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EARLY EOCENE BRONTOTHERIIDAE (PERISSODACTYLA) FROM THE EUREKA SOUND GROUP, ELLESMERE ISLAND, CANADIAN HIGH ARCTIC—IMPLICATIONS FOR BRONTOTHERE ORIGINS AND HIGH-LATITUDE DISPERSAL

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ABSTRACT—The northernmost records of early Eocene brontotheres, fossils of cf. *Eotitanops* and Brontotheriidae gen. et sp. indet., are described here from late Wasatchian-aged strata of upper parts of the Eureka Sound Group on central Ellesmere Island (~79°N). Although the fossils were initially tentatively identified on faunal lists as *Lambdotherium*, their larger size and dental morphology ally them more closely to mid-latitude *Eotitanops* and *Palaeosyops*. The Ellesmere Island specimens are dentally most similar to mid-latitude *Eotitanops*, but can be distinguished from the latter by derived characters on their premolars that are shared with the younger (i.e., Bridgerian) *Palaeosyops*. The presence of brontotheres in early Eocene strata on Ellesmere Island implies that the group's evolution was well underway early in its history at northern high latitudes, and is consistent with either an Asian or North American origin and trans-Beringian dispersal. While cf. *Eotitanops* from Ellesmere Island appears dentally too advanced to be ancestral to mid-latitude co-eval *Eotitanops*, it may be a suitable ancestor to *Palaeosyops*. The presence of cf. *Eotitanops* on Ellesmere Island may reflect a high-latitude lineage that subsequently dispersed to mid-latitudes during early middle Eocene (Bridgerian) time.

INTRODUCTION

Brontotheres are an extinct family of perissodactyls or odd-toed ungulates that inhabited North America from the Wasatchian through the Chadronian North American land mammal ages (NALMA), equivalent to the entirety of the Eocene (Prothero, 1995). Their molars bear a characteristic bunoselenodont pattern with a well-developed 'W'-shaped ectoloph (Mader, 1998). Here, fossils of early Eocene brontotheres are described from upper levels of the Eureka Sound Group in the Canadian High Arctic. Discovered on expeditions to Ellesmere Island in the 1970s through 2001, these fossils initially were identified tentatively on faunal lists as *Lambdotherium* (e.g., West et al., 1977; Marincovich et al., 1990; Eberle and McKenna, 2002). However, detailed study clearly distinguishes the High Arctic specimens from *Lambdotherium*, and allies them more closely to mid-latitude brontotheres *Eotitanops* and *Palaeosyops*. Early Eocene brontothere specimens described below are from smaller, more primitive brontotheres than the large diplacodont brontothere known from tooth fragments from middle Eocene strata on nearby Axel Heiberg Island (Eberle and Storer, 1999).

Strata of the Eureka Sound Group preserve the northernmost known record of early Tertiary mammals. The first fauna from these strata was discovered in 1975 on central Ellesmere Island (Dawson et al., 1976), with subsequent discoveries in the late 1970s–2001 in Eureka Sound Group strata on Ellesmere Island and nearby Axel Heiberg Island (e.g., Dawson, 1990; Dawson et al., 1993; Eberle and Storer, 1999). In addition to fossil mammals, a diverse lower vertebrate fauna that includes land tortoises, monitor lizards, snakes, and crocodilians strongly corroborates long-standing paleobotanical evidence for a mild temperate arctic climate during the Eocene (Estes and Hutchison, 1980; McKenna, 1980).

Early Eocene brontotheres from Ellesmere Island are among the oldest known representatives of the Brontotheriidae, and consequently may be key to understanding the group's origin and early dispersal patterns. While brontothere origins have long been contended, more recently it has been hypothesized that the group originated in Asia and subsequently dispersed into North America across Beringia (Beard, 1998; Hooker and Dashzeveg, 2003). Early Eocene occurrence of brontotheres on Ellesmere Island implies that the group's evolution was well underway early on at northern high-latitudes, and seems consistent with an Asian origin, although North America also needs to be considered. Further paleobiogeographic implications are discussed below.

GEOLOGIC AGE AND FAUNA

On central Ellesmere Island near Bay Fiord (Fig. 1), Eocene terrestrial vertebrates occur in two stratigraphic levels in upper parts of the Eureka Sound Group, the lower of which contains the brontothere specimens described below. The diverse fauna from the lower faunal level, comprising fishes, amphibians, reptiles, birds, and over 20 mammalian taxa, indicates an early Eocene age, equivalent to the younger part of the Wasatchian NALMA (West et al., 1981; Dawson et al., 1993; Eberle and McKenna, 2002). Specifically, Perissodactyla, Hyaenodontidae, *Miacis*, and cf. *Vulpavus*, all of which first appear in the Wasatchian, and *Anacodon*, which last appears in the Wasatchian (Robinson et al., 2004), are known from the lower faunal level in the Eureka Sound Group (Eberle and McKenna, 2002). Additionally, *Pachyaena*, an index taxon for the Wasatchian, occurs in the lower faunal level, as do *Coryphodon*, *Paramys*, and *Viverravus* (see Eberle and McKenna, 2002), all typical of the Wasatchian at mid latitudes (Robinson et al., 2004). Although the known sample from the upper faunal level is considerably less diverse, it is interpreted as early middle Eocene in age, equivalent to the Bridgerian NALMA (McKenna, 1980; West et al., 1981; Dawson, 1990; Dawson et al., 1993), based upon presence of an anosteirine turtle (Estes and Hutchison, 1980) and a larger, more derived brontothere to be described elsewhere. Palynology supports an early to middle Eocene age range for terrestrial vertebrate-bearing strata of the Eureka Sound Group near Bay Fiord (Norris and Miall, 1984).

The lithology of the terrestrial vertebrate-bearing strata of the Eureka Sound Group, supported by the fossil flora and fauna, indicates a lush, proximal, delta-front to delta-plain environment with abundant channels and lowland swamps (Miall, 1986).

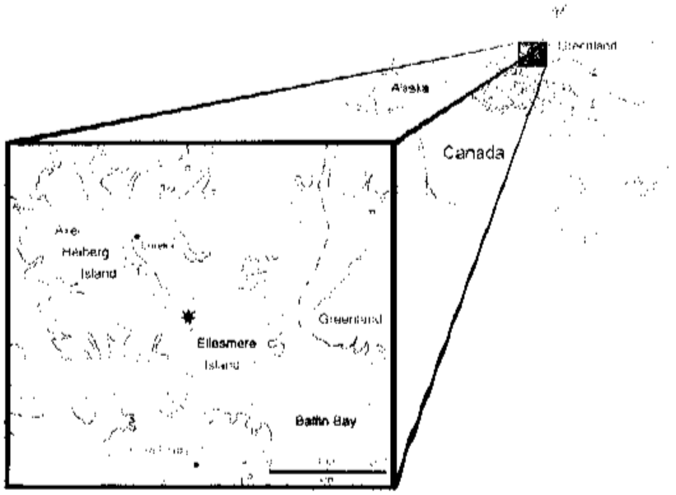

FIGURE 1. Map of Ellesmere and Axel Heiberg Islands, Nunavut. Star indicates the general location of terrestrial vertebrate-bearing localities in upper parts of the Eureka Sound Group in the Bay Fiord area, central Ellesmere Island.

MATERIALS AND METHODS

Brontothere specimens described here were recovered from the 1970s through 2001 by field parties headed by the Carnegie Museum of Natural History (1970s and 1980s) and the California Academy of Sciences and Canadian Museum of Nature (2001). The specimens are curated at the Canadian Museum of Nature in Ottawa. They are from four localities at the same stratigraphic level in the Wasatchian-aged lower faunal level near Bay Fiord on central Ellesmere Island. While the stratigraphic relationships among terrestrial vertebrate localities in the Bay Fiord area are just beginning to be understood, the Wasatchian brontothere-bearing localities are among the stratigraphically lowest in the area, a few tens of meters above marine strata. More detailed locality information is on file at the Canadian Museum of Nature and the Carnegie Museum of Natural History.

In describing the specimens, all of which are teeth and tooth fragments, I follow dental terminology outlined by Hooker (1989). Measurements follow Mihlbachler (2005). Specifically, the length of upper premolars and molars is the maximum anteroposterior length measured along the labial side. The width of upper premolars is measured from the labial side of the paracone to the lingual side of the protocone, and the width of upper molars is measured from the labial margin of the mesostyle to the lingual margin of the protocone. Measurements were taken using a SPOT Insight camera (Diagnostic Instruments, Inc.) attached to a Leica MZ16 microscope, and using SPOT Version 3.5.8 measuring software, and are in millimeters (mm).

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, NY; **CMN**, Canadian Museum of Nature, Ottawa, Ontario; **NUFV**, Nunavut Fossil Vertebrate collection (housed at CMN); **UCM**, University of Colorado Museum of Natural History, Boulder, Colorado.

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Family BRONTOTHERIIDAE Marsh, 1873
EOTITANOPS Osborn, 1907
cf. *EOTITANOPS*
(Fig. 2A–G, Tables 1, 2)

Referred Specimens—CMN 32249, associated left P2, P3, partial P4, M1, M2 and jaw fragments, and NUFV 34, RM1, from Mac's Bone Pile locality; CMN specimens 32279 and 32280, RM1s from Locality 76-45; CMN 32247, incomplete LMX and associated jaw fragments; CMN 52062, associated Lmx fragment, Rm1, partial Rm2 and m3 talonid, incisor, and tooth enamel and root fragments from Locality 76-50; and CMN 32240, Lmx fragment from D7 locality; all Eureka Sound Group (late Wasatchian), central Ellesmere Island near Bay Fiord, Nunavut.

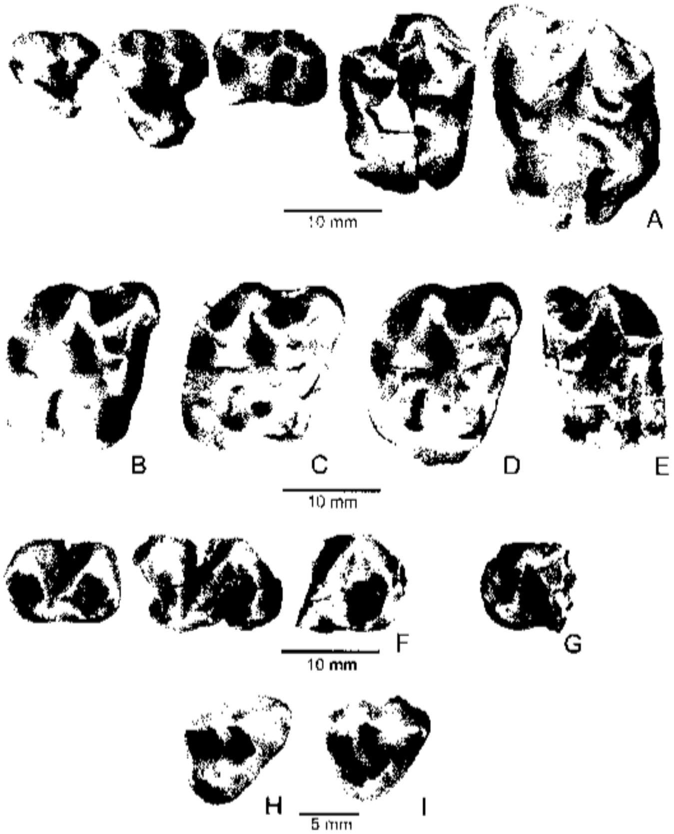

FIGURE 2. Brontothere teeth from the Eureka Sound Group, Ellesmere Island, Nunavut, **A–G**, cf. *Eotitanops*. **A**, CMN 32249, associated left P2, P3, partial P4, M1, and M2 from Mac's Bone Pile locality; **B** and **C**, CMN specimens 32279 and 32280, respectively, RM1s from Locality 76-45; **D**, NUFV 34, RM1 from Mac's Bone Pile locality; **E**, CMN 32247, incomplete LMX from Locality 76-50; **F**, CMN 52062, probable Rm1, partial m2 and talonid of m3 from Locality 76-50; **G**, CMN 32240, Lmx fragment from D7 locality (A–G are at the same scale). **H** and **I**, CMN 52060 and CMN 52061, respectively, RP2s of Brontotheriidae, gen. et sp. indet., from the D7 locality.

Description—While initially identified tentatively as *Lambdotherium* in faunal lists of the Eureka Sound Group (e.g., Marincovich et al., 1990; Eberle and McKenna, 2002), specimens referred here to cf. *Eotitanops* can be distinguished from *Lambdotherium* on the basis of both their larger size and differences in dental morphology (see description below). Additional specimens, recovered in the late 1980s and 2001, preserve several characters that ally them most closely with *Eotitanops* and *Palaeosyops*.

The most complete specimen (CMN 32249; Fig. 2A), which includes associated left upper premolars and molars, is similar in size to mid-latitude, early Eocene (i.e., latest Wasatchian–earliest Bridgerian) *Eotitanops borealis*. Specifically, measurements of premolars and M2 of CMN 32249 fall within size ranges of *E. borealis* given by Gunnell and Yarborough (2000) and Mihlbachler (pers. comm., 2004). M1 of the Arctic brontothere is distinctly smaller than that of *E. borealis* and similar in size to

TABLE 1. Measurements of upper dentition (in mm) of cf. *Eotitanops* from the Eureka Sound Group, Ellesmere Island, Nunavut

Specimen No.	Tooth position	Length	Width
CMN 32249	P2	10.00	0.66*
CMN 32249	P3	10.95	12.69
CMN 32249	P4 fragment	11.87	—
CMN 32279	M1	15.70	17.67
CMN32280	M1	15.80	18.23
NUFV 34	M1	15.40	17.63
CMN 32249	M2	17.30	21.00

*Estimated measurement due to breakage.

TABLE 2. Measurements of lower dental specimens (in mm) of CMN 32247, cf. *Eotitanops*, from the Eureka Sound Group, Ellesmere Island, Nunavut

Tooth position	Length	Width trigonid	Width talonid
Rm1	12.24	8.52	8.39
Rm2 fragment		—	9.71*
Rm3 fragment—		—	10.40*

*Estimated measurement due to breakage.

that of *E. minimus*. All dental measurements of the Arctic specimens are noticeably greater than those of *Lambdotherium* measured by Wallace (1980:tables 6, 8, 9).

Although the P2 of CMN 32249 (Fig. 2A) is missing its posterolingual corner, it nevertheless preserves several characters that differentiate it from P2s of *Lambdotherium*, and ally it more closely with *Eotitanops* and *Palaeosyops*. The P2s of *Lambdotherium* measured by Wallace (1980:tables 6, 8) are roughly two-thirds the size of the P2 of CMN 32249. Moreover, the P2 of CMN 32249 bears a relatively strong preprotocrista that is typical of early brontotheres, but is lacking on P2s of *Lambdotherium* (Mihlbachler, pers. comm., 2004). As in *E. minimus* (see Gunnell and Yarborough, 2000:fig. 6), the P2 of CMN 32249 has a tiny protocone that is relatively posterior in placement. There is no mesostyle or ectocingulum, although a narrow cingulum occurs anterolingual to the paracone. The P2 of CMN 32249 bears a large paracone and an incipient metacone that is directly posterior and separated from the paracone by a lingual crease. This contrasts with mid-latitude *Eotitanops*, which lacks a metacone, but is similar to *Palaeosyops*, which typically bears one (Gunnell and Yarborough, 2000). On the P2 of CMN 32249, cristae extend anteriorly and posteriorly from the para- and metacones.

The P3 of CMN 32249 is larger and more transverse than P2, and bears a preprotocrista but lacks a postprotocrista, which is typical of early brontotheres. In contrast, premolars of *Lambdotherium* have a distinct postprotocrista (Wallace, 1980; Mihlbachler, pers. comm., 2004). The para- and metacones on the P3 of CMN 32249 are similar in size, whereas on P3s of *E. borealis*, the paracone is noticeably larger than the metacone. Extending anteriorly from the paracone and posteriorly from the metacone, respectively, the preparacrista and postmetacrista bend slightly labially towards the tooth margin. As in *Eotitanops* (see Gunnell and Yarborough, 2000), the protocone on P3 of CMN 32249 is much lower than the labial cusps, and is not nearly so inflated as on P3s of *Palaeosyops*. As Osborn (1929) noted on the P3 and P4 of *E. borealis*, a very weak cingulum occurs labial to the metacone on the P3 of CMN 32249. However, there is essentially no buccal ridge extending from the paracone to the buccal margin. Weak buccal ridges characterize P3s and P4s of *Eotitanops*, whereas *Palaeosyops* has moderate to strong buccal ridges on its premolars (Gunnell and Yarborough, 2000). Similarly, the para- and metacones on premolars of *Lambdotherium* are buccally inflated and bear 'vertical ribs' (Wallace, 1980). The P3 of CMN 32249 also bears a narrow anterior cingulum, while breakage obscures morphologic details of its posterior margin. The width of P3 of CMN 32249 falls within the range for P3s of *E. borealis* measured by Gunnell and Yarborough (2000), but its length is roughly 10% less than for *E. borealis*. The P3s of *Lambdotherium* measured by Wallace (1980:tables 6, 8, 9) are 22–40% smaller than the P3 of CMN 32249.

Although only the labial half of P4 is preserved on CMN 32249, it nevertheless shows similarities to early brontotheres. As in *E. borealis*, the para- and metacones are subequal in size, and their labial margins are flat to slightly convex; as in P3, there is essentially no buccal ridge. In contrast, P4s of *Palaeosyops* have moderate to strong buccal ridges, whereas P4s of *Lambdotherium* possess relatively strong vertical ribs on the labial margins of both the para- and metacones (pers. observ.: Wallace, 1980). The parastyle on the P4 of CMN 32249 appears relatively larger and more distinct than on P4s of *Eotitanops*, and there is a weak cingulum labial to the metacone, including a slight swelling in the mesostyle region. Although rare, an incipient mesostyle on P4 is found in nearly all species of brontotheres (Mihlbachler, 2005). The P4s of *Palaeosyops* have noticeably greater buccal ectoloph expansion than the P4 of CMN 32249, including the cingulum labial to the metacone, which appears relatively wider and better developed on *P. paludosus* and *P. fontinalis* (see Gunnell and Yarborough, 2000:fig. 6). The length of the P4 of CMN 32249 falls within ranges of length for P4s of *E. borealis* measured by Gunnell and Yarborough (2000:table 6), and is approximately 25–40% longer than the P4s of *Lambdotherium* measured by Wallace (1980:tables 6, 8, 9).

The three M1s of cf. *Eotitanops* from Ellesmere Island are comparable in size to those of *E. minimus* and roughly 12–17% smaller than the average for specimens of *E. borealis* measured by Gunnell and Yarborough (2000). M2 of CMN 32249 falls within size ranges of M2s of *E. borealis* given by Gunnell and Yarborough (2000). However, their relative dimensions are more similar to those of *E. minimus*, but differ from those of *E. borealis* and *Palaeosyops* in that their transverse width is visibly greater than their length. Specifically, the transverse width of M1s of cf. *Eotitanops* is 12–15% greater than the length, while the single known M2 (on CMN 32249) is about 21% wider than it is long. In contrast, M1s and M2s of *E. borealis* tend to be more square in outline, with a transverse width ranging from 0–10% greater than the length (Mihlbachler, pers. comm., 2004). Based upon measurements of two M1s by Gunnell and Yarborough (2000), M1 of *E. minimus* is 18–20% wider than it is long, while M2 (based upon a single specimen) is approximately 11% wider than it is long. Molars of *Lambdotherium* are roughly 20–30% wider than they are long, based upon measurements by Wallace (1980:tables 6, 8, 9).

Characteristic for early brontotheres, the M1 and M2 of cf. *Eotitanops* from Ellesmere Island bear a protocone that is noticeably broader than the hypocone. In contrast, on molars of *Lambdotherium*, the protocone and hypocone are nearly equal in size (pers. observ.; Wallace, 1980). As in *Eotitanops*, the proto- and hypocones on molars of the Arctic brontothere are lower than the para- and metacones (which are subequal). A valley is formed between the two lingual cusps, closed labially by the prehypocrista and lingually by a cingulum running between the proto- and hypocones. There is no cingulum lingual to the protocone or around the hypocone, in contrast to molars of *Lambdotherium*, which typically bear a cingulum around the hypocone and occasionally lingual to the protocone (e.g., UCM 70193). However, as in *Lambdotherium* and early brontotheres, a relatively strong anterior cingulum runs the length of the molars on the Arctic specimens. As in *Eotitanops* and *Palaeosyops*, M1 and M2 of the Arctic brontothere possess a small paraconule from which the preparaconule crista extends to the anterolingual margin of the paracone. Molars of *Lambdotherium* have a much larger, triangular paraconule with a relatively longer preparaconule crista that connects to the paracone more labially. The M1 and M2 of the Arctic brontothere have a distinct prehypocrista, which occurs on molars of *Lambdotherium* and is occasionally present on *Eotitanops* and *Palaeosyops* (see Wallace, 1980). However, the prehypocrista on molars of *Lambdotherium* tends to be straight, while that on the Arctic specimens has a distinct anterolabial curve or bend to it. Development of a metaconule on molars of the Arctic brontothere appears variable, as is also the case for *Lambdotherium* and early brontotheres. The M1 on CMN 32249 appears to have a metaconule (although this region of the tooth is damaged); however the M2 of CMN 32249 lacks any swelling along its prehypocrista. CMN specimens 32279 and 32280 (Fig. 2B–C), identified as RM1s based upon their dimensions, lack a metaconule cusp, while NUFV 34 (Fig. 2D), also a RM1, shows a slight swelling at the anterior end of its prehypocrista. Although NUFV 34 was discovered well over a decade after CMN 32249, the two specimens are from the same locality and may belong to the same individual. NUFV 34 is similar in size and morphology, and shows similar wear patterns, to M1 on CMN 32249. The para- and mesostyles on molars of the Arctic brontothere appear larger and more inflated than on *Lambdotherium* and *E. minimus*, but are comparable in development to *E. borealis*.

CMN 32247 (Fig. 2E), a partial left upper molar, is referred to cf. *Eotitanops* based upon similarity to molars (particularly M1) of CMN 32249. CMN 52062 (Fig. 2F), consists of associated, incomplete lower molars and enamel fragments that were found alongside CMN 32247 at Locality 76-50, and may be from the same individual. These specimens also are referred to cf. *Eotitanops*, based upon their similarity to specimens of *E. borealis*. While lower molars of *Eotitanops* do not appear to be particularly diagnostic morphologically, they are noticeably smaller than those of *Palaeosyops* (at least 20%; Novacek et al., 1991). The probable Rm1 of CMN 62062 is roughly 20–25% smaller than m1s of *E. borealis* measured by Gunnell and Yarborough (2000:table 6), and is similar in size to those of *E. minimus* (Mihlbachler, pers. comm., 2004). This m1 is unusual in having an entoconid that is noticeably smaller than the hypoconid, and not as buccally placed as on m1s of *Eotitanops*. Wallace (1980) noted that for m1s of *Palaeosyops* (in which he also included *Eotitanops*), the hypo- and entoconids are subequal in height. Given its small size, small entoconid, and relatively large paralophid, the tooth in question on CMN 52062 may actually be a p4. However, it seems more plausible that it is an m1 because the p4s of *Palaeosyops* and *Eotitanops* typically lack an entoconid altogether, and the protoconid is more posterior in placement (i.e., nearly across from the metaconid; see Wallace, 1980). The more anterior placement of the protoconid on the probable m1 of CMN 52062 is more in keeping with m1s (rather than p4s) of *Eotitanops*. A probable Rm2 fragment of CMN 52062 indicates a tooth larger than m1, and, as in *Eotitanops* and *Palaeosyops*, it bears subequal hypo- and entoconids. A probable Rm3 talonid on CMN 52062 is morphologically comparable to, and falls within the range of widths for m3s of *E. borealis* measured by Gunnell and Yarborough (2000).

CMN 32240 (Fig. 2G) is a Lmx fragment preserving the trigonid and anterior part of the talonid. It probably belongs to the same taxon as CMN 52062, based on similarities in size and morphology.

Discussion—While the Arctic specimens appear dentally most similar to mid-latitude *Eotitanops*, they nevertheless can be differentiated from the latter by the following characters: (1) presence of a metacone on P2; (2) buccal ridges essentially lacking on premolars; (3) P4 with a relatively larger parastyle; and (4) upper molars with a distinct, antero-labially bending prehypocrista. Two of these characters, the metacone on P2 and P4 with a larger parastyle, are characteristic of the younger, more derived *Palaeosyops* (see Gunnell and Yarborough, 2000). Given the mixture of primitive and derived characters, and the fragmentary nature of the Arctic specimens, I only tentatively refer them to *Eotitanops*.

Despite their indefinite taxonomic position within early brontotheres, the Arctic specimens are not *Lambdotherium*, as earlier tentative identifications had suggested. They differ from *Lambdotherium* in being larger, and having: premolars that lack a postprotocrista and vertical ribs, and molars with a small paraconule, a protocone that is noticeably broader than the hypocone, an anterolabially-bending prehypocrista, larger, more inflated para- and mesostyles, and the absence of a posterolingual cingulum around the hypocone.

BRONTOTHERIIDAE, gen. et sp. indet.
(Fig. 2H–I)

Referred Specimens—CMN 52060, RP2, and CMN 52061, RP2; both from the D7 locality, Eureka Sound Group, central Ellesmere Island near Bay Fiord, Nunavut (late Wasatchian).

Description and Discussion—CMN specimens 52060 and 52061 (Figs. 2H and I, respectively), isolated RP2s, are similar in size to the P2 on CMN 32249 (Fig. 2A). Although there are notable morphologic differences, premolar morphology is highly variable in most species of brontothere (Mihlbachler, 2005). More specifically, Wallace (1980) concluded that the cusp morphology on P2s of *Palaeosyops* (in which he also included *Eotitanops*) is probably more variable than on any other tooth. Consequently, morphologic differences among CMN specimens 52060, 52061, and 32249 may simply reflect intraspecific variation. Importantly, CMN specimens 52060 and 52061 occur at the same locality (D7 locality) as a specimen identified above as cf. *Eotitanops*. However, I hesitate to assign CMN specimens 52060 and 52061 to the same taxon as CMN 32249 until more complete material is recovered.

Although its occlusal surface is pitted and some enamel is eroded away, CMN 52060 has a similar outline as the P2 of CMN 32249, and both have a small, posteriorly placed protocone. However, CMN 52060 bears a relatively larger metacone that is subequal in size to the paracone. In addition, CMN 52060 has a swelling (i.e., paraconule) along its preprotocrista, while P2 on CMN 32249 lacks a paraconule. In fact, in descriptions of P2s of *Eotitanops* and *Palaeosyops* by others (e.g., Gunnell and Yarborough, 2000; Wallace, 1980), there is no mention of a paraconule.

CMN 52061 differs from the P2 of CMN 32249 in having a relatively larger metacone (although it is still visibly smaller than the paracone), a somewhat smaller, more anteriorly placed protocone, and a significantly shorter preprotocrista. As on CMN 32249, there is no paraconule on CMN 52061.

PALEOBIOGEOGRAPHIC IMPLICATIONS

Eotitanops is a rare element in Eocene, mid-latitude faunas. The appearance of *Eotitanops* and *Palaeosyops* traditionally defined the onset of the Bridgerian NALMA (Robinson et al., 2004). However, rare Wasatchian occurrences of *Eotitanops* have been documented, and a single specimen of *Palaeosyops* has been reported from purportedly Wasatchian strata (Guthrie, 1971), although its locality information has been questioned (Wallace, 1980). West (1973) first reported co-occurrence of *Eotitanops* with *Lambdotherium* (index taxon for the Wasatchian), from late Wasatchian (i.e., Lostcabinian) strata of the Wasatch Formation. More recently, Smith and Holroyd (2003) documented an incomplete left maxillary of *E. borealis* from a classic Lostcabinian fauna in the northern Green River Basin. A lower molar of *Eotitanops* was reported from the Lomas las Tetas de Cabra fauna of Baja California, which has been correlated with Wasatchian faunas of North America (Novacek et al., 1991).

However, Novacek et al. (1991) were uncertain of the provenance of this specimen, and noted that they could not rule out the possibility that it was a contaminant from younger strata capping the Wasatchian.

Cf. *Eotitanops* occurs at several late Wasatchian localities on central Ellesmere Island, although its fossils are not nearly as common as those of *Coryphodon* (the most abundant mammal in the Eocene high Arctic), and tapiroids (Eberle, in press). The Ellesmere occurrences represent the northernmost known range for early Eocene brontotheres, and imply that brontothere evolution was well underway early in the history of the group at high latitudes. It begs the question: from where did brontotheres originate?

Dispersal into North America across high-latitude corridors is the most popular explanation for the abrupt appearance of several mammalian taxa in North America during the early Eocene (Hooker and Dashzeveg, 2003; Krause and Maas, 1990, and references therein). Moreover, Asia has been hypothesized as a likely source area (Beard, 1998). While the origin of brontotheres has long been contended, *Danjiangia* from the late early Eocene of China, initially identified as the earliest known chalicothere (Wang, 1995), may be a stem brontothere (Beard, 1998; Hooker and Dashzeveg, 2003, 2004). High Arctic occurrence of cf. *Eotitanops* appears consistent with an Asian origin for brontotheres and subsequent dispersal across northern high-latitude Beringia. On the other hand, North America need also be considered. Recent cladistic analyses suggest *Lambdotherium*, appearing in late Wasatchian strata of North America (Robinson et al., 2004), may be the sister taxon to brontotheres (Froehlich, 1999; Mihlbachler, pers. comm., 2005). If this relationship is accepted, then North American occurrence of both *Lambdotherium* and the earliest brontothere *Eotitanops* would suggest an origin from this continent and trans-Beringian dispersal to Asia. Incidentally, cladistic analysis of High Arctic tapiroids suggests this lineage may represent an instance wherein a North American taxon invaded Asia during the early Eocene (Eberle, in press). In either scenario, trans-Beringian dispersal was probably mediated by a warm, temperate climate during early Eocene time (Krause and Maas, 1990), as suggested in the High Arctic by fossils of alligators and land tortoises from the Eureka Sound Group fauna (Estes and Hutchison, 1980).

Although cf. *Eotitanops* from Ellesmere Island appears dentally too advanced to be ancestral to mid-latitude co-eval *Eotitanops*, it seems a plausible ancestor to the younger, Bridgerian-aged *Palaeosyops*, given the derived characters of its upper premolars. Presence of cf. *Eotitanops* on Ellesmere Island may reflect a high-latitude lineage that subsequently dispersed to mid-latitudes during the early middle Eocene (i.e., Bridgerian), perhaps with onset of the Cenozoic cooling trend purported to have begun by this time (Wade et al., 2001).

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