New genus of minute Berothidae (Neuroptera) from Early Eocene amber of British Columbia

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Abstract—*Microberotha macculloughi* **gen. nov.** and **sp. nov.** from Early Eocene Okanagan Highlands amber of Hat Creek, British Columbia, Canada, is described. This new genus and species represents one of the smallest members of the family Berothidae and the first occurrence of the family in the New World Tertiary. The systematic position of the genus *Microberotha* within the family is rather unclear, but the structure of the male genitalia indicates a close association with the subfamily Cyrenoberothinae. Stratigraphy and palaeoenvironment of the Hat Creek locality are briefly discussed.

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Résumé—On trouvera ici la description de *Microberotha macculloughi* **gen. nov.** et **sp. nov.** provenant de l'ambre de l'éocène inférieur de Hat Creek, dans les hautes terres de l'Okanagan, Colombie Britannique, Canada. Cet insecte appartenant à un nouveau genre et une nouvelle espèce est l'un des plus petits de la famille des Berothidae; il représente aussi la première mention de la famille du tertiaire du Nouveau Monde. La position systématique de la genre *Microberotha* dans la famille est plutôt incertaine, mais les organes sexuels mâles indiquent une forte association avec la sous-famille des Cyrenoberothinae. La stratigraphie et le paléoenvironnement du site de Hat Creek font l'objet d'une courte discussion.

[Traduit par la Rédaction]

Introduction

The extant family Berothidae is a small family comprising about 100 species in 22 genera, excluding the subfamily Rhachiberothinae (Aspöck and Nemeschkal 1998). The status of the latter subfamily, with 13 living species of 3 genera from Africa, is unclear. It has been considered a subfamily of Berothidae (Tjeder 1959; MacLeod and Adams 1967; Grimaldi 2000) and of the family Mantispidae (Willmann 1990, 1994), or as a separate family (Aspöck and Mansell 1994; Aspöck and Aspöck 1997). The subfamily Rhachiberothinae is characterized in particular by raptorial forelegs, which it shares with Mantispidae. Here we follow Grimaldi (2000) in considering the subfamily Rhachiberothinae within the family Berothidae, although the problem of the status of Rhachiberothinae/-dae is outside the scope of this paper.

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Species of the family Berothidae are discontinuously distributed, primarily throughout the tropical and warm-temperate regions of the world, although some species extend into temperate regions as far north as southern Canada and as far south as New Zealand (Aspöck 1986). Some are known to be termitophiles, at least the larvae of the North American species *Lomamyia latipennis* Carpenter (Neuroptera: Berothidae), which are known to feed on the termite *Reticulitermes hesperus* Banks (Isoptera: Rhinotermitidae) within their subterranean galleries (Tauber and Tauber 1968; Johnson and Hagen 1981). Larvae of the Australian *Spermophorella* sp. (Neuroptera: Berothidae) occur under bark (New 1991).

Thirteen fossil species representing 11 extinct genera have hitherto been described in the family Berothidae. These genera range from the Late Jurassic through mid-Paleogene: *Oloberotha* Ren *et* Guo from the Late Jurassic of Liaoning Province, China (Ren and Guo 1996); *Banoberotha* Whalley and *Paraberotha* Whalley from the Early Cretaceous of Lebanon (Whalley 1980); *Araripeberotha* Martins-Neto *et* Vulcano and *Caririberotha* Martins-Neto *et* Vulcano from the Early Cretaceous (Aptian) of Brazil (Martins-Neto and Vulcano 1990); *Jersiberotha* Grimaldi, *Nasciberotha* Grimaldi, and *Rhachibermissa* Grimaldi from the Late Cretaceous (Turonian) of New Jersey, United States of America (Grimaldi 2000); *Retinoberotha* Schlüter from the Late Cretaceous (Cenomanian) of France (Schlüter 1978), *Plesiorobius* Klimaszewski *et* Kevan from the Late Cretaceous of Canada and northern Siberia (Klimaszewski and Kevan 1986; Makarkin 1994); and *Proberotha* Krüger from Eocene Baltic amber (Krüger 1923). The genera possessing raptorial forelegs (*Retinoberotha*, *Paraberotha*, and *Rhachibermissa*) may belong to the subfamily Rhachiberothinae (Grimaldi 2000), whereas the subfamily affinities of the other genera are uncertain, although some have been tentatively associated with various extant subfamilies.

Six specimens of the family Berothidae representing 3–4 species have been previously reported from the Tertiary, all from Baltic amber. Of these, three specimens belong to *Proberotha prisca* Krüger, which is described but not illustrated (Krüger 1923). Two other specimens, which are photographed but neither described nor named, are certainly not congeneric with the genus *Proberotha* (Bachofen-Echt 1949, Fig. 122; Weitschat and Wichard 1998, Figs. 55*a*, 55*b*). Finally, there is "an undescribed amber berothid in the collection of the Museum of Comparative Zoology which, judging from Krüger's rather incomplete description of *P. prisca*, is probably not congeneric, has long hypocaudae and is obviously a berothine" (MacLeod and Adams 1967, p 258).

In the present paper, we describe a new genus of the family Berothidae from Early Eocene Hat Creek amber of British Columbia and discuss its systematic position within the family and its paleoenvironmental context. Hitherto, only one paper has been published on the insects of Hat Creek, containing some preliminary identifications (Poinar *et al.* 1999).

Morphological terminology largely follows that of Ulrike Aspöck (*e.g.*, Aspöck and Mansell 1994; Aspöck and Nemeschkal 1998), except for the forewing venation: "MP" is simply M and "MA" is the most proximal branch of Rs (as interpreted in the family Hemerobiidae by Oswald 1993).

Materials and methods

A small number of insects in amber, including the present specimen, were collected at Hat Creek in the mid-1990s and donated by David Langevin to the Kelowna Centennial Museum (Kelowna, British Columbia), which then loaned us the present specimen. In the years of collecting since that time (SBA), no other Neuroptera have been recovered from Hat Creek, although a quantity of amber remains to be prepared.

The amber piece is pale yellow and generally clear, except as noted below. The collector did initial polishing; the specimen was further prepared by Alex Brown in Berkeley, California. As is common with Hat Creek amber, this piece was somewhat opaque in places; bubbles, fractures that act as internal reflective surfaces, discolouration between subsequent flow surfaces, and bits of organic matter somewhat obscured the specimen. Consequently, the amber was further prepared at the American Museum of Natural History fossil insect laboratory by Paul Nascimbene, according to the protocols of Nascimbene and Silverstein (2000). It was ground to a small chip on a disc grinder, embedded in clear resin under reduced pressure in a bell jar, and repolished. As the dorsal aspect of the abdomen remained obscured by imperfections in the amber, further preparation by sanding with 1500 grit sandpaper and polishing using German dental polish with beeswax (unknown brand) was done at Harvard under the direction of Gary Alpert. Digital photography was done using a JVC 3-CCD camera adapted to interface with AUTO-MONTAGE version 4.0 (Syncroscopy 2002) and a Leica MZ 12.5 dissecting microscope.

Stratigraphy and palaeoenvironment of Hat Creek

George Mercer Dawson visited the Hat Creek deposit for the Geological Survey of Canada (GSC) in 1877 to examine the coal beds that had long been known; on this expedition, Dawson collected the first reported discoveries of Eocene fossil insects from British Columbia in shale deposits on the Fraser River at Quesnel and in the Allenby Formation on the Similkameen River (Dawson 1879). Almost 50 years later, another GSC geologist, BR MacKay, reported that “parts of the coal are characterized by small lenses, globules, and irregular-shaped masses of light-yellow, semi-transparent fossilized amber or retinite” (MacKay 1926, p A327). Fossil inclusions in this amber were unreported until a small collection of fossil insects (above) was first brought to the attention of one of us (SBA) by the collector in 1997.

The amber is found within sub-bituminous coal situated between Cache Creek and Lillooet in south-central British Columbia. This is the thickest coal deposit in the world, about 425 m (Church 1981) and with over 2 billion tonnes of reserve indicated by core drilling (Kim 1979). The Hat Creek locale is part of a series of Eocene fossil-bearing sites known collectively as the Okanagan Highlands (Archibald and Mathewes 2000), which extend from Republic, Washington, in the south through about 1000 km north to Driftwood Canyon, west-central British Columbia. This series was formed by regional tectonic uplift, which resulted in fault-bounded grabbens in which coal and lacustrine shales were deposited (Ewing 1981; Read 2000).

Coal is often associated with richly fossiliferous shales throughout the Okanagan Highlands; other deposits have been extensively mined since the late 19th century. At some sites coal lies in direct contact with lacustrine shales, as the depositional environment grades between swamp and offshore open water (Wilson 1980). At times these coal deposits contain amber; however, no other occurrence in the Okanagan Highlands has yet been found to contain fossil inclusions.

Hat Creek amber ranges from clear to pale yellow (Poinar *et al.* 1999), although it may be bright red (and extremely fragile) in areas next to burn zones. The coal within which it occurs is commonly harder than the amber, making amber extraction difficult without breakage or extensive fracturing. Nuclear magnetic resonance (NMR) spectroscopy indicated that the amber was formed by resin from the genus *Agathis* (Araucariaceae) (Poinar *et al.* 1999); however, NMR spectroscopy indicating the origins of various Cretaceous ambers from Araucariaceae may be problematic (Grimaldi *et al.* 2000). The determination of an araucariaceous origin of Hat Creek amber was further supported by the reported occurrence of compression fossils of the genus *Araucaria* (Araucariaceae) from the Early Eocene McAbee locality, about 30 km east of Hat Creek (Verschoor 1974); however, this determination is not now considered likely, as these fossils are more probably of the genus *Cunninghamia* (Cupressaceae) (R Stockey, personal communication).

Hat Creek amber is significant primarily for two reasons. First, it is apparently Early Eocene. Potassium–argon dating of overlying rhyolite indicates a minimum age of 51.2 ± 1.4 Ma (million years), and unconformably underlying basalt indicates a maximum age of 91.6 ± 3 Ma (Church *et al.* 1979). More than 550 m of Medicine Creek lacustrine sediments lie below the dated rhyolite and above the amber-bearing coal (Kim 1979). Read (2000), however, suggests that the dated rhyolite may have been superimposed above the Medicine Creek sediments in Quaternary time. Tephra samples from within Hat Creek coal are currently undergoing radiometric analysis for precise age determination of the deposit (JK Mortensen and SB Archibald, current research). Palynological analysis suggests that this deposit is no older than Eocene (Church 1981).

Hat Creek amber then appears to have been formed in a period of time relatively less known in the world amber record. Most well-known Tertiary amber deposits range from Middle Eocene and younger, including amber from the Baltic region, the Dominican Republic, and Chiapas. Cretaceous amber from Alberta and Manitoba, Canada; New Jersey, United States of America; Alava, Spain; Lebanon; and Myanmar are being or have been extensively studied (McAlpine and Martin 1966; Alonso *et al.* 2000; Grimaldi *et al.* 2000, 2002). Fossiliferous amber from the intervening time period remains less studied, including Paleocene amber from Sakhalin, Russia; the recently discovered Early Eocene amber from Oise, France (Nel 1997); Middle to Early Eocene (40–53 Ma) Chinese (Fu Shun) amber; and Early Eocene Clairbourne, Arkansas, United States of America (Poinar 1992).

Secondly, Hat Creek amber is significant because it is situated among roughly coeval insect-bearing lacustrine shale sites. The Early Eocene McAbee (“about 51 Ma”; Ewing 1981) lacustrine shale site (also in the Kamloops Group) is only about 30 km to the east. This locality is extremely rich in fossil insects, which allows for unprecedented comparison between insect assemblages preserved in amber and shale deposits, with their respective environmental and taphonomic biases.

The thickness of the Hat Creek coal deposit indicates that it was likely deposited for a period of between 1.66 and 2.5 Ma (Church 1981). With minor variations, the pollen record indicated a “remarkedly” consistent plant assemblage with no zonation, interpreted as a broad marsh with little or no water circulation in a warm to subtropical lowland environment (Kim 1979; Church 1981). This climatic inference is based on the presence of subtropical *Alnus* spp. (Betulaceae), walnut (*Juglans* spp. (Juglandaceae)), and fungus. Poinar *et al.* (1999) also ascribe a tropical or subtropical environment based on the presence of insect taxa that today are restricted to low latitudes.

Taxon-independent climate analysis (of leaf physiognomy) at McAbee, however, indicates a temperate mean annual temperature at that locality of about 10.7 °C (Greenwood and Wing 1995). Leaf-margin analysis at Okanagan Highlands sites indicate mean annual temperatures consistently microthermal, or <13 °C (reviewed in Archibald and Mathewes 2000) (except for the oldest of the series, the Quilchena locality, which is lower mesothermal at 13–14 °C; Mathewes 2003), and Eocene climate is considered seasonally equable (*e.g.*, Wing and Greenwood 1993; Greenwood and Wing 1995). Therefore, the presence of thermophilic organisms in Okanagan Highland sites (many examples of plants, including palms (Erwin and Stockey 1994), banana (Wehr and Manchester 1996), cycads (Hopkins and Johnson 1997), and such insects as tropical cockroaches, termites, and Hemiptera (Archibald and Mathewes 2000)) may be the result of reduced temperature seasonality (milder winters) rather than increased mean annual temperature (Archibald and Mathewes 2000; Archibald and Farrell 2003). Pollen analysis (Church 1981) also indicates the presence of temperate-associated taxa at Hat Creek including the genera *Betula* (Betulaceae), *Tsuga* (Pinaceae), and *Castanea* (Fagaceae). Modern analogue assemblages of thermophilic/temperate mixture may only exist in mountains of tropical regions (Archibald and Farrell 2003). The possibility must then be considered that Hat Creek, as is hypothesized for other Okanagan Highlands sites, was a temperate, yet equable upland.

Taphonomy

The amber has several sequential internal surface layers. Some internal surfaces indicate cylindrical resin flows; the insect was presumably trapped on a "stalactite" resin flow, likely on the surface of the tree. Such pieces, which resemble wax melted on the side of a candle, are not uncommon in Hat Creek amber and elsewhere. The insect was presumably trapped on its back on the surface of one layer, with the forewings and right hind wing stuck to the resin. The internal flow layer that was the surface to which the insect adhered is clearly visible (layer 3 in Fig. 2). A subsequent flow then engulfed it, forcing the left hind wing upward and twisting it, and tearing off both hind legs (for an example of serial resin flow taphonomy see Grimaldi 1996, p 76). One hind leg was tangled in the right middle leg, and the other was transported a few millimetres to its left in the direction of the downward resin flow. Therefore, we surmise that the insect was trapped with its left side facing downward. The second flow must have been slow and viscous, hardening shortly after engulfing the insect, as the broken hind leg was transported a short distance and the left hind wing was not strongly twisted to the left.

Family Berothidae Handlirsch, 1906

Microberotha Archibald *et* Makarkin, gen. nov.

Type species

Microberotha macculloughi **sp. nov.** (single known species).

Etymology

The generic name is from the Greek *mikros*, "small", and *Berotha*, a genus-group name of the family Berothidae. Gender is feminine.

Diagnosis

The new genus may be easily distinguished from all other genera of the family Berothidae, both extant and fossil, by only one branch of Rs and absence of outer gradate series of crossveins in forewing.

Description

See Description below under *Microberotha macculloughi* **sp. nov.**

Microberotha macculloughi **Archibald *et* Makarkin, sp. nov.**

(Figs. 1–7)

Type material

Holotype: No. NH.998.015.002. Labelled: "HOLOTYPE *Microberotha macculloughi* Archibald et Makarkin". A well-preserved, nearly complete, but somewhat crumpled male specimen in amber; deposited in the Kelowna Centennial Museum (Kelowna, British Columbia, Canada).

Etymology

The species is named in honour of Terry McCullough, in appreciation of his efforts in support of paleontology at Hat Creek. The specific epithet "*macculloughi*" is formed ("*mac-*" not "*mc-*") in accordance with recommendations of the *International Code of Zoological Nomenclature* (refer to "Appendix D: Recommendations on the formation of names; part III. Names based on personal names; Article 21*a*" in International Trust for Zoological Nomenclature 1985).

Description

Head. Approximately as wide as long, with prominent eyes (Fig. 4*b*). Face (between antennae and clypeus) short, apparently not extending ventral to eyes. Vertex moderately elevated, with rather distinct lateral tubercles, covered with rather long fine hairs not confined to tubercles. Postocular zone not particularly inflated. Antennae widely separated, moniliform; scape enlarged, comparatively short, about 2.5 times as long as wide; flagellum with approximately 20 segments. Mouthparts poorly visible, maxillary and labial palps moderately long (Fig. 4*a*). **Thorax.** Pronotum large, rather short, approximately as wide as long (dorsal aspect), somewhat narrowed toward the anterior margin (the latter was almost straight in dorsal aspect), deflected laterally, with two distinct transverse furrows (Fig. 4*c*). Pronotum and mesonotum covered with long fine hairs. Metanotum mostly obscured (Fig. 3). **Legs.** Cursorial, slender, rather scarcely covered with fine hairs. Tibial spurs not present. Tarsi of all legs five-segmented. Claws small. **Forewing.** Length 3.36 mm (presumed when straightened: wing sharply curved, approximately 2.65 mm, seen from above; Fig. 5*a*), maximal width 1.05 mm (Fig. 5*a*, 5*b*); elongate oval with rounded apex, with no suggestion of falcation. Trichosors prominent along entire wing margin. Veins somewhat bulbous at tips, like trichosors. Costal space narrow, dilated maximally at proximal one-forth. Humeral vein not branched, not recurrent. All subcostal veinlets simple. Subcostal space broad. Pterostigma present. Sc, R1 widely spaced distally, 1 apical crossvein between. Sc slightly bent towards R1 at crossvein; distal-most portion of Sc poorly visible (within pterostigma, possibly partly atrophied). Basal crossvein sc-r1 located well basad of origin of Rs. R1 with two marginal forks. Origin of Rs located far from base of wing. Rs and its single branch parallel, both veins not forked before marginal dichotomous branching. R, M fused basally. M forked slightly distal to origin of Rs. M1 dichotomously branched near wing margin. M2 pectinately branching, most proximal branch again pectinately branched near wing margin. Cu forked near base of wing. CuA, CuP parallel to each other; both not forked before marginal branching of 2–3 short branches. 1A, 2A with 3–4 pectinate branches each. 3A not detected. Five crossveins posterior to R1 detected: r1-rs distad to origin of Rs branch; rs-m1, m2-cua distad to forking of M; cup-a1 distad to forking of Cu; a1-a2 proximal to cup-a1. Two basal crossveins not detected: r-m (vein "b") obscured by bubbles in both forewings, m-cu (possibly absent or indistinct). No outer gradate series of crossveins. Anterior margin of wing, longitudinal veins with moderately long hairs;

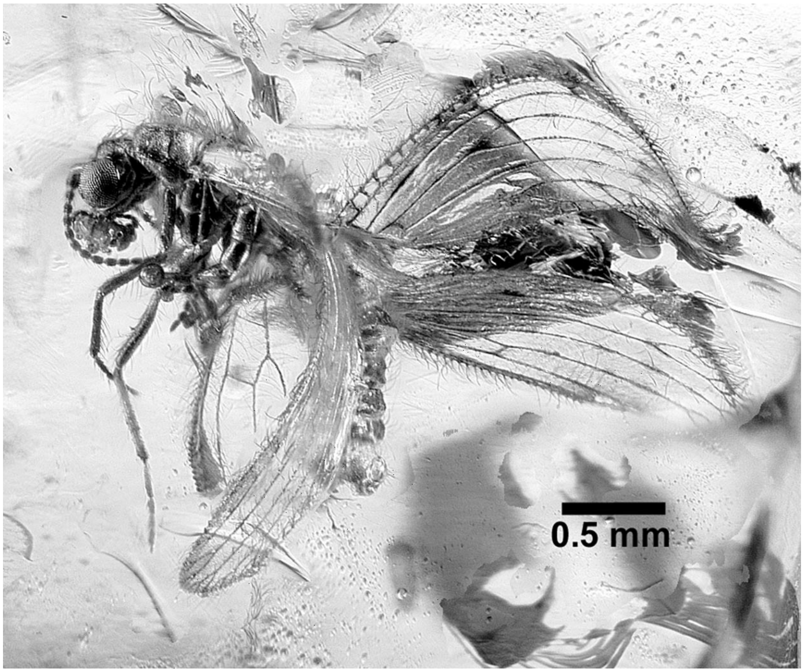

FIGURE 1. ***Microberotha macculloughi*, lateral aspect.**

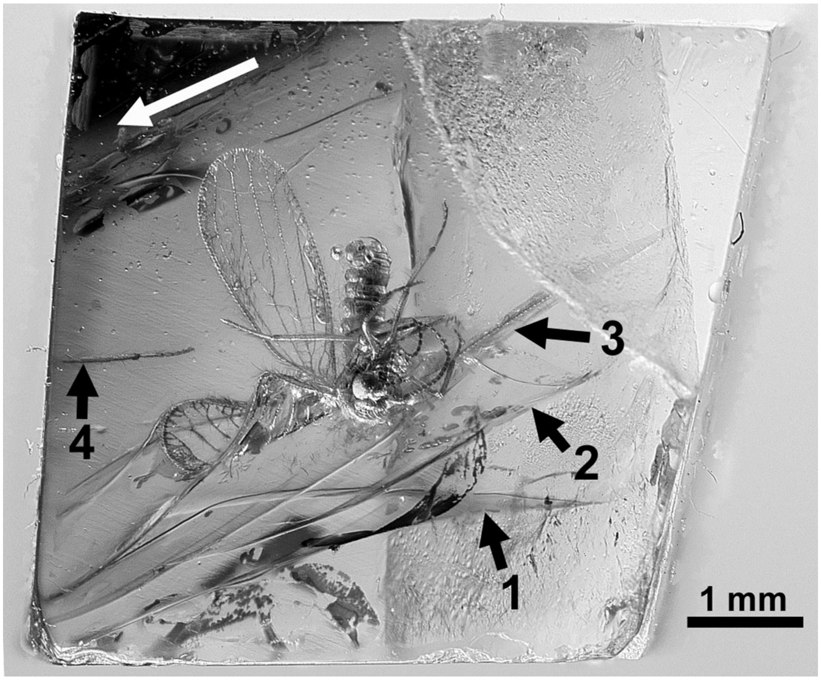

FIGURE 2. Photograph showing flow-layer sequence (1–3) and disarticulated leg (4). White arrow indicates flow direction.

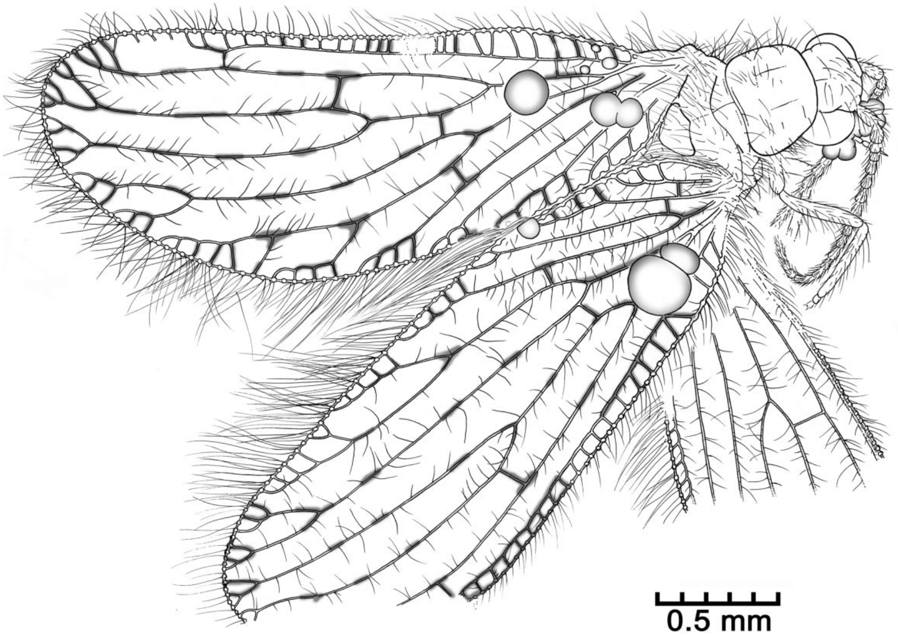

FIGURE 3. ***Microberotha macculloughi*** **habitus, dorsal aspect. Hairs on body reduced for clarity.**

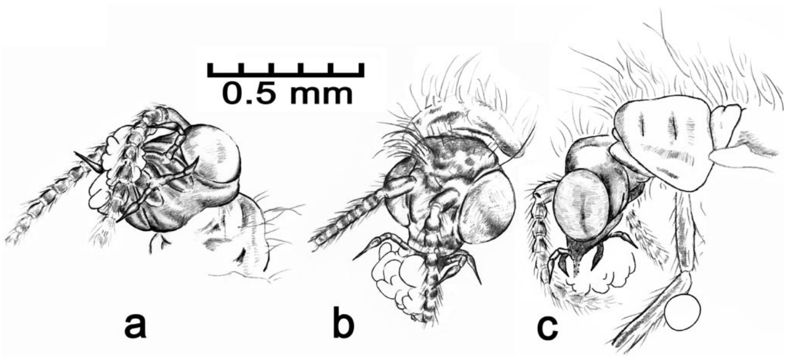

FIGURE 4. ***Microberotha macculloughi*** **head: *a*, lateroventral view; *b*, laterofrontal view; *c*, lateral view. Hairs reduced for clarity.**

posterior margin fringed with long hairs. Membrane of forewings colourless, hyaline, with narrow shading along fuscous interruptions of veins, at some forkings, at ends of crossveins. Longitudinal veins pale, with few short fuscous interruptions. Almost all crossveins fuscous (Fig. 3). **Hind wing** (Fig. 6). Trichosors prominent along entire wing margin. Costal space extremely narrow, developed basally (lesser extent) and apically (greater extent), otherwise C and Sc run nearly adjoining. Subcostal veinlets visible only in apical dilation of costal space, probably unforked. Pterostigma present. Entire subcostal space wide except for basal-most portion; 1–2 apical crossveins present in space. Sc poorly visible apically, possibly partly atrophied. R1 branches few, pectinately branched distally. Rs origin rather close to wing base; arrangement of Rs similar to forewing. Basal "b" vein ("basal piece of MA") present, crossvein-like, located proximal to forking of MP. R and M appear not fused basally (bases of both hind

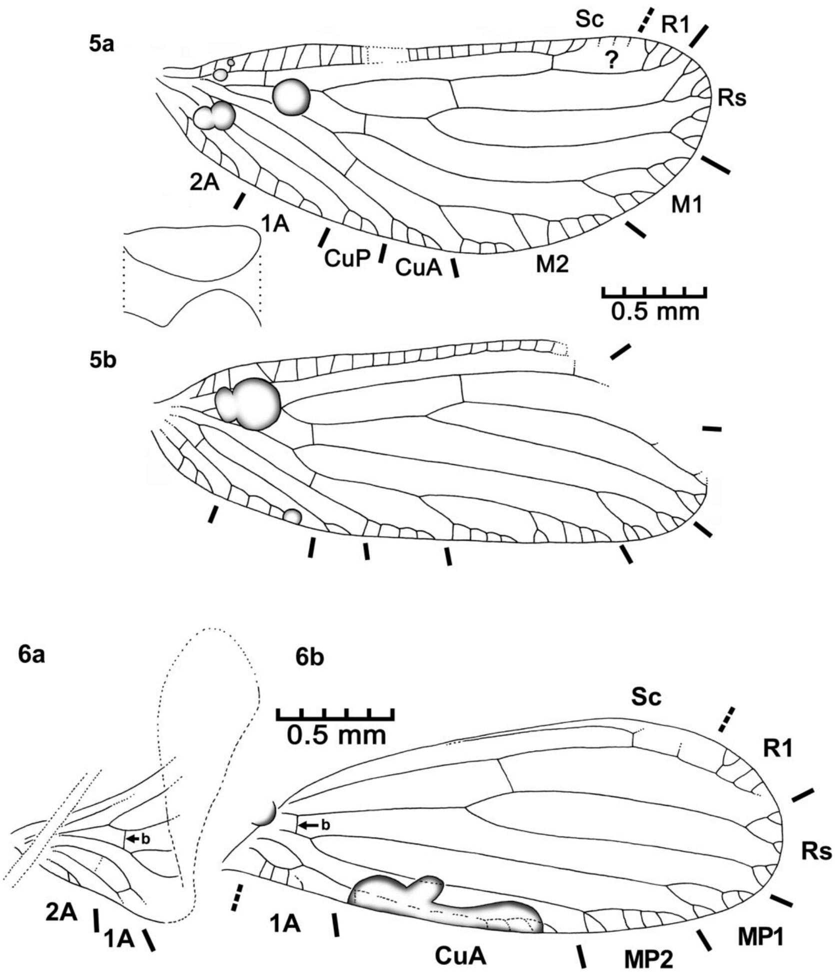

Figure 5, 6. ***Microberotha macculloughi*** **wing venation: 5*a*, left forewing (converted to standard right dorsal view); 5*b*, right forewing; 6*a*, left hind wing, base of wing (dorsal aspect, converted to standard right dorsal view); 6*b*, ventral aspect of same wing. 1A–2A, Anal veins; *b*, basal "*b*" vein ("basal piece of MA"); CuA, anterior cubitus; CuP, posterior cubitus; M, media; MP, media posterior; Rs, radial sector; R1, first branch of radius; Sc, subcosta. "?" indicates indistinct (or atrophied?) venation in pterostigmal region (see text). All figures drawn to scale.**

wings not clearly visible). MP forked distal to origin of Rs; MP1, MP2 branched near wing margin, MP1 dichotomously, MP2 pectinately. Basal crossvein m-cu not detected. CuA long, running close to hind margin of wing, pectinately branched. CuP not detected. 1A branches few, pectinate, connected with CuA by short crossvein cua-1a at level of forking of MP. 2A short, with one or few branches. 3A not detected. Posterior margin of wing fringed with long hairs basally, other margins and longitudinal veins with relatively shorter hairs. Membrane of hind wings entirely colourless, hyaline; all veins pale, without detectable colouration. **Abdomen** (Figs. 7*a*–7*c*). Tergite and sternite numbers given here as probabilities; see below. Segments 5–8 well developed, of unspecialized morphology. Ninth tergite clearly visible, appears as narrow segment, long hairs few; alternately, 9T fused with ectoprocts (= 10T) and "9T?" (Fig. 7*a*) is 8T (less

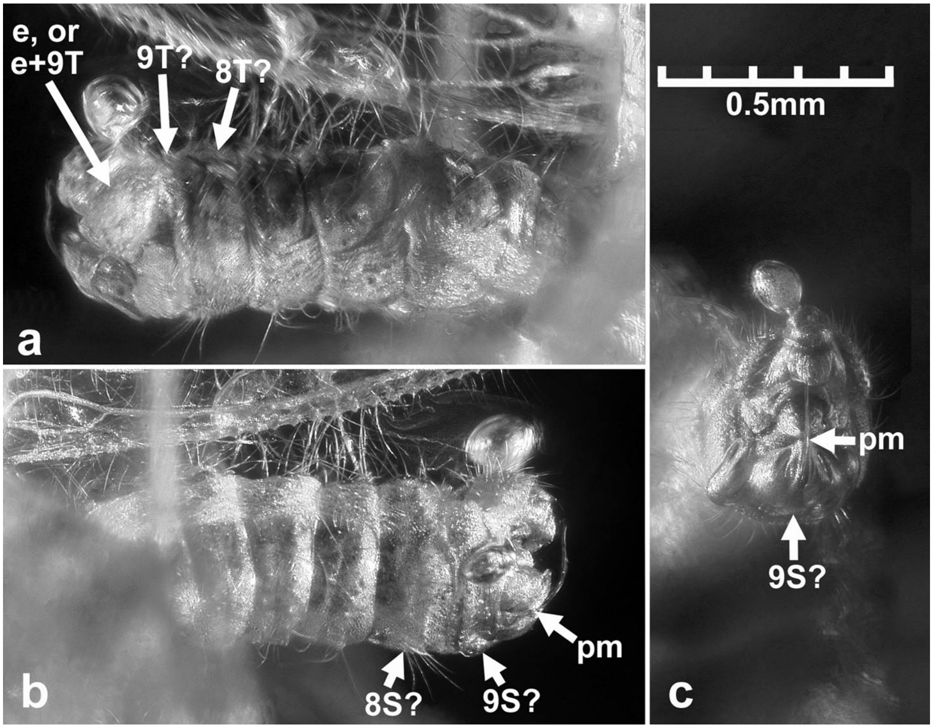

FIGURE 7. ***Microberotha macculloughi*** **apex of abdomen: *a*, dorsolateral aspect; *b*, ventrolateral aspect; *c*, caudal aspect. e, Ectoproct; pm, paramere–mediuncus complex; 8T and 9T, 8th and 9th tergites; 8S and 9S, 8th and 9th sternites. "?" indicates uncertainty (see text).**

likely, see Discussion below). Ninth sternite short, transverse. Ectoproct more or less rounded, without caudal or ventral projections, covered with long setae; *callus cerci* not detected. Inner genitalia: only distal portion of paramere–mediuncus complex ("free portion of mediuncus" from MacLeod and Adams 1967) clearly visible, long, bent dorsally, strongly pigmented, gradually narrowed towards apex, without bristles at tip and not serrate.

Locality and age

Hat Creek Coal Formation, Kamloops Group, British Columbia, Canada; Early Eocene.

Discussion

Microberotha macculloughi is one of smallest members of the family Berothidae; all extant species of the family are larger. The smallest extant species are *Nyrma kervillea* Navás (Neuroptera: Berothidae, Nyrminae) and *Manselliberotha neuropterologorum* Aspöck *et* Aspöck (Neuroptera: Berothidae, Cyrenoberothinae), which have a minimum forewing length of 3.8 and 3.6 mm, respectively (Aspöck and Aspöck 1988; Aspöck 1989). All others have a minimum forewing length of approximately 5 mm or larger. Of fossil Berothidae, all species from the New Jersey amber are small (Grimaldi 2000), ranging in forewing length from approxiamtely 2.6 mm (an undescribed species closely related to *Jersiberotha luzzii* Grimaldi, estimated from Fig. 19) to 4.3 mm (*Nascimberotha picta* Grimaldi). Other fossil Berothidae are larger.

The genus *Microberotha* has a slender forewing, 3.2 times as long as wide (calculated in flattened wing). It might be expected that this forewing morphology (small and slender) is the cause of the reduction of venation; however, the small size and narrow wings do not necessarily lead to this character state. The smallest species of the family Berothidae ("near *Jersiberotha luzzi*"; Grimaldi 2000, Fig. 19) possess a two-branched Rs and an outer gradate series of crossveins.

The head structure of the genus *Microberotha* is rather generalized within the family. In particular, the short face and short antennal scape are plesiomorphic at the family level (Aspöck and Nemeschkal 1998). The postocular zone, which is not particularly inflated, may be considered plesiomorphic as well.

A short pronotum with two transverse furrows is considered plesiomorphic in the family Berothidae and occurs in several genera (former) or in the vast majority of genera (latter), whereas the heavy pronotal shape found in the genus *Microberotha* is apomorphic within the family and is thought to have evolved in parallel in the genera *Nyrma* Navás (Nyrminae), *Spiroberotha* Adams (Neuroptera: Berothidae, Nosybinae), and most of the genera of subfamily Berothinae (Aspöck and Nemeschkal 1998).

A ribbon-like forewing shape (*i.e.*, not distinctly widest in middle third) has been considered an autapomorphy of the genus *Stenobiella* Tillyard (Neuroptera: Berothidae) (Aspöck and Nemeschkal 1998). The forewing of the genus *Microberotha* has a similar appearance in that it is slender, with the anterior and posterior margins nearly parallel through the mid-region. The apparent widening seen in the left mid-wing is due to the perspective from bending (Fig. 5*a*); ribbon-like morphology is evident in the more flatly preserved right wing (Fig. 5*b*). As these genera probably belong to different lineages (see below), this character state may be considered homoplasious between the genera *Stenobiella* and *Microberotha*.

The venation is, in general, characteristic of the family Berothidae, although simplified. In the forewing, the basal fusion of M and R is distinctive and is generally agreed to be apomorphic within the family. This fusion is interpreted (Aspöck and Nemeschkal 1998) as having arisen independently in the subfamilies Trichomatinae and Nosybinae and in the genera *Quasispermophorella* Aspöck *et* Aspöck (Neuroptera: Berothidae, Berothinae) and *Mucroberotha* Tjeder (Neuroptera: Berothidae, Rhachiberothinae). Two other characters found in the genus *Microberotha* are interpreted here as autapomorphies of the genus *Microberotha*: (1) Rs with a single branch (Rs with two or more branches in other genera) and (2) outer gradate series absent (present in other genera). The entire (apparent) loss of CuP in the hind wing is considered apomorphic and occurs in the genera *Cyrenoberotha* MacLeod *et* Adams (Neuroptera: Berothidae, Cyrenoberothinae), *Naizema* Navás (Neuroptera: Berothidae, Nosybinae), and *Berlekrumyia* Aspöck *et* Aspöck (Neuroptera: Berothidae, Berothinae).

Understanding the identity of the terminal abdominal segments then is key to subfamily placement. The placement, however, is confounded by the inability to determine with certainty the identity of some of the terminal abdominal segments from the only known specimen. The aspects available (*i.e.*, dorsolateral, ventrolateral, and caudal) present individual difficulties. In caudal view, the individual segments become difficult to separate owing to perspective. Furthermore, the identity of the first segment is difficult to detect owing to bending of the insect and intervening imperfections in the amber. In lateral views, only the terminal half-dozen segments are visible. Therefore, reference to the identity of particular sternites and tergites is mindful of these difficulties and is intended only as theoretical possibilities.

Depending on the identity of terminal segments (*i.e.*, is the tergite proximal to the ectoproct; 8T or 9T?), several interpretations seem plausible. In the vast majority of extant species of the family Berothidae, 9T is entirely fused with the ectoproct. The exceptions are the genera *Cyrenoberotha*, *Manselliberotha* Aspöck *et* Aspöck, and all genera of the subfamily Rhachiberothinae. The morphology of the terminal segments of the genus *Microberotha* may be hypothesized as in the latter; if so, then the tergite proximal to 9T + ectoproct is 8T. This, however, requires that 8T to be narrower in this genus than in other known Berothidae. In addition, the corresponding sternite (8S) is then also narrow, and 9S is either entirely lost or even more reduced. We consider this possibility doubtful; it is more parsimonious to consider the apparent distal-most sternite to be 9S, and to consider 9T and the ectoproct to be separate, in which case the segments proximal to 9T and 9S are normally developed as in other extant species of the family Berothidae (those of fossil species are poorly known). Because this view, however, is somewhat speculative, we take the conservative stance in determination of subfamily affinity without regard to this hypothesis.

Systematic position of the genus *Microberotha*

Six subfamilies are currently recognized within the family, excluding the subfamily Rhachiberothinae (see above): Nyrminae, Cyrenoberothinae, Protobiellinae, Trichomatinae, Nosybinae, and Berothinae (Aspöck and Nemeschkal 1998). Extinct subfamilies have not been proposed for fossil genera.

The minute size of the genus *Microberotha* and the associated reduced venation make determination of the systematic position of this genus within the family Berothidae problematic. External characters such as the structure of the head, antennae, palps, thorax, and legs found in this genus are generalized (above), and therefore are not useful in the determination below the family level, although some are useful in comparison with apomorphic states in certain groups (below). The venation is distinctive, but this state may be derived from almost any of the subfamilies (even from Nyrminae, which, in spite of their small size, have complex venation) by means of reduction. The male genitalia are quite well preserved, they do show considerable similarity with those of subfamily Cyrenoberothinae, but they alone do not provide evidence of subfamily affinity with certainty. All other subfamilies, although none should be excluded *a priori*, are lower possibilities for this genus.

We may state that this genus certainly does not belong to the subfamily Rhachiberothinae (if considered within the family) because of its cursorial forelegs with five tarsomeres (in the subfamily Rhachiberothinae, the forelegs are raptorial with four tarsomeres in males), and the basal vein “b” (“basal part of MA”) in the hind wing is vertical and short (Fig. 6) (in the hind wing of the subfamily Rhachiberothine, this vein is sinuate and long). In all genera of the subfamilies Protobiellinae, Trichomatinae, Nosybinae, and Berothinae, the male genitalia are different; in particular, they possess bristles in the paramere–mediuncus complex (synapomorphy of Protobiellinae + Trichomatinae + Nosybinae + Berothinae in Aspöck and Nemeschkal 1998), so this group is excluded. The paramere–mediuncus complex occurs without bristles only in two relictual subfamilies: Nyrminae and Cyrenoberothinae.

The subfamily Nyrminae is composed of only one genus, *Nyrma* Navás (with one known species, *Nyrma kervillea* Navás, from Asia Minor), which was originally described within the family Hemerobiidae (as tribe Nyrmini), then subsequently transferred from this family and elevated to subfamily rank within the family Berothidae (Aspöck 1989). The genus *Nyrma* has a elongate head, small eyes, the postocular zone is strongly inflated, the male genitalia has 9T fused with the ectoproct, 9S is long, and the distal portion of the paramere–mediuncus complex is relatively short and dorsally serrate (also the wing venation differs, but as we note above, the venation in the genus *Microberotha* could theoretically have been derived through simplification from the subfamily Nyrminae) (Aspöck and Aspöck 1979; Aspöck 1989). All of these character states are contrary to those found in the genus *Microberotha*. Therefore, this subfamily is the least possibility for this genus.

The subfamily Cyrenoberothinae was created for the genus *Cyrenoberotha*, which has a single species from Chile (MacLeod and Adams 1967). Later, the South African monotypic genus *Manselliberotha* was assigned to this subfamily, based mainly on the following synapomorphies: (1) elongate face, (2) humeral vein recurrent in forewing, (3) 9T and ectoproct separated, and (4) paramere–mediuncus complex lacking bristles (Aspöck and Aspöck 1988). Character state (1) is now considered to be an apomorphy of the genera *Nyrma*, *Manselliberotha*, and *Cyrenoberotha*; character state (2) is now believed to be plesiomorphic with regards to the family and occurs in many genera of various subfamilies; character state (4) was subsequently found in the subfamily Nyrminae as well and is now considered to be plesiomorphic for the family (Aspöck and Nemeschkal 1998). Aspöck and Nemeschkal (1998), in their cladistic analysis, found that the genera *Nyrma*, *Manselliberotha*, and *Cyrenoberotha* constitute an unresolved trichotomy. Although this fact supports the monophyly of this group, the relationship between these genera remains unknown. Nevertheless, the authors retained the composition of these two subfamilies unchanged "unless further clear results are available" (Aspöck and Nemeschkal 1998, p 61).

Indeed, although some aspects of their genitalic features are dissimilar (*e.g.*, greatly differing structures of gonarcus and ninth gonocoxites), the genera *Manselliberotha* and *Cyrenoberotha* are similar in their external characters (the structure of the head, pronotum, and wing venation), as well as the genitalic characters (3) and (4). The external features characteristic of these two genera, however, are dissimilar to those of the genus *Microberotha*: in the genera *Cyrenoberotha* and *Manselliberotha*, the head and pronotum are elongate (in particular, the face is conspicuously extended ventrad of the lower margin of the eyes), 9S is long, and the venation is markedly different (in particular Sc and R1 are apically fused); unlike in the genus *Microberotha* where the head, pronotum, and 9S are short (the pronotum is "heavy") and the venation is quite reduced (Sc and R1 are widely spaced distally). The structure of the visible portion of the paramere–mediuncus complex of the genus *Microberotha* (long and bent dorsally) is undoubtedly much more similar to the genus *Cyrenoberotha* (practically identical in both genera) than to the genus *Manselliberotha* (not so long and directed almost caudally). The main diagnostic character of the subfamily Cyrenoberothinae is the separation of the 9th and 10th tergites. Unfortunately, in the genus *Microberotha*, this character state is hypothetical, because of the inability to confidently identify segment number in this specimen (see above). Additionally, this character state is plesiomorphic for the order (for Dilaridae + Mantispidae + Rhachiberothidae + Berothidae in Aspöck and Nemeschkal 1998). The similar morphology of the visible portion of the paramere–mediuncus complex remains the only character shared by the genera *Microberotha* and *Cyrenoberotha*.

The subfamily Cyrenoberothinae is unquestionably relictual, with two monotypic genera greatly separated spatially (Chile and South Africa) and sharing similar external and genitalic characters; if the structure of the paramere–mediuncus complex is evolutionarily more stable than external features, the genus *Microberotha* might be referred to this subfamily. This seems to be a reasonable possibility: in various neuropteran families there are taxa in which species have similar genitalia but differ significantly in external characters (*e.g.*, the genus *Micromus* Rambur (Neuroptera: Hemerobiidae) is represented in the Hawaiian Islands by numerous species that are similar to each other in male genitalia but diverse in wing shape; Zimmerman 1957).

Similarly, the genera of the subfamily Apochrysinae (Neuroptera: Chrysopidae) are similar in genitalia but vary in wing venation (Brooks and Barnard 1990).

On the other hand, the separated 9T and ectoproct and the absence of bristles in the paramere–mediuncus complex are plesiomorphic for the family Berothidae (although the possibility also exists that the paramere–mediuncus complex in the ancestral lineage of the genus *Microberotha* had bristles, and that amalgamation of these is indistinguishable here from their absence), so the new genus may possibly represent another, extinct Berothidae group basal to all described subfamilies (excluding the subfamily Rhachiberothinae). This assumption is supported by many plesiomorphic character states that were found in this genus such as in structures of the head, antennae, and pronotum (see the above Discussion and Aspöck and Nemeschkal 1998), although the wings possess numerous apomorphies. The family Berothidae (s.l.), however, have a long history (known at least since the Late Jurassic), and until a careful analysis of the characters available in all described fossil species are done, this basal placement of the genus *Microberotha* is tentative.

Thus, in spite of the inability to confirm the diagnostic feature (*i.e.*, separated 9T and ectoproct), the genitalic features visible suggest a closer relationship between the genus *Microberotha* and the subfamily Cyrenoberothinae than with any other subfamily. Yet this remains unresolved, as other characters available are not clearly diagnostic.

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