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An Eocene brontothere and tillodonts (Mammalia) from British Columbia, and their paleoenvironments.

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Draft

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25 paleoenvironments.

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27 **Abstract:**

28 We describe Eocene fossils of the tillodont *Trogosus* from the Allenby Formation in Princeton,
29 British Columbia (B.C.) as well as teeth of Brontotheriina from the lower Australian Creek
30 Formation near Quesnel, B.C. These fossils represent the only occurrence of Tillodontia and
31 Brontotheriidae in B.C. Further, the presence of the largest species of *Trogosus* – *T. latidens* – as
32 well as a smaller species identified only as *Trogosus* sp. supports a late early – early middle
33 Eocene (Bridgerian) age for the Vermilion Bluffs Shale of the Allenby Formation. Based on their
34 morphology and large size, the teeth referred here to Brontotheriina represent one of the larger,
35 more derived brontothere genera, and suggest a Uintan – Chadronian (middle – late Eocene) age
36 range for the lower Australian Creek Formation that is consistent with radiometric ages of
37 underlying volcanic rocks. Paleobotanical data from sediments correlative to those that produced
38 these Eocene mammal fossils suggest they inhabited forested landscapes interspersed with
39 swamps and open water environments, under mild and wet temperate climates (MAT ~10–16 °C;
40 CMMT -4–4 °C; MAP > 100 cm/yr). These mixed conifer-broadleaf forests included tree genera
41 typical of modern eastern North American forests (e.g., *Tsuga*, *Acer*, *Fagus*, and *Sassafras*),
42 together with genera today restricted to east Asia (e.g., *Metasequoia*, *Cercidiphyllum*, *Dipteronia*,
43 and *Pterocarya*). The paleobotanical evidence is consistent with the hypothesized habitats of
44 both tillodonts and brontotheres.

Introduction

The Eocene Epoch (ca. 56 – 33.9 Ma; Cohen et al. 2013) saw significant global climate change, including a pulse of hyperthermals near its onset that marked the height of global warming since dinosaur extinction (Zachos et al. 2008). Cooling began in the middle Eocene and culminated in a significant global temperature drop and rapid expansion of continental ice sheets on Antarctica near the Eocene-Oligocene boundary – the transition from a greenhouse to an icehouse (Miller et al. 1987; Zanzazi et al. 2007 and references therein). Importantly, North America saw major reorganization of its mammalian fauna in the early Eocene, marked by appearance of Perissodactyla, Artiodactyla, hyaenodontid creodonts, and Euprimates at its onset and multiple dispersal events throughout the Eocene (Beard 1998), while the end of the Eocene marked extinction in marine and terrestrial realms, although the North American mammalian fauna was largely unaffected (Zanzazi et al. 2007). Most of what we know about the North American fauna and flora during the Eocene comes from localities in the U.S. Western Interior, although discoveries in the Canadian Arctic have shed light on early – middle Eocene polar fauna and flora (Dawson et al. 1976; Eberle and Greenwood 2012 and references therein), and Saskatchewan's Cypress Hills Formation has produced late Uintan – Chadronian (middle – late Eocene) mammalian faunal assemblages (Robinson et al. 2004 and references therein; Prothero and Emry 2004). In British Columbia, whereas its Eocene flora and insect fauna have been studied since the 1890s (e.g., Dawson 1883, 1890; Archibald et al. 2010; Greenwood et al. 2016a and references therein), the Eocene mammalian fauna is poorly known.

Eocene mammals are rare in British Columbia. The most taxonomically diverse fauna, with some seven orders represented, is from the Kishenehn Formation cropping out along the North Fork in southern B.C., and is tentatively assigned a latest Eocene (Chadronian) age

(Constenius et al. 1989; M.R. Dawson (personal communication to JE, 2017)). Outside of the Kishenehn, however, the number of Eocene mammal fossils in B.C. drops dramatically. Russell (1935) briefly described one and a half tillodont lower molars from a coal mine in the Allenby Formation near Princeton, referring them to “*Trogosus minor*” (a species that is no longer valid), while Gazin (1953) noted a second tillodont specimen from Princeton. An undescribed jaw of an erinaceid (hedgehog family) is purported to have also come from the Princeton area (Mathews and Monger 2005, pp. 229–230), although the specimen appears to be lost. Further north, near Quilchena, a fragment of a tiny lower molar (Q5508, Simon Fraser University) of an indeterminate lipotyphlan was collected by Glen Guthrie in the early 1990s from the west side of Quilchena Creek in strata of the Coldwater Formation that also preserve a diverse flora and insect fauna, fossil fishes, and rare fossil feathers (Mathewes et al. 2016). Brontothere teeth were collected from the lower Australian Creek Formation near Quesnel in central B.C., though never described (Rouse and Mathews 1979). Ludvigsen (2001) reported postcranial material of a small mammal from Driftwood Canyon Provincial Park near Smithers, northern B.C. (Fig. 1), but in the absence of cranial and dental remains this specimen is probably unidentifiable. More recently, Eberle et al. (2014) described two fossil mammals – the erinaceid *Silvacola acares* and the tapiroid cf. *Heptodon* from an unnamed formation of the Eocene Ootsa Lake Group (coined the Driftwood Creek beds) in Driftwood Canyon Provincial Park. These fossils are the first early Eocene (Wasatchian) mammals from mid-latitude Canada, although a diverse late Wasatchian mammal fauna is known from Ellesmere Island (Dawson et al. 1976; Eberle and Greenwood 2012).

Here, we describe the tillodont fossils from Princeton and the brontothere teeth from Quesnel. The presence of both groups refine the age of the strata, and are the first records of

Tillodontia and Brontotheriidae from British Columbia. Tillodontia are a small group of medium- to large-sized archaic herbivores that range in age from the late Paleocene to the middle Eocene in North America. They appear earlier in the Paleocene in Asia and are hypothesized to have originated on that continent and crossed into North America via Beringia by late Paleocene time (Stucky and Krishtalka 1983; Miyata 2007a and references therein). Their distinctive tooth morphology, considered alongside skeletal anatomy, suggests tillodonts were diggers that fed on tough vegetation, roots, and tubers that introduced soil and grit to their diet, which may account for the heavy wear on their teeth (Lucas and Schoch 1998; Rose 2006). The fossils from B.C. are the only undoubted occurrence of tillodonts in Canada, although a small piece of tusk from Ellesmere Island, Nunavut may belong to the group (Schoch 1986; M.R. Dawson (personal communication to Eberle, 2017)).

The Brontotheriidae is a clade of medium- to very large-sized browsers that inhabited North America and Asia throughout the Eocene, going extinct at the Eocene-Oligocene boundary (Mihlbachler 2008). By latest Eocene time, they had evolved into giant horned forms comparable in size to large rhinos. Stratigraphically the earliest known occurrence of North American brontotheres is from Arctic Canada, where their fossils occur in late Wasatchian and early Bridgerian-aged strata of the Margaret Formation on Ellesmere Island (Eberle 2006; Eberle and Eberth 2015). Like the tillodonts, the clade was hypothesized to have originated in Asia and dispersed across Beringia into North America (Beard 1998), although recently others have suggested the reverse – a North American origin and subsequent dispersal into Asia (Mihlbachler 2008). That early forms occur in Arctic Canada suggests that at least some brontotheres were adapted to Arctic environments, supporting the hypothesis for trans-Beringian dispersal during early and middle Eocene time (Eberle and Eberth 2015). The brontothere teeth from Quesnel are

the only documented occurrence of brontotheres in B.C. and belong to one of the larger, geologically younger taxa (discussed below).

To place these Eocene mammals from British Columbia into a paleoenvironmental context, we also summarize available paleobotanical data for the associated sediments to reconstruct the paleoclimate, and present a new analysis of the paleoclimate of the Australian Creek Formation.

Geologic Setting

Princeton Basin - Allenby Formation.

The tillodont fossils described below come from the Allenby Formation in the Princeton Basin, which extends in a north-south axis from just north of the town of Princeton B.C. (Fig. 1), paralleling the Similkameen River. A minor associated coal basin (Tulameen Basin) occurs to the west near the towns of Tulameen and Coalmont. The prevailing major rock units of the Princeton Basin – the Princeton Group – are composed of up to 1370 m of volcanic rocks, and a 1600 to 2100 m thick sedimentary sequence containing major coal seams, shales, and sandstones together with minor volcanics (Shaw 1952; McMechan 1983; Read 1987, 2000). The Princeton Basin is considered to be formed within a complex half graben, with structural features including major faults, synclines and anticlines, indicating a complex structure that included considerable volcanic activity during its formation (McMechan 1983). The depositional low was likely a consequence of crustal extensional activity associated with the uplift of the Rocky Mountains and the underplating of rafted terranes (McMechan 1983; Ickert et al. 2009).

Shaw (1952) divided the Princeton Group into a Lower Volcanic Formation, the Allenby Formation, and an Upper Volcanic Formation. McMechan (1983) divided the predominantly sedimentary Allenby Formation into three informal members – the volcanic, lower, and coal-

bearing members – and provided correlation data for the major coal seams mined in the Princeton Basin. Read (1987, 2000) further refined the stratigraphic framework of the Allenby Formation, subdividing it into 14 units, including (in ascending stratigraphic order) the Hardwick Sandstone, Vermilion Bluffs Shale, Summers Creek Sandstone, and the uppermost Ashnola Shale (Fig. 2). Read's (1987, 2000) nomenclature is followed here. The tillodont fossils, as well as most of the coal mined from the Princeton Basin, came from seams that are part of the Vermilion Bluffs Shale (Read 2000). The coal seam mined in Pleasant Valley Mine #2 (= Wilson Mine) is the Princeton #1 seam, which is the Princeton basin 0 m datum used by McMechan (1983) and Read (1987, 2000). Read (2000) stated for the Pleasant Valley Mine #2 that the Princeton #1 seam is 140 m below the top of the Vermilion Bluffs Shale. The published section for Pleasant Valley Mine #2 (Shaw 1952; McMechan 1983) shows a thickness of about 2.5m of coal with two shale partings, an underlying sandstone, and the top of the mined seam grading into a shaly-coal at about 2.6–3.0m above the base of the Princeton #1 seam. The Thomas Ranch megaf flora (Dillhoff et al. 2013) corresponds to fossil locality F25 in Read (1987, Table 4A), in the Vermilion Bluffs Shale, up-section from the Princeton #1 seam.

The age of the Allenby Formation and the fossil assemblages reported from the formation have been problematic, with earlier reports stating Miocene, Oligocene, or Eocene (e.g., Dawson, 1890; Penhallow 1908; Russell 1935; Shaw 1952; Arnold 1955b). Early K-Ar dates of ~50 Ma, combined with palynology and mammalian biostratigraphy (specifically the tillodont fossils), were correlated using the geochronometric scales in use at the time to place the Allenby Formation as Middle Eocene (Hills and Baadsgaard 1967). However, based on the current geochronometric scale, the early-middle (Ypresian-Lutetian) Eocene boundary is at 47.8 Ma (Cohen et al. 2013), placing the Allenby Formation as early Eocene (Ypresian) based on the

older K-Ar dates (Fig. 2). More recent $^{40}\text{Ar}/^{39}\text{Ar}$ and U-Pb dates from Allenby Formation volcanics are even older, at ~ 52 Ma (e.g., Moss et al. 2005; Ickert et al. 2009; summarized in Greenwood et al. 2016a), with the top of the Allenby Formation likely ~ 48.7 Ma based on an unpublished date for Ash #22 in the Princeton Chert (Little et al. 2009; Pigg et al. 2016). Moss et al. (2005) reported an unpublished age using U-Pb from zircons for the Vermilion Bluffs Shale at Hospital Hill in the town of Princeton as 52.08 ± 0.12 Ma, which is consistent with an $^{40}\text{Ar}/^{39}\text{Ar}$ age of 52.0 ± 1 Ma for the overlying Sunday Creek Sandstone of Read (1987, 2000) by Ickert et al. (2009).

Quesnel area - Australian Creek Formation.

The valley of the Fraser River around Quesnel in central B.C. (Fig. 1) preserves a series of outcrops exceeding 320 m of extrusive volcanic rocks and minor sediments correlative with the Eocene Kamloops Group to the south, but more recently mapped as the Eocene Endako Group (Piel 1971; Rouse and Mathews 1979; Hora and Hancock 1994; Massey et al. 2005; Bordet et al. 2014). These rock units are capped by a series of mostly sedimentary rocks of the Australian Creek Formation initially considered to be early Oligocene in age, and the Miocene Fraser Bend and Crownite formations, overlain by late Miocene sheet basalts of the Neogene Chicoltin Group. These rock units are in turn capped by Pleistocene sediments (Rouse and Mathews 1979; Hora and Hancock 1994; Bordet et al. 2014) (Fig. 3). Initial K-Ar ages for the volcanics of the Kamloops Group in the Quesnel area ranged from 48.8 ± 1.5 Ma to 41.6 ± 1.9 Ma (Rouse and Mathews 1979) (Fig. 2), although these rocks are now mapped as Endako Group, which has $^{40}\text{Ar}/^{39}\text{Ar}$ ages ranging from 51-45 Ma (Grainger et al. 2001; Bordet et al. 2014). Extensive

slumping of the Miocene Fraser Bend and Crownite formations obscures local stratigraphic sequences (Rouse and Mathews 1979; Hora and Hancock 1994) (Fig. 3).

The approximately 500 m thick Australian Creek Formation was defined by Rouse and Mathews (1979) from a section near the confluence of Australian Creek and the Fraser River. The brontothere teeth (ROM 6088) were recovered from the lower part of the formation, at the base of a coal seam near river level, on the west side of the Fraser River approximately 35 km south of Quesnel (K. Seymour (personal communication to JE, 2017)). The lower part of the formation is composed of claystones and mudstones, silty to sandy lenses, and lignite seams, while the upper part is predominantly conglomerate and pebbly sandstones containing volcanic clasts (Rouse and Mathews 1979) (Fig. 3).

The Australian Creek Formation was deposited in lacustrine, fluvial and paludal settings of a lowland floodplain in a graben or half graben. Minor occurrences of fossil leaves have been reported from a clay beneath a breccia west of Quesnel (Rouse and Mathews 1979), and a series of samples from the lower beds of the Australian Creek Formation include a microflora that has been described (Piel 1971; Rouse and Mathews 1979). The early Oligocene age assignment of the Australian Creek Formation is based in part on diagnostic palynomorphs in these microfloras (Piel 1971; Rouse and Mathews 1979), and the identification of the brontothere ('titanotherium' in these reports) from the lower beds of the Australian Creek Formation as suggesting a Chadronian age (Piel 1971; Rouse and Mathews 1979; Hora and Hancock 1994). Under the current geochronology for the North American Land Mammal Ages (NALMA), however, the Chadronian is late Eocene (Prothero and Emry 2004 and references therein) (Fig. 2).

Materials and methods

205 *Vertebrate paleontology*

206 The tillodont fossils described here were recovered from the Pleasant Valley Mine #2,
207 also called the W.R. Wilson Coal Mine, near Princeton, B.C. in the 1930s. According to its
208 associated catalog card (dated December 2 1934), the larger and more complete specimen CMN
209 8709 came from the.... ‘mouth of mine 430 feet below surface’, whereas CMN 8687 (= GSC
210 8687) was collected by B.R. MacKay and C. Stubbs from the W. R. Wilson Mine in 1933. Based
211 on the stratigraphic nomenclature of Read (1987, 2000), the sediments that hosted the coal seam
212 mined in the Pleasant Valley Mine #2 are part of the Vermilion Bluffs Shale, with the coal being
213 the Princeton #1 seam (Table 5 in Read 1987). Read (1987, Table 4A) indicated that the tillodont
214 was collected from the Vermilion Bluffs Shale.

215 The brontothere teeth (ROM 6088) were collected in the 1960s by G.E. Rouse from the
216 west bank of the Fraser River, 2.5 km south of the mouth of Australian Creek (UTM grid 349390;
217 Rouse and Mathews 1979, appendix 1); the specimen is curated at the Royal Ontario Museum
218 (ROM).

219 Identifications of the tillodont specimens were made via comparison with specimens in
220 the University of Colorado Museum of Natural History (UCM) Fossil Vertebrate Collection as
221 well as published descriptions and images, while the brontothere teeth were compared to
222 specimens at the University of California Museum of Paleontology (UCMP) and UCM.

223 Tillodont dental terminology follows Bown and Kraus (1979) and Miyata (2007b, fig. 1).
224 We follow brontothere dental terminology outlined by Osborn (1929, fig. 221) and Mhlbachler
225 (2008, fig. 4). Dental measurements were obtained using Mitutoyo Absolute Digimatic digital
226 calipers. Brontothere classification follows Mhlbachler (2008), while tillodont classification
227 follows Lucas and Schoch (1998).

Institutional abbreviations—**AMNH**, American Museum of Natural History, New York, U.S.A.; **CMN**; Canadian Museum of Nature, Ottawa, ON; **GSC**, Geological Survey of Canada, Calgary, Canada; **ROM** Royal Ontario Museum, Toronto, ON; **UCM**, University of Colorado Museum of Natural History, Boulder, CO; **UCMP**, University of California Museum of Paleontology, Berkeley, CA, **YPM**, Yale Peabody Museum, New Haven, CT.

Dental Terminology—**L**, Left; **R**, Right; **P/p**, upper/lower premolar; **M/m**, upper/lower molar, **A–P length**, Anteroposterior length; **Wtri**, Trigonid Width; **Wtal**, Talonid Width.

Paleobotanical climate reconstruction

For the Allenby Formation, we compiled available reports of fossil flora attributed to the Vermilion Bluffs shale of Read (1987, 2000) to provide an account of the paleovegetation and paleoclimate. In particular, Dillhoff et al. (2013) provided a detailed systematic appraisal of the Thomas Ranch flora, which was collected from within the Vermilion Bluffs shale on the north bank of the Tulameen River, proximal to Pleasant Valley Mine #2. These authors also provided estimates of annual temperature and precipitation as well as seasonal values, based on both a nearest living relative (NLR) analysis and leaf physiognomy. As only microflora is described in detail for the Australian Creek Formation, we applied the same NLR approach to the flora (Table 1) as used by Dillhoff et al. (2013) to allow comparability of the data.

In the NLR method, fossil plant taxa have their nearest living relative identified and the climate limits of all identified NLRs are compared to find the zone of overlap where all taxa can co-exist. Dillhoff et al. (2013) used a variant of the NLR method, bioclimatic analysis (Greenwood et al. 2005), where the estimate is derived using the 10th and 90th percentiles of the assemblage of NLRs to weight against so-called outliers, taxa whose climate range may fall

outside the range of the majority of other NLRs. The estimate is expressed as the midpoint of the maximum and minimum estimates, with the full range of the estimate expressed as an uncertainty value (Greenwood et al. 2005; Thompson et al. 2012; Mathews et al. 2016). Climate range data for modern plant genera identified as NLRs used in our analysis (Table 1) were derived principally from Thompson et al. (2012) and Fang et al. (2011), with additions as described in Mathews et al. (2016). Recent analyses of the NLR method for North American plant taxa show that estimates derived from plant genera are accurate (Thompson et al. 2012; Harris et al. 2017).

Systematic Paleontology

Order Tillodontia Marsh, 1875

Family Esthonychidae Cope, 1883

Subfamily Trogosinae Gazin, 1953

Trogosus Leidy, 1871

Comments: *Trogosus* was a large, derived tillodont primarily known from the late early – early middle Eocene of western North America, but also known from Asia (Miyata 2007a). and considered an index taxon for the Bridgerian North American Land Mammal Age (Robinson et al. 2004). It was a stout, bear-like herbivore that weighed 150 kg or more, it had a short neck and long tail, large claws on its manus, a long rostrum and deep mandible, and its second incisors were large evergrowing tusks (Lucas and Schoch 1998; Miyata 2007a, b). *Trogosus* is hypothesized to have used its large tusks and claws to dig up roots and tubers, and this appears to be borne out by the heavy wear on most *Trogosus* dentitions, suggesting that it ingested soil and

grit while eating (Gingerich and Gunnell 1979). Four to six North American species of *Trogosus* are considered valid, diagnosed primarily by cranial, mandibular, and dental characters (Miyata 2007a, b; Lucas and Schoch 1998). It is arguably the best-known tillodont, and is considered an index taxon for the Bridgerian North American Land Mammal Age (Robinson et al. 2004).

Trogosus latidens (Marsh, 1874)

Figure 4, Table 2

REFERRED SPECIMEN: CMN 8709, mandibular fragment with worn Lm1-3 and Rm2.

LOCALITY: CMN 8709 was recovered from the Princeton #1 coal seam at the mouth of the Pleasant Valley Mine #2 (=W.R. Wilson Coal Mine), near Princeton, B.C. The coal seam is part of the Vermilion Bluffs Shale, Allenby Formation, Princeton Basin, B.C.

KNOWN DISTRIBUTION: Huerfano Formation, CO; Aycross Formation, Big Horn Basin, WY; Bridger Formation, Green River Basin, WY; Vermilion Bluffs Shale, Allenby Formation, Princeton Basin, B.C. (all Bridgerian).

DESCRIPTION AND DISCUSSION: CMN 8709, which comprises a mandibular fragment with worn Lm1-3 and Rm2 (Fig. 4), was collected in the 1930s from the mouth of the Pleasant Valley Mine #2 near Princeton, B.C. It was identified in 1934 as “*Trogosus minor*” (= nomen dubium; Gazin 1953), but subsequently Gazin (1953) tentatively identified it as ?*Trogosus latidens* due to its large size, although didn’t describe the specimen. *T. latidens* is known primarily from isolated

cheek teeth, and is diagnosed only by its large size (Gazin 1953; Gunnell et al. 1992). More recently, Miyata's (2007a) analysis of the size range of *T. latidens*, that included measurements of a cast of CMN 8709, concluded that lower molars referred to *T. latidens* are 25% longer and wider than those of other North American species of *Trogosus*.

As noted for tillodonts in general, the mandible on CMN 8709 is deep, and the trigonid and talonid on the molars are U-shaped. Although the teeth exhibit considerable wear (e.g., the smallest molar, Lm1, is completely worn, save for the posterolabial corner of the tooth), the trigonid is nonetheless taller than the talonid on each of the molars. The m2s and m3 on CMN 8709 show that the paraconid was as lingual as the metaconid, and the latter is the tallest cusp on the tooth on m3, although this may be related to the heavy wear over the rest of the tooth. A short metastylid occurs posterior to the metaconid on Lm2 and m3. A short, heavily worn entoconid is present on the Lm2 and m3, though this region is completely worn down on the Rm2. The m3 talonid is incomplete, and consequently the presence of a third lobe basin cannot be ascertained. The cristid obliqua joins the posterior wall of the trigonid lingual of the anteroposterior midline of the tooth.

Trogosus sp.

Figure 4

REFERRED SPECIMEN: CMN 8687, a Lm1 talonid fragment and nearly complete Lm2.

318 LOCALITY: CMN 8687 was recovered in 1933 from the Princeton #1 coal seam at the mouth of
319 Pleasant Valley Mine #2 (=W.R. Wilson Coal Mine) near Princeton, B.C. The coal seam is part
320 of the Vermilion Bluffs Shale, Allenby Formation, Princeton Basin, B.C.

321 DESCRIPTION AND DISCUSSION: CMN 8687, a Lm1 talonid fragment and nearly complete
322 Lm2, was briefly described and referred to “*Trogosus minor*” by Russell (1935). However,
323 “*Trogosus minor*” was disregarded as a valid species by Gazin (1953) because the type (YPM
324 11083, a Rm2) cannot be differentiated from m2 of *T. hyracoides* or *T. castoridens*. Gazin (1953)
325 further suggested that *T. hyracoides* and *T. castoridens* may represent morphologic variants of
326 the same species (perhaps males and females), although some workers have since considered
327 both species valid (e.g., Miyata 2007a, b; Miyata and Deméré, 2016; but see Lucas and Schoch
328 1998).

329 CMN 8687 is unusual for a tillodont fossil in that the teeth are essentially unworn (Fig. 4).
330 The m1 on CMN 8687 consists only of the labial part of the talonid which preserves a large
331 hypoconid, whereas the m2 is nearly complete, missing only its paraconid and part of the labial
332 wall of the talonid. The m2 on CMN 8687 has a length of 20.0 mm, WTri of 17.8 mm, and WTal
333 of 16.1 mm, placing it within the size range of m2s of *T. castoridens* and *T. hyracoides* measured
334 by Gazin (1953) and *T. grangeri* measured by Robinson (1966).

335 On the m2 of CMN 8687, the labial cusps and lophids of the trigonid and talonid form a
336 U-shaped pattern in occlusal aspect, as in CMN 8709, but unlike *Trogosus gazini* from the
337 Bridger Formation in Wyoming in which the talonid on m1-m2 is V-shaped (see Miyata 2007b).
338 On the m2 of CMN 8687, the trigonid is noticeably taller than the talonid, and comparable in
339 relative height and hypsodonty to an m1 of *Trogosus hillsii* (UCM 69094) from the Huerfano
340 Formation in Colorado; both are more hypsodont than lower molars of *T. gazini* that Miyata

(2007b) described as relatively brachydont. Although the paraconid has been broken off, the m2 on CMN 8687 preserves a large protoconid (the largest cusp on the tooth), and a metaconid that is subequal in height and posterolingual to the protoconid. A crenulated protolophid runs between the proto- and metaconids. CMN 8687 bears a well-developed metastylid posterior to, and lower than, the metaconid, contrasting *T. gazini* which has a weak metastylid (Miyata 2007b). The talonid basin of the m2 on CMN 8687 is deeper than the trigonid basin, and is open lingually with a deep notch occurring on the lingual margin between the metastylid and entoconid. The m2 on CMN 8687 lacks a precingulid, although it has a weak discontinuous cingulid on the posterolabial margin of the m2 talonid. Like m2s of some other trogosines, including some specimens of *T. latidens* (UCM 42723) and *Tillodon fodiens* (see Miyata 2007b), the m2 on CMN 8687 has a small second talonid basin – the hypoconulid-entoconid basin – although the basin is not completely closed in that a notch exists along its lingual margin directly posterior to the entoconid. The second talonid basin does not appear to be restricted to m2s of *Trogosus*, as UCM 69094, an m1 referred to *T. hillsii*, also shows the feature.

According to Gazin (1953), molars of *T. castoridens* and *T. hyracoides* are comparable in size, and the primary difference between these two genera relates to the length of the rostrum – *T. hyracoides* has a longer rostrum than *T. castoridens*. Subsequently, Robinson (1966) suggested that *T. grangeri* and *T. hillsii* may be synonymous and had similar-sized upper dentitions. Lucas and Schoch (1998) considered *T. hyracoides* a junior synonym of *T. castoridens*, and they synonymized *T. hillsii* with *T. grangeri*, following Robinson (1966). Recently, Miyata and Deméré (2016) suggested that *T. castoridens* and *T. hyracoides* as well as *T. hillsii* and *T. grangeri* represented sympatric pairs of short- and long-faced species in the Green River and Huerfano basins, respectively, although this idea, initially put forward by Gazin (1935), has been

questioned due to small sample size and the fragmentary nature of most *Trogosus* fossils. Concerning the identification of CMN 8687, it seems too small to be *T. latidens*, and it is morphologically distinct in a number of characters from *T. gazini*. However, due to the overlap in size and morphology of lower molars of the other species and questions concerning synonymies, we cannot refer CMN 8687 to any previously known species of *Trogosus*, and as such refer the specimen only to *Trogosus* sp.

Order Perissodactyla Owen, 1848

Family Brontotheriidae Marsh, 1873

Subtribe Brontotheriina Marsh, 1873

Comments: The Brontotheriidae is an Eocene clade of perissodactyls (odd-toed ungulates) known from North America, Asia, and Europe (Mihlbachler 2008 and references therein). They are differentiated from other perissodactyls by several cranial and dental characters, including an elongate postorbital cranium, a short face with the orbit above M2, a W-shaped ectoloph and isolated proto- and hypocones on their upper molars, as well as an M-shaped lophid pattern, reduced paraconid, and large m3 hypoconulid on lower molars. However, the cranial morphology is primarily used to differentiate among the later, larger more derived brontothere genera (Mader 1989; Mihlbachler 2008). With regard to lower molars such as those on ROM 6088, primarily size is used to refer this specimen to Brontotheriina – a clade that includes large-bodied, horned brontothere species from North America and Asia (Mihlbachler, 2008).

Brontotheriina, gen. et. sp. indet.

Figure 5

DESCRIPTION: ROM 6088, found in the lower Australian Creek Formation cropping out on the west side of the Fraser River approximately 32 km south of Quesnel, comprises a partial Rm3 (missing its hypoconulid, metaconid, and entoconid) and the talonid of Rm2 (Fig. 5). Although incomplete, the length of m3 clearly exceeded 63 mm, and the trigonid and talonid widths are 40.1 and 39.9 mm, respectively; the m2 talonid was at least 40 mm wide. Its large size places ROM 6088 within the size range of m3s of latest Eocene (Chadronian) *Megacerops* spp. and about a mm wider than m3s of late Uintan *Eubrontotherium clarnoensis* and about 2 mm wider than m3s of *Protitanops curryi* and *Protitanotherium emarginatum* measured by Mhlbachler (2008, appendix 1). ROM 6088 is also within the size range of middle Eocene Asian taxa, including *Gnathotitan berkeyi*, *Rhinotitan* spp., and *Metatitan relictus* (Mhlbachler, 2008, appendix 1). Genera within the Brontotheriina are differentiated from one another based largely upon cranial characters, whereas their lower molars are morphologically very similar and overlap in size. Like the lower molars of these taxa, ROM 6088 has shallow trigonid and talonid basins, a ridge-like paraconid, and a notch midway along the lingual margin of the talonid basin. The labial cingulid on ROM 6088 is discontinuous, like *Eubrontotherium clarnoensis* (see Mhlbachler 2007), although this character seems variable in *Megacerops*, with most of the UCM specimens from the White River Formation showing a continuous labial cingulid (e.g., UCM 43751 and 94369). The m3 on ROM 6088 differs from m3s of *Megacerops* from the White River Formation (UCM specimens 43751, 47863, 20504, and 94369) and *Eubrontotherium clarnoensis* (UCMP 126102) in having a larger, more linguall-projecting metacristid, and the protolophid and cristid obliqua are straight, not bowed or rounded, although

the latter may be a factor of wear (i.e., ROM 6088 is not as worn as most *Megacerops* specimens with which it was compared). However, presence of a lingually expanded metacristid on m3s of *Megacerops* is variable, with some dentitions from the Cypress Hills Formation in Saskatchewan showing similar development to ROM 6088 (Mihlbachler, pers. comm. to JE, 2017). ROM 6088 also bears an entocristid along the lingual margin of the tooth anterior to the entoconid. The entocristid is smaller than the metacristid, which bears a tiny wear facet, and the notch in the talonid basin is between the two. Although the hypoconulid is not preserved on the m3 of ROM 6088, the pattern of breakage indicates that it was lingual in placement, as in all Brontotheriidae (Mihlbachler 2008).

DISCUSSION: Brontotheriina is a subtribe within the family Brontotheriidae that includes several middle – late Eocene, large-bodied genera from North America and Asia (Mihlbachler 2008). Compared to the North American genera included within the Brontotheriina, the m2 talonid and partial m3 of ROM 6088 are considerably wider than lower molars of middle Eocene *Duchesneodus*, and fall within (or near) the size range of *Megacerops* spp., *Eubrontotherium clarnoensis*, *Protitanotherium emarginatum*, and *Protitanops curryi*. With regard to age, these taxa range from late Uintan to Chadronian. Specifically, *Eubrontotherium clarnoensis* is from the Hancock Quarry in the Clarno Formation, Oregon, which is considered ca. 40 Ma or slightly older, based upon Ar/Ar dates of 39.49 – 39.99 Ma for a welded tuff directly above the Hancock Quarry in the basal John Day Formation (Hanson 1996; Lucas et al. 2004 and references therein). Lucas et al. (2004) also suggested the Hancock Quarry fauna fits best with a late Uintan age, based upon its mixture of North American endemics and Eurasian immigrants. *Protitanotherium*

emarginatum is from a late Uintan locality in the Uinta Formation in Utah, while both *Megacerops* and *Protitanops* are Chadronian (latest Eocene) in age (Mihlbachler 2008).

Paleoenvironment

Princeton Basin - Allenby Formation (tillodont)

Megaflora remains from the Allenby Formation in the Princeton area were first reported by Dawson (1890) and Penhallow (1908), and remain under study (Greenwood et al. 2016a, 2016b; Pigg et al. 2016). Fossils discovered in outcrop and in mine tailings in the Princeton Basin include compression fossils of plants in shales and coals (e.g., Thomas Ranch; Dillhoff et al. 2014; Greenwood et al. 2016a). Three-dimensionally preserved plant organs occur in silicified peats of the Princeton Chert, part of the Ashnola Shale of Read (1987, 2000), on the east bank of the Similkameen River, south of Princeton (Pigg et al. 2016). The outcrops at Whipsaw and Nine-mile creeks are intersected in the abandoned Blue Flame mine, and are stratigraphically equivalent to the shales and coal seams mined in Pleasant Valley Mine #2 (McMechan 1983; Read 2000). Geographically close to the Pleasant Valley Mine #2 and Vermilion Cliff (Vermilion Bluffs of modern works) is the Thomas Ranch fossil locality, part of the Vermilion Bluffs Shale unit of Read (2000) (Dillhoff et al. 2013).

Penhallow (1908) listed a range of gymnosperm and angiosperm leaf and fruit taxa from his Tulameen locality, and Arnold (1955a, 1955b) reported on the floating water fern *Azolla* as well as conifers (Cupressaceae and Pinaceae) from the tailings of the Pleasant Valley mine on the south banks of the Tulameen River. At Thomas Ranch, Dillhoff et al. (2013) reported a comparable list of plant genera as reported by Penhallow (1908) and Arnold (1955b) for Tulameen River and the Pleasant Valley Mine, confirming a common flora across the area for

the time span encompassed by the Pleasant Valley and Princeton #1 coal seams, but adding a number of key conifer and broadleaf angiosperm genera. Many genera are typical of today's mixed deciduous forests of eastern North America and Asia (Greenwood et al. 2005, 2016b). Dillhoff et al. (2013) reconstructed the Thomas Ranch paleoclimate using bioclimatic analysis of the plant fossils' nearest living relatives as mesothermal and moist, with a mean annual temperature (MAT) of 12.8 ± 2.5 °C, cold month mean temperature (CMMT) of -3.9 ± 4.1 °C, and mean annual precipitation (MAP) of 115 ± 39 cm/yr; slightly cooler temperatures were estimated by Dillhoff et al. (2013) from leaf physiognomy (MAT 9.0 ± 2.0 °C and CMMT -1.2 ± 3.4 °C).

Quesnel area - Australian Creek Formation (brontothere).

J.W. Dawson (1877), G.M. Dawson (1883) and Penhallow (1908) reported megaflora from the confluence of the Quesnel and Fraser rivers, from strata Rouse and Mathews (1979) later correlated with their Australian Creek Formation. Taxa included maples (*Acer*), birch (*Betula*), hickory (*Carya*), chestnut (*Castanea*), beech (*Fagus*), walnut (*Juglans*), sycamores (*Platanus*), oaks (*Quercus*) and conifers (likely *Metasequoia*). No recent studies have been made of the plant fossils from the sediments from which the brontothere fossils were collected. However, Piel (1971) and Rouse and Mathews (1979) provided lists of spores and pollen found in lignite and clays of the Australian Creek Formation near the confluence of the Narcoisi and Fraser Rivers (Table 1) near where the brontothere teeth were collected and at another nearby outcrop. Rouse and Mathews (1979) reported a limited megaflora in the clays of the Australian Creek Formation, including *Equisetum* and leaves of beech (*Fagus*), oak (*Quercus*), katsura (*Cercidiphyllum*), and leafy shoots of the conifer *Metasequoia*.

A diverse tree and herbaceous plant microflora is reported from the Australian Creek Formation, including both terrestrial and aquatic forms (Piel 1971; Rouse and Mathews 1979). The tree pollen flora included the conifer families Cupressaceae and Pinaceae (Table 1). Piel (1971) listed several bisaccate grain types he identified as *Podocarpus* (Podocarpaceae); however, these grains more likely represent extinct Pinaceae (Greenwood et al. 2013 and references therein). The Pinaceae genera present in the pollen flora are all dryland forest trees typical of western Canada and montane areas across North America (i.e., *Abies* / fir, *Picea* / spruce, *Pseudotsuga* / Douglas fir, and *Tsuga* / hemlock), although black spruce (*Picea mariana*) is more typical of treed fens in present-day boreal forests. The Cupressaceae recorded by Piel (1971) (Table 1, e.g. *Glyptostrobus*, *Metasequoia*, and *Taxodium*) are today associated with swamp forest environments, with all but *Taxodium* restricted today to eastern Asia. Similarly, the umbrella pine *Sciadopitys* found in the samples, is today restricted to Japan, whereas *Cedrus* is Eurasian in distribution. Rouse and Mathews (1979) also recorded *Sequoia* (California redwood) in blue-grey clays they associated with stable bottomlands.

The broadleaf tree (i.e., angiosperm) pollen flora from the Australian Creek Formation (Table 1) includes temperate forest genera typical of southeastern North American and east Asian deciduous forests, but also genera restricted today to eastern Asia (e.g., *Engelhardia* and *Pterocarya*, both Juglandaceae). Included in the angiosperm pollen flora were swamp trees and shrubs (e.g., alders / *Alnus*, tupelo / *Nyssa*), as well as aquatic herbaceous plants (e.g., water primrose / *Jussiaea-Ludwigia*, and the pond weed / *Potamogeton*). The understorey of the dryland forests and wetland margins likely were rich in mosses and ferns, including *Equisetum* (horsetails) and *Osmunda* (royal fern and similar species) (Table 1).

Rouse and Mathews (1979) recognized three separate palynofacies in their Australian Creek Formation; the *Osmunda* facies associated with lignitic clays (peat swamps), a *Parviprojectus* facies of laminated carbonaceous silts and clays (small lakes and ponds on the alluvial plain), and a *Carya* facies reflecting weakly bedded blue-grey clays (bottomlands with ponds and backwaters). The overall impression from the spore and pollen flora and the sedimentary facies is of a landscape supporting mixed conifer-broadleaf forests (i.e., mixed mesophytic forest of Rouse and Mathews 1979) interspersed with wetland areas, including treed fens and swamps, and open water. The mixture of genera listed by Piel (1971) and Rouse and Mathews (1979) is consistent with a mesothermal moist climate, with MAT 15-17 °C and MAP 100-150 cm/yr according to Rouse and Mathews (1979). Applying the same bioclimatic analysis method to the modern plant genera listed in Table 1 as used by Dillhoff et al. (2013) for the Thomas Ranch flora, MAT is estimated at 13.6 ± 3.0 °C, CMMT 4.0 ± 4.2 °C, and MAP 129 ± 34 cm/yr, consistent with the prior estimates.

Conclusions

With regard to the tillodont fossils described above, Robinson et al. (2004) considered *Trogosus* an index taxon for the Bridgerian NALMA, which temporally ranges from approximately 51 – 48 Ma (Smith et al. 2008). Consequently, the relative age inferred for the Vermilion Bluffs Shale based upon presence of *Trogosus* corroborates the $^{40}\text{Ar}/^{39}\text{Ar}$ and U-Pb age estimates for the Allenby Formation ranging from 52 – 48.7 Ma (Moss et al. 2005; Ickert et al. 2009; Little et al. 2009; Greenwood et al. 2016a; Pigg et al. 2016) (Fig. 2). From a paleobiogeographic perspective, *Trogosus latidens* and *Trogosus* sp. from the Eocene of B.C.

support the hypothesis for trans-Beringian dispersal of this genus from Asia into North America during Bridgerian time, initially suggested by Beard (1998).

Our inability to assign the brontothere teeth from the lower Australian Creek Formation (ROM 6088) to a known genus has implications for estimating the age of this rock unit, because the late Eocene (Chadronian) age – originally considered early Oligocene based on the geochronology in use for the Chadronian NALMA at the time – assigned to these beds by earlier studies (Rouse and Mathewes 1979) is based largely on the brontothere fossils. Given their size and morphologic similarities with later, larger members of Brontotheriina, the brontothere teeth are consistent with a Chadronian age for the Australian Creek Formation, but they may be as old as late Uintan. The late Uintan – Chadronian NALMA range from 40 – 33.7 Ma (Robinson et al. 2004; Prothero and Emry 2004). Volcanic rocks underlying the Australian Creek Formation originally mapped as cf. Kamloops Group south of Quesnel have K-Ar ages of 48.8 ± 1.5 Ma to 41.6 ± 1.9 Ma (Rouse and Mathewes 1979) (Fig. 2). These underlying volcanic rocks are now mapped as the Endako Group (Fig. 3), which has $^{40}\text{Ar}/^{39}\text{Ar}$ ages ranging from 51-45 Ma (Grainger et al. 2001; Bordet et al. 2014). Therefore, the radiometric ages of the rocks underlying the Australian Creek Formation are consistent with a late Uintan – Chadronian age for the brontothere teeth (Fig. 2).

Climate and forest character in the area where the tillodont lived during the early Eocene (Dillhoff et al. 2013) were comparable to that reconstructed for the late Eocene brontothere; warm and wet (MAT 12.8 ± 2.5 °C, CMMT -3.9 ± 4.1 °C, and MAP 115 ± 39 cm/yr), supporting mixed conifer-broadleaf forest rich in temperate forest tree genera.

The paleoenvironmental reconstruction for the Australian Creek Formation – a warm and wet (MAT 13.6 ± 3.0 °C, CMMT 4.0 ± 4.2 °C, and MAP 129 ± 34 cm/yr) mixed conifer-

broadleaf forest rich in temperate forest tree genera (Table 1) – fits well with the hypothesized habitat of the large late Eocene brontotheres, which based on carbon isotope analysis of their teeth (Zanazzi and Kohn, 2008), were folivores that preferred mesic forested environments.

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782 **Table 1.** List of pollen and spore plant taxa from the Australian Creek Formation (Piel 1971),
 783 and additional megaflora listed by Rouse and Mathews (1979). Those with an * were
 784 not used in the bioclimatic analysis of the nearest living relatives (NLR).

Palynomorph / major plant type	NLR	Common name
Pteridophytes		
<i>?Equisetum sp.</i>	<i>Equisetum</i> *	horsetail
<i>Lycopodium annotinioides</i>	<i>Lycopodium</i> s.l.*	Club moss
<i>Osmunda claytonites</i> , <i>O. irregulites</i> , <i>O. regalites</i>	<i>Osmunda</i>	interrupted fern, royal fern
Gymnosperms		
<i>Abies sp.</i>	<i>Abies</i> (Pinaceae)	fir
<i>Cedrus sp.</i> & <i>C. perialata</i>	<i>Cedrus</i> (Pinaceae)	True cedar
<i>Ephedra sp.</i>	<i>Ephedra</i> *	Mormon tea
<i>Glyptostrobus sp.</i> & <i>G. vacuipites</i>	<i>Glyptostrobus</i> (Cupressaceae)	Chinese water pine
<i>Metasequoia papillapollenites</i>	<i>Metasequoia</i> (Cupressaceae)	Dawn redwood
<i>Picea sp. 1-3</i>	<i>Picea</i> (Pinaceae)	spruce
<i>Pinus sp. 1 & 2</i>	<i>Pinus</i> (Pinaceae)	pine
<i>Podocarpus sp. 1-3</i>	likely Pinaceae*	
<i>Pseudotsuga sp.</i>	<i>Pseudotsuga</i> (Pinaceae)	Douglas fir
<i>Sciadopitys serratus</i>	<i>Sciadopitys verticillata</i>	Japanese umbrella pine
<i>Sequoia megafossils</i>	<i>Sequoia sempervirens</i>	California redwood
<i>Taxodium sp.</i> , <i>T. kiatipites</i> & <i>T. rousei</i>	<i>Taxodium</i> (Cupressaceae)	Swamp cypress

<i>Tsuga sp., T. alexandriana, T. heterophyllites, T. minisacca</i>	<i>Tsuga</i> (Pinaceae)	Hemlock & western hemlock
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Arboreal Angiosperms

<i>Acer sp. 1 & 2</i>	<i>Acer</i> (Sapindaceae)	maple
<i>Alnus sp. & A. verus</i>	<i>Alnus</i> (Betulaceae)	alder
<i>Betula claripites</i>	<i>Betula</i> (Betulaceae)	birch
<i>Carya juxtaoripites, C. viridifluminipites, C.</i>	<i>Carya</i> (Juglandaceae)	hickory or buckeye
<i>Castanea sp.</i>	<i>Castanea</i> (Fagaceae)	chestnut
<i>Cercidiphyllum</i> leaf fossils	<i>C. japonicum</i>	katsura
<i>Corylus sp.</i>	<i>Corylus</i> (Betulaceae)	hazelnut
<i>Engelhardia sp. cf. E. chrysolepis</i>	<i>Engelhardia</i> (Juglandaceae)	
<i>Fagus granulata</i>	<i>Fagus</i> (Fagaceae)	beech
<i>Fraxinus sp. & Fraxinus columbiana</i>	<i>Fraxinus</i> (Oleaceae)	ash
<i>Juglans horniana</i>	<i>Juglans</i> (Juglandaceae)	walnut
<i>Liquidambar sp.</i>	<i>Liquidambar</i> (Altingiaceae)	Sweet gum
<i>Myrica annulites</i>	<i>Myrica</i> (Myricaceae)	Sweet gale
<i>Nyssa sp.</i>	<i>Nyssa</i> (Cornaceae)	Tupelo / sweet gum
<i>Prosopis quesnelli</i>	<i>Prosopis</i> (Fabaceae)*	mesquite
<i>Pterocarya stellatus</i>	<i>Pterocarya</i> (Juglandaceae)	wing nut
<i>Quercus shiabensis</i>	<i>Quercus</i> (Fagaceae)	oak
<i>Tilia crassipites</i>	<i>Tilia</i> (Malvaceae)	Linden or basswood
<i>Ulmus/Zelkova sp. 1 & 2</i>	<i>Ulmus</i> (Ulmaceae)	elm

Other Angiosperms

<i>Diervilla echinata</i>	<i>Diervilla</i> (Caprifoliaceae)*	Bush honeysuckle
? <i>Dorstenia</i> sp.	cf. <i>Dorstenia</i> (Moraceae)*	
<i>Jussiaea</i> sp.	<i>Ludwigia</i> (Onagraceae)*	Water primrose
<i>Pachysandra</i> sp. or <i>Sarcococca</i> sp.	<i>Pachysandra</i> (Buxaceae)*	
<i>Potamogeton narcoslii</i>	<i>Potamogeton</i> * (Potamogetonaceae)	Pond weed
<i>Psilastephanocolpites marginatus</i>		
? <i>Symplocos</i> sp.	cf. <i>Symplocos</i> (Symplocaceae)	Yellow wood

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Table 2. Tooth measurements (in mm) of CMN 8709, *T. latidens* from Vermilion Bluffs Shale, Allenby Formation, Princeton, B.C.

Element	A-P Length	WTri	WTal
Lm1	20.8	19.2	17.2
Lm2	23.2	23.5	21.5
Rm2	25.9	22.6	21.7
Lm3 (incomplete)	>30	22.8	19.4

Figures

Figure 1. Location maps for the fossil occurrences. (A) Map of North America showing the location of areas outside of British Columbia mentioned in the text. (B) Map of British Columbia showing locations of sites with Eocene mammals reported from British Columbia and other fossil sites mentioned in the text. Nearby cities and towns are shown as solid black circles for reference. Adapted from a map in Greenwood et al. (2016b).

Figure 2. Chart showing the stratigraphic relationships of the Princeton Group, including the Allenby Formation, and a summary of available radiometric age data for the Princeton Group and the Kamloops Group. (A) K-Ar dates from Allenby Fm. from sources cited in Read (1987, 2000), and (B) from Kamloops Gp. near Quesnel from Rouse & Mathews (1979). (C) ^{40}Ar - ^{39}Ar of Princeton Group volcanics from Ickert et al. (2009). (D) Rock unit relationships adapted from Read (1987, 2000). Minor units and intercalated ash layers not shown. (E) ^{40}Ar - ^{39}Ar and Pb-U from tephra reported in Villeneuve and Mathewes (2005), Moss et al. (2005), Archibald et al. (2010), DeVore & Pigg (2010), and summarized in Greenwood et al. (2016a); *A*, 48.7 Ma from ash layer #22 from the Ashnola Shale / Princeton Chert; *B*, Vermilion Bluffs shale; *C*, Hardwick ss. Epoch and Stage chronology from Cohen et al. (2013, updated 2015); NALMA (North American land mammal ages) from Woodburne (2004). Adapted from a figure in Greenwood et al. (2016b).

Figure 3. Diagrammatic representation of structural and stratigraphic relationships of major

rock units along the Fraser River Valley near Quesnel. Dashed lines represent minor faults associated with surface slumping of the Miocene Fraser Bend Formation. Dotted lines indicate uncertain relationships. Redrawn from Hora and Hancock (1994). Not to scale.

Figure 4. (A–B) Mandibular fragment with worn Lm1-m3 and Rm2 of *Trogosus latidens*: left lateral (A) and occlusal views (B), respectively; CMN 8709. (C–D) Lm1 talonid fragment and nearly complete Lm2 of *Trogosus* sp.: occlusal (C) and labial views (D), respectively; CMN 8687. Both CMN 8709 and 8687 are from the Pleasant Valley Mine #2, Vermilion Bluffs Shale, Allenby Formation, Princeton Basin, B.C. (Bridgerian). Abbreviations: en = entoconid, hyc = hypoconulid, mtst = metastylid; hypoconulid-entoconid basin is indicated by a dashed white line on (C).

Figure 5. Incomplete talonid of Rm2 and nearly complete Rm3 referred to *Brontotheriina*, gen. et. sp. indet.; ROM 6088, from the lower Australian Creek Formation, west side of Fraser River near Quesnel, B.C. Abbreviations: mter = metacristid.

Location maps for the fossil occurrences. (A) Map of North America showing the location of areas outside of British Columbia mentioned in the text. (B) Map of British Columbia showing locations of sites with Eocene mammals reported from British Columbia and other fossil sites mentioned in the text. Nearby cities and towns are shown as solid black circles for reference. Adapted from a map in Greenwood et al. (2016b).

168x176mm (300 x 300 DPI)

Chart showing the stratigraphic relationships of the Princeton Group, including the Allenby Formation, and a summary of available radiometric age data for the Princeton Group and the Kamloops Group. (A) K-Ar dates from Allenby Fm. from sources cited in Read (1987, 2000), and (B) from Kamloops Gp. near Quesnel from Rouse & Mathews (1979). (C) 40Ar-39Ar of Princeton Group volcanics from Ickert et al. (2009). (D) Rock unit relationships adapted from Read (1987, 2000). Minor units and intercalated ash layers not shown. (E) 40Ar-39Ar and Pb-U from tephra reported in Villeneuve and Mathewes (2005), Moss et al. (2005), Archibald et al. (2010), DeVore & Pigg (2010), and summarized in Greenwood et al. (2016a); A, 48.7 Ma from ash layer #22 from the Ashnola Shale / Princeton Chert; B, Vermilion Bluffs shale; C, Hardwick ss. Epoch and Stage chronology from Cohen et al. (2013, updated 2015); NALMA (North American land mammal ages) from Woodburne (2004). Adapted from a figure in Greenwood et al. (2016b).

172x102mm (300 x 300 DPI)

Diagrammatic representation of structural and stratigraphic relationships of major rock units along the Fraser River Valley near Quesnel. Dashed lines represent minor faults associated with surface slumping of the Miocene Fraser Bend Formation. Dotted lines indicate uncertain relationships. Redrawn from Hora and Hancock (1994). Not to scale.

90x41mm (300 x 300 DPI)

(A–B) Mandibular fragment with worn Lm1–m3 and Rm2 of *Trogosus latidens*: left lateral (A) and occlusal views (B), respectively; CMN 8709. (C–D) Lm1 talonid fragment and nearly complete Lm2 of *Trogosus* sp.: occlusal (C) and labial views (D), respectively; CMN 8687. Both CMN 8709 and 8687 are from the Pleasant Valley Mine #2, Vermilion Bluffs Shale, Allenby Formation, Princeton Basin, B.C. (Bridgerian). Abbreviations: en = entoconid, hyc = hypoconulid, mtst = metastylid; hypoconulid-entoconid basin is indicated by a dashed white line on (C).

182x219mm (300 x 300 DPI)

Incomplete talonid of Rm2 and nearly complete Rm3 referred to *Brontotheriina*, gen. et. sp. indet.; ROM 6088, from the lower Australian Creek Formation, west side of Fraser River near Quesnel, B.C.
Abbreviations: mtr = metacristid.

86x190mm (300 x 300 DPI)