant Mecoptera. J. Kans. Entomol. Soc. 48: 331–350.

Ponomarenko, A. G., and A. P. Rasnitsyn. 1974. New Mesozoic and Cenozoic Protomecoptera. Paleont. J. 4: 493–507.

Rasnitsyn, A. P., and V. V. Zherikhin. 2002. Alphabetical list of selected insect fossil sites: impression fossils, pp. 437–444. *In* A. P. Rasnitsyn and D.L.J. Quicke [eds.], History of insects. Kluwer Academic, Dordrecht, The Netherlands.

Raven, P. H., and D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Mo. Bot. Gard. 61: 539–673.

Rebolledo, R. R., L. L. Alda, M. S. Gutiérrez, and B. S. Guiñez. 1990. Antecedentes biológicos de *Notiothauma reedi* MacLachlan (Mecoptera: Eomeropidae) en el Monumento Natural Cerro Ñielol (Temuco, Chile). Rev. Chilena Entomol. 18: 25–28.

Romero, E. J. 1986. Fossil evidence regarding the evolution of *Nothofagus* Blume. Ann. Mo. Bot. Gard. 73: 276–283.

Rouse, G. E., W. S. Hopkins, Jr., and K. M. Piel. 1971. Palynology of some Late Cretaceous and Early Tertiary deposits in British Columbia and adjacent Alberta. Geol. Soc. Am., Special Paper 127: 213–246.

Savolainen, V., M. W. Fay, D. C. Albacj, A. Backlund, M. van der Bank, K. M. Cameron, S. A. Johnson, M. D. Lledo, J.-C. Pintaud, M. Powell, et al. 2000. Phylogeny of the eudicots: a nearly complete familial analysis based on *rbcL* gene sequences. Kew Bull. 55: 257–309.

Sequeira, A. S., and B. D. Farrell. 2001. Evolutionary origins of Gondwanan interactions: how old are Araucaria beetle herbivores? Biol. J. Linn. Soc. 74: 459–474.

Sequeira A. S., B. B. Normark, and B. D. Farrell. 2000. Evolutionary assembly of the conifer fauna: distinguishing ancient from recent associations in bark beetles. Proc. R. Soc. B 267: 2359–2366.

Solbrig, O. T. 1972. The floristic disjunctions between the "Monte" in Argentina and the "Sonoran Desert" in Mexico and the United States. Ann. Mo. Bot. Gard. 59: 218–223.

Tanai, T. 1974. Evolutionary trend of the genus *Fagus* around the northern Pacific basin, pp. 62–83. *In* Symposium on Origin and Phytogeography of Angiosperms. Birbal Sahni Institute of Palaeobotany, Special Publ. No. 1.

Tanai, T. 1995. Fagaceous leaves from the Paleogene of Hokkaido, Japan. Bull. Natl. Sci. Mus., Tokyo Ser. C 21: 71–101.

Taylor, D. W. 1990. Paleobiogeographic relationships of angiosperms from the Cretaceous and early Tertiary of the North American area. Bot. Rev. 56: 279–417.

Tiffney, B. H. 1985. Perspectives on the origin of the floristic similarity between eastern Asia and eastern North America. J. Arnold Arb. 66: 73–94.

Tiffney, B. H., and S. R. Manchester. 2001. The use of geological and paleontological evidence in evaluating plant phylogenetic hypotheses in the Northern Hemisphere Tertiary. Int. J. Plant Sci. 162 (6 suppl.): S3–S17.

Tribe, S. 2005. Eocene paleo-physiography and drainage directions, southern Interior Plateau, British Columbia. Can. J. Earth Sci. 42: 215–230.

Veblen, T. T., C. D. Donoso, T. Kitzberger, and A. J. Rebertus. 1996. Ecology of southern Chilean and Argentinean *Nothofagus* forests, pp. 11–24. *In* T. T. Verblen, R. S. Hill, and J. Read [eds.], The ecology and biogeography of *Nothofagus* forests. Yale University Press, New Haven, CT.

Wehr, W. C. 1998. Middle Eocene insects and plants of the Okanogan highlands, pp. 99–109. *In* J. E. Martin [ed.], Contributions to the paleontology and geology of the West Coast; in honor of V. Standish Mallory: Thomas Burke Memorial Washington State Museum Research Report 6.

Willmann, R. 1978. Mecoptera (Insecta, Holometabola). Fossilium Cat. (Animalia) 124: 1–139.

Willmann, R. 1981. Phylogenie und Verbreitungsgeschichte der Eomeropidae (Insecta: Mecoptera). Ein Beispiel für die Anwendung der phylogenetischen Systematik in der Paläontologie. Paläont. Z. 55: 31–49.

Willmann, R. 1983. Widersprüchliche Rekonstruktionen der Phylogenese am Beispiel der Ordnung Mecoptera (Schnabelfliegen; Insecta: Holometabola). Paläont. Z. 57: 285–308.

Willmann, R. 1989. Evolution und Phylogenetisches System der Mecoptera (Insecta: Holometabola). Abh. Senckenb. Natf. Ges. 544: 1–153.

Wing, S. L., and D. R. Greenwood. 1993. Fossils and fossil climate: the case for equable continental interiors in the Eocene, pp. 243–253. *In* J.R.L. Allen, B. J. Hoskins, B. W. Sellwood, and R.A. Spicer [eds.], Paleoclimates and their modeling with special reference to the Mesozoic Era. Phil. Trans. R. Soc. Lond. B 341.

Wolfe, J. A. 1979. Temperature parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the northern hemisphere and Australasia. U.S. Geol. Surv. Prof. Paper 1106.

Wolfe, J. A. 1994. Tertiary climatic changes at middle latitudes of western North America. Palaeogeogr. Palaeoclimatol. Palaeoecol. 108: 195–205.

Wolfe, J. A., and W. Wehr. 1987. Middle Eocene dicotyledonous plants from Republic, northeastern Washington. U.S. Geol. Surv. Bull. 1597: 1–25.

Wolfe, J. A., C. E. Forest, and P. Molnar. 1988. Paleobotanical evidence of Eocene and Oligocene paleoaltitudes in midlatitude western North America. Geol. Soc. Am. Bull. 110: 664–687.

Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science (Wash. DC) 292: 686–693.

Zherikhin, V. V. 1978. Razvitie i smena melovykh i kainozoiskikh faunisticheskikh kompleksov (trakheinye i khelitserovye). Nauka Press; Moscow. Trudy Paleontologicheskogo Instituta 165: 1–200.

Received 26 November 2004; accepted 20 April 2005.