Boreameryx, an unusual new artiodactyl (Mammalia) from the Pliocene of Arctic Canada and endemism in Arctic fossil mammals

Mary R. Dawson and C.R. Harington

Abstract: ***Boreameryx braskerudi***, gen. et sp. nov., from Early Pliocene (about 5–4 Ma) deposits of Ellesmere Island, Nunavut, is represented by the posterior portion of a dentary with three molars, a partial calcaneum, unciform, and fragments of long bones and ribs. The incompletely known structure of *Boreameryx* must leave open the questions of its relationships within the pecoran ruminants. Even its possible affinities with early cervoids and the North American blastomerycines are speculative. We favour the tentative association of *Boreameryx* within the Cervoidea. Rather than evolving hypsodonty to deal with abrasive northern foods, *Boreameryx* apparently retained plesiomorphic dental structures—even augmenting those structures in a unique morphological development. We hypothesize, based on recorded relationships and ranges (both geological and geographical) of several Beaver Pond site mammals, including *Boreameryx*, that they indicate a significant interval of endemic development in a high northern biotic province prior to 5 Ma.

Résumé : ***Boreameryx braskerudi***, gen. et sp. nov., issu de dépôts du Pliocène précoce de l'île Ellesmere (Nunavut), est représenté par la partie postérieure du dentaire comptant trois molaires, un calcanéum partiel, un os unciforme et des fragments d'os longs et de côtes. Étant donné la connaissance incomplète de la structure de *Boreameryx*, des questions demeurent quant à ses liens au sein des ruminants de l'infra-ordre des Pecora et même ses affinités éventuelles avec les premiers cervoïdes et les blastoméryines nord-américaines sont conjecturales. Nous privilégions l'association provisoire de *Boreameryx* au sein des Cervoidea. Plutôt que d'adopter l'hypsodontie en réponse aux aliments abrasifs des régions nordiques, *Boreameryx* a apparemment préservé des structures dentaires plésiomorphes qui ont même développé des caractères morphologiques uniques. À la lumière des relations et des étendues observées (tant stratigraphiques que géographiques) pour plusieurs mammifères du site de Beaver Pond, dont *Boreameryx*, nous émettons l'hypothèse que ces derniers reflètent un important intervalle de développement endémique dans une province biotique de haute latitude nordique, avant 5 Ma.

[Traduit par la Rédaction]

Introduction

The first comprehensive view of late Neogene vertebrates and their environment from very high northern latitudes in North America has been based on fossils collected from peat deposits at 78°33′N, 82°22′W near Strathcona Fiord (Fig. 1) in central Ellesmere Island, Nunavut (Harington 2001). The sediments, interpreted as representing a beaver pond environment, were discovered by geologists of the Geological Survey of Canada in 1961 (Fyles 1989). This locality preserves not only the oldest and most northerly evidence of beaver-cut wood but also contains a remarkable fossil record of the biota of the time. The peat deposits contain fossils of mosses, mostly of extant species, and vascular plants, mainly wetland species. Included vascular plants are a fossil species of larch, *Larix groenlandi*, spruce (*Picea*), pine (cf. *Pinus pumila*), alder (*Alnus*), birch (*Betula*), and more than 30 other taxa (Matthews and Ovenden 1990). The invertebrate fauna includes at least 16 species of beetles (Coleoptera), the assemblages of which suggest warmer (+15 °C) than modern mean winter temperatures and warmer (+10 °C) summer temperatures (Elias and Matthews 2002). Molluscs include *Gyraulus albus*, a European species (Barry Miller, personal communication to CRH, 1995). The pond appears to have been located in an open larch woodland, near the tree line of the time.

In 1988, vertebrate fossils were first found in the sediments. The known vertebrates now include fishes, frogs, birds, and mammals. Of these the most diverse are the mammals. Twelve taxa are currently recognized (Table 1), of which five are carnivores, one is an insectivore, and several lagomorphs and rodents are present. Of larger herbivores, only one perissodactyl of the family Equidae has been previously described. Another herbivore, a new ruminant artiodactyl, is here added to the Strathcona Fiord Beaver Pond site assemblage. The mammalian fauna supports an age of Early Plio-

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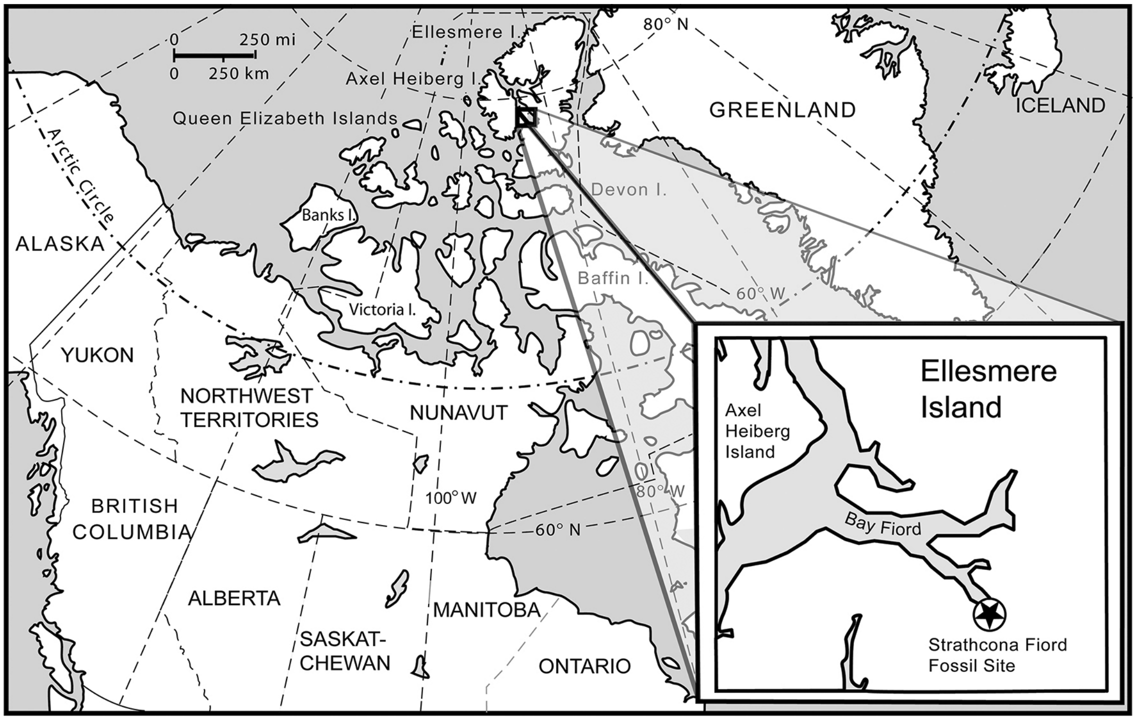
Fig. 1. Map showing location of the Beaver Pond site, Ellesmere Island, Nunavut (inset).



cene (5–4 Ma) for the peat deposit (Tedford and Harington 2003).

Abbreviations

AMNH, American Museum of Natural History, New York, N.Y., USA; CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; GSC, Geological Survey of Canada, Ottawa, Ontario; L.F., local fauna; m, lower molar; NHM, The Natural History Museum, London, England; PCSP, Polar Continental Shelf Project, Ottawa, Ontario.

Systematic paleontology

Order Artiodactyla Owen, 1848

?Superfamily Cervoidea Goldfuss, 1820

The only artiodactyl now known from the Beaver Pond site is represented by one incomplete dentary with m1–m3, one carpal, one tarsal element, and some other postcranial fragments. Previously referred to as a primitive deerlet cf. *Blastomeryx* (Hutchison and Harington 2002), this animal is here described as a new genus and species of artiodactyl of uncertain familial relationships. It is characterized by a complex occlusal pattern on its lower molars that clearly sets it apart from other artiodactyls.

Family indet.

Boreameryx gen. nov.

Type species of genus. *Boreameryx braskerudi* sp. nov.

DIAGNOSIS: Small selenodont artiodactyl having complex lower molar pattern with large ectostylid, well-developed *Palaeomeryx* fold, metastylid, anterobuccal cingulum on trigonids and anterobuccal and posterobuccal cingulids on talonids of lower molars, as well as strong lingual fold into metaconid and entoconid. Hypolophulid of m3 open posteriorly. Differs from other selenodont artiodactyls in the extremely well-developed accessory structures on the molars.

Boreameryx braskerudi sp. n.

HOLOTYPE: Canadian Museum of Nature (CMN 52710), incomplete left dentary with m1–m3.

HYPODIGM: Holotype (CMN 52710) and partial left calcaneum (CMN 52711); unciform (CMN 52712); fragments of long bones and ribs (CMN 52713 – CMN 52719).

HORIZON AND LOCALITY: Early Pliocene (5–4 Ma). Beaver Pond site near the southwestern end of Strathcona Fiord (78°33′N, 82°22′W; 367 m above sea level), beneath Braskerud Plain, Ellesmere Island, Nunavut, Canada. Holotype from main locality, in place 2.5 cm below the top of the original exposure near its western end, and 1.61 m above the base of the deposit.

DIAGNOSIS: Only known species of genus.

ETYMOLOGY: *Boreameryx*, from Greek, *boreas*, north, and *meryx*, a ruminant; and *braskerudi*, for Ove Braskerud, member of the Norwegian Arctic Expedition (1898–1902) for whom the Braskerud Plain was named. Unfortunately Braskerud died during the expedition, one of its two fatalities.

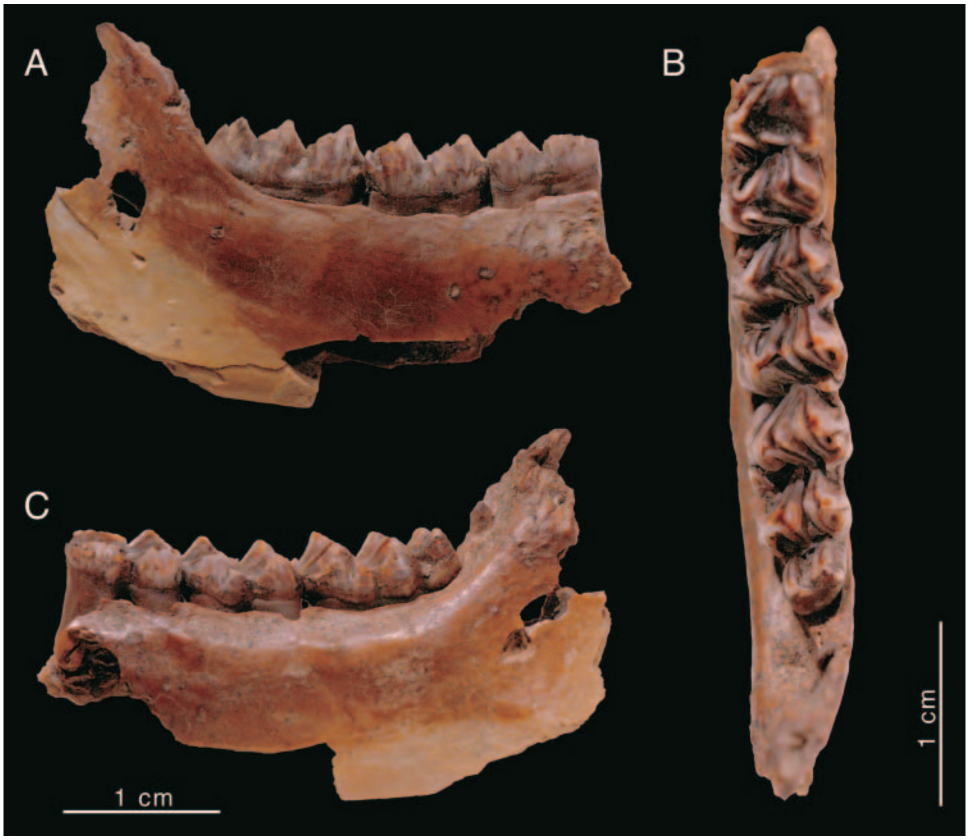
DESCRIPTION: The only known dentary of *Boreameryx* (CMN 52710) is incomplete (Figs. 2, 3), little more than the tooth-bearing section preserved. What appear to be tooth cusp indentations of a relatively small predator or scavenger, possibly a mustelid, occur on the posteromedial surface of the preserved bone. The specimen has moderately worn teeth, but enough of their surface is retained to show that all of the molars have similarly complex occlusal patterns. The surface

Table 1. First recorded appearance and geographic distribution of Beaver Pond site mammalian genera.

Beaver Pond site	Mid-latitude North America	Asia	Europe
Arctisorex polaris	—	—	—
cf. *Hypolagus*	Early Miocene	Late Miocene	Late Miocene
ochotonid	—	—	—
Dipoides	Late Miocene	Late Miocene	Late Miocene
cf. *Baranomys*	—	—	Early Pliocene
Eucyon	Middle Miocene	Early Pliocene	Late Miocene
Arctomeles sotnikovae	—	Early Pliocene	Early Pliocene
cf. *Plesiogulo*	Late Miocene	Middle Miocene	Late Miocene
Martes	Late Miocene	Late Miocene	Early Miocene
cf. *Mustela*	—	—	—
Ursus abstrusus	Pliocene[1]	—	—
cf. *Plesiohipparion*	—	—	—
Boreameryx braskerudi	—	—	—

[1] Hagerman L.F., White Bluffs L.F., Buckeye Creek L.F., Lower Cita Canyon L.F. (Woodburne, 2004).

Fig. 2. Photograph of *Boreameryx braskerudi*, holotype, left jaw fragment with m1–m3 (CMN 52710). (A) medial view; (B) occlusal view; (C) lateral view.



of the tooth enamel itself is smooth, and cusps and crests are rounded. The teeth are brachydont.

The basic four-cusped selenodont structure of m1–m2, most clearly shown on the less worn m2, is augmented by additional lophids and folds (Fig. 4). On the trigonid the anterior cingulid has two parts: a rounded buccal cuspid and an elongate cingulid that slopes down toward the lingual side of the tooth. There is also a small anterolingual cingulid on the trigonid. The large, elongated ectostylid fills the buccal valley between trigonid and talonid. On the posterior side of the protoconid the *Palaeomeryx* fold is short but distinct. The metastylid is well developed; anterior to it a wide fold creases the lingual side of the metaconid. The talonid also is complex, having one buccal cingulid extending anteriorly from the hypoconid and another extending posteriorly from it. There is a posterolingual fold into the entoconid that

Fig. 3. *Boreameryx braskerudi*, holotype, left jaw fragment with m1–m3 (CMN 52710). (A) medial view; (B) occlusal view; (C) lateral view.

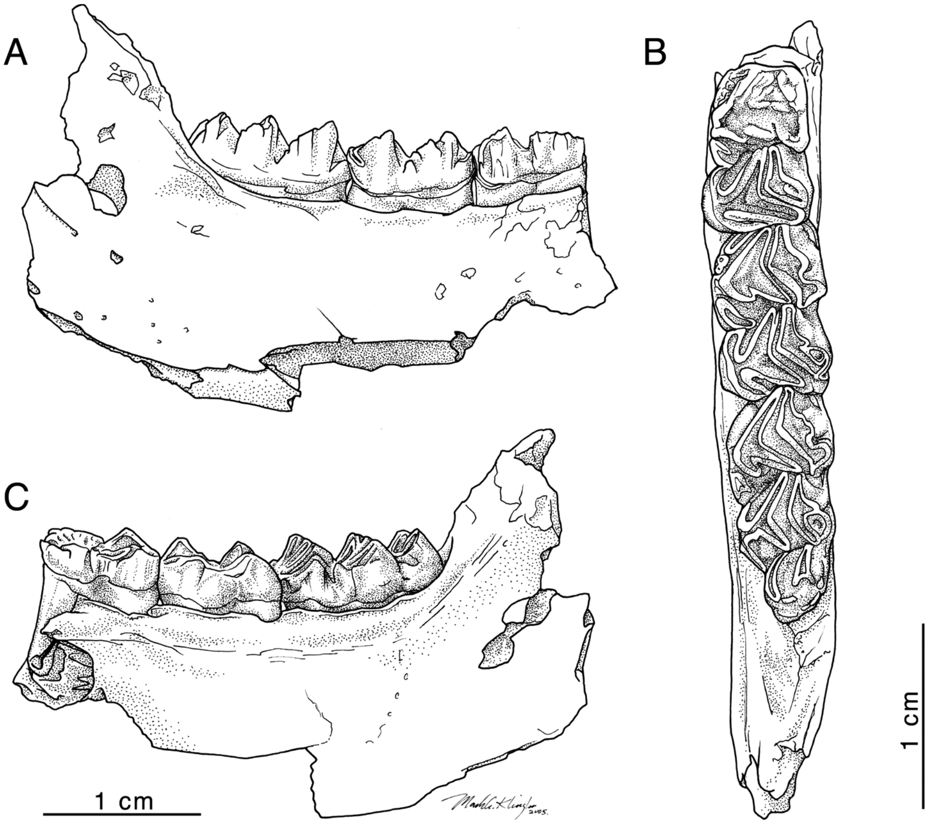
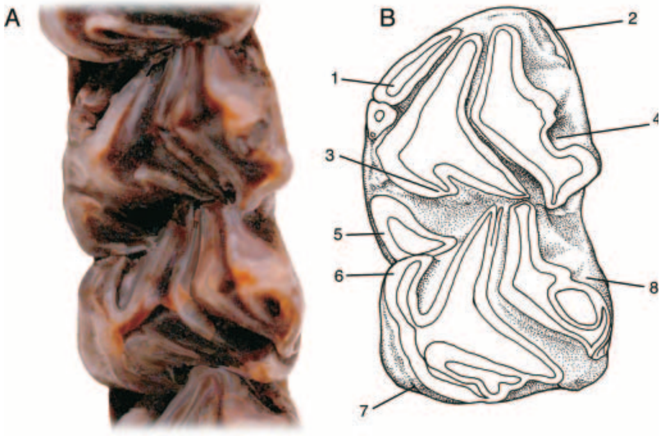


Fig. 4. *Boreameryx braskerudi*, holotype, left m2 (CMN 52710), enlarged in photo and line drawing, anterior end to the top. (1) anterior cingulid; (2) anterolingual cingulid; (3) *Palaeomeryx* fold; (4) metastylid fold; 5. ectostylid; 6. anterobuccal cingulid of talonid; 7. posterobuccal cingulid of talonid; 8. entoconid fold.



forms an isolated, enamel-rimmed lake, suggesting presence of an entostylid similar to the metastylid. In the central valley, the preentocristid extends to the postprotocristid, and the cristid obliqua terminates posterobuccal to the postprotocristid. Both metaconid and entoconid have a short posteriorly extending crest. The development of structures on the buccal side of the lower molar results in tooth proportions that are relatively wide. The posterior surface of the trigonid and anterior surface of the talonid wear to produce a fairly distinct, V-shaped transverse valley.

Trigonid and talonid of m3 resemble those of m1–m2, but the morphology of the hypoconulid lobe of m3 is distinctive. The buccal cuspid is normal, but the lingual hypoconulid cuspid is unusual in having a short transverse crest extending buccad into the basin. There is a small posterior gap between the two cuspids of the hypoconulid, so the third lobe is open posteriorly.

The complex pattern of the occlusal surfaces of the lower molars seems to suggest a relatively fibrous diet. This is emphasized also by an analysis of dental microwear of m2 of *Boreameryx* (Dompierre and Harington 1997, where the taxon is referred to as *Parablastomeryx* sp.?) that showed a high number of scratches in the enamel, oriented in one predominant direction, and relatively few pits.

A partial calcaneum, CMN 52711, from the Beaver Pond site appears referable to *Boreameryx* on the basis of its morphology and size (Fig. 5). It is incomplete, lacking the tuber calcis. The bone is slightly larger than that of the early Barstovian blastomerycine *Blastomeryx gemmifer*, AMNH 9449, from the Pawnee Creek Formation west of Pawnee Buttes, Colorado (Frick 1937; Tedford 1999). In *Boreameryx* the fibular facet is one continuous convexity, whereas in *Blastomeryx*, the facet is clearly divided by a transverse groove into a larger, more proximal convexity and a smaller, more distal convexity. The sustentaculum tali is more robust in *Boreameryx* and the distal articular surface for the naviculocuboid is more concave. Whereas most of these differences probably indicate different functional adaptations, the shape of the fibular facet has been suggested as a character

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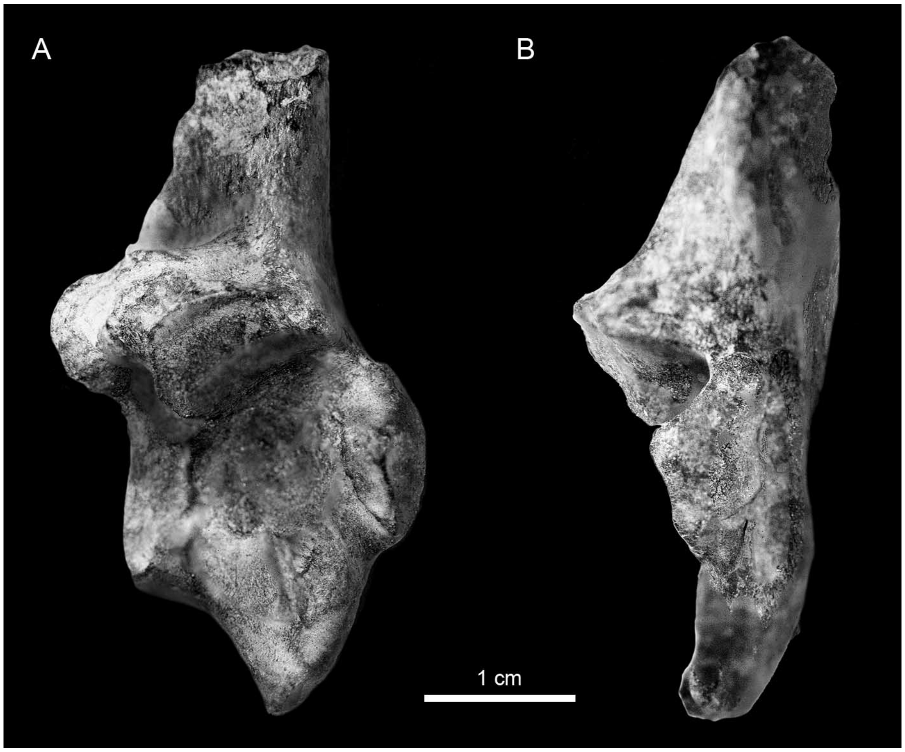
Fig. 5. *Boreameryx braskerudi* left calcaneum (CMN 52711). (A) medial view; (B) anterolateral view.



of some phylogenetic significance in an analysis of relationships among hornless ruminants (Webb and Taylor 1980).

COMPARISONS: The currently known material of *Boreameryx* is incomplete, lacking as it does the most utilized diagnostic characters for ruminants, including dental formula, spacing of teeth, morphology of premolars, upper molars, and most cranial and postcranial features, including presence or absence of cranial appendages. This record limits greatly most significant comparisons with other ruminant artiodactyls. Presence of several dental characters that are considered derived for early pecorans and that have been interpreted as having a low likelihood of homoplasy (Scott and Janis 1993), namely the lower molar metastylid, anterior cingulum, and *Palaeomeryx* fold, suggests reference to this group. The posteriorly open hypoconulid lobe of M_3 found in *Boreameryx* is known also in *Hoplitomeryx* and *Amphimoschus* (Leinders 1984) and in the *Leptomeryx speciosus–evansi–elissae* lineage (Korth and Diamond 2002).

The complex occlusal morphology of the lower molars that characterizes *Boreameryx* excludes most pecorans from further appropriate comparisons. Development of varied extra folds in ruminant lower molars can be found in some other artiodactyls (Janis 1987), but the combination of folds seen in *Boreameryx* has not been previously reported, nor has the pronounced development of the additional crests. The *Palaeomeryx* fold occurs in the more brachydont cervoids and the *Dorcatherium* fold in tragulids; a presumably homologous counterpart of the former is present and the latter absent in *Boreameryx*.

Matthew (1908) regarded the Oligocene North American ruminant *Leptomeryx* as an ancestral cervid, based at least in part on the presence of a *Palaeomeryx* fold as the main character of resemblance. Later, Janis and Scott (1987) considered the *Palaeomeryx* fold of *Leptomeryx* to be a remnant of the buccal part of the traguloid *Dorcatherium* fold. More recently, Korth and Diamond (2002) showed that a *Palaeomeryx* fold and separation of entoconulid and hypoconulid on m3 characterize the *Leptomeryx speciosus–evansi–elissius–Pronodens* lineage. A *Palaeomeryx* fold is present in the most brachydont blastomerycines *Problastomeryx* and *Parablastomeryx* (both considered synonyms of *Blastomeryx* by McKenna and Bell 1997), as well as in some specimens of *Eumeryx* and *Rutitherium* (Janis and Scott 1987).

The cervid or palaeomerycid *Dromomeryx* (Prothero and Liter in press) has traces of anterior and posterior cingulids and an ectostylid but lacks the other dental complications that characterize *Boreameryx*. The closest morphological approach to the lower molars of *Boreameryx* appears to be in the puzzling, and incompletely known, Eurasian cervoid incertae sedis (Rössner and Mörs 2001) or palaeomerycid (Vislobokova 2005) *Orygotherium* Meyer, 1838. Similarities between the lower molars of *Orygotherium* (Rössner and Mörs 2001) and those of *Boreameryx* include the basic pecoran structure plus the following additional developments: the enlarged, elongated ectostylid; *Palaeomeryx* fold; large metastylid; posterobuccal cingulum; and hypertrophied entoconulid on m3. *Boreameryx* has even more complex lower molars than *Orygotherium*, however, in having the extra pre-hypoconid crest and the lingual folds into metaconid and entoconid.

Boreameryx, with its brachydont teeth, retains primitive pecoran characters that tend to be lost in more hypsodont taxa (Scott and Janis 1993). Rather than evolving hypsodonty to deal with tooth wear, the evolutionary path followed

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Table 2. Measurements (in mm) of *Boreameryx braskerudi*, holotype (CMN 52710).

Maximum width of mandible at m3	6.3
Alveolar length m1–m2 (labial)	17.4
Maximum cusp height (m2) above cingulum (labial)	4.7
m1 length	8.8
m1 width	5.9
m2 length	8.8
m2 width	5.8
m3 length	11.8
m3 width	5.7

by *Boreameryx* appears to have been to retain plesiomorphic pecoran dental structures and even to augment those structures in a unique morphological development.

Relationships

The incompletely known structure of *Boreameryx* must leave open the question of its relationships within the pecoran ruminants. Even its possible affinities with early cervoids, such as *Dremotherium* (Sigogneau 1968), and the North American blastomerycines (Webb and Taylor 1980) can be only speculative.

Phylogenetic connections among the pecoran artiodactyls are far from well established (Scott and Janis 1993; Hassanin and Douzery 2003). Distinct differences of opinion can be related both to interpretations of the phylogenetic significance and polarity of varied characters and to the extensive homoplasy that characterizes ruminant evolution (compare, for example, Webb and Taylor 1980; Leinders 1984; Gentry and Hooker 1988; Janis and Scott 1988; Scott and Janis 1993). One source of the different opinions of pecoran interrelationships can be traced to the question of the affinities, and content, of the Moschidae. A number of mid-Tertiary Eurasian and North American hornless pecorans have been associated with this family, along with its living representative, the Asian musk deer, *Moschus*. McKenna and Bell (1997) and Janis and Scott (1988) support the affinities of moschids as cervoids, a concept rejected by Webb and Taylor (1980). A recent morphological–molecular analysis calls into question most previous interpretations of the family Moschidae, and supports a sister group relationship between Moschidae and Bovidae (Hassanin and Douzery 2003). This study must reopen the question of the relationships among these Holarctic artiodactyls.

As currently known, *Boreameryx* does not contribute significantly to solving any problems of ruminant interrelationships. We favour the tentative association of *Boreameryx* within the Cervoidea based on the definition of cervoids as possessing a *Palaeomeryx* fold on the lower molars (Janis and Scott 1987, 1988).

Endemism among the Beaver Pond site mammals

Mammals from the Beaver Pond locality are divisible into two or three groups based on whether their closest relatives occur in North America, in Eurasia, or can be found across the Holarctic (Tedford and Harington 2003). The leporid *Hypolagus* (Rybczynski and Harington 1997), castorid *Dipoides*, and canid *Eucyon* have significant Miocene records in more southerly latitudes in North America, although all three genera also occur in Eurasia. The cricetid cf. *Baranomys*, mustelid *Arctomeles*, ursid *Ursus abstrusus*, and neomyine soricid *Arctisorex*, on the other hand, are considered to be closer to Eurasian groups. Relationships of the hipparionine equid, as of *Boreameryx*, are too unclear to determine their closest biogeographic connections. Outside of rather broad paleogeographic associations, however, the Beaver Pond site mammals that have been examined in detail so far all show striking differences from presumed relatives from more southerly latitudes. These differences and the highly unusual morphology of *Boreameryx* led to advancing the hypothesis that at least some mammals living in the Beaver Pond environment document a significant interval of endemic development in a biotic province located at high northern latitudes.

This could be suggested not only for *Boreameryx* but also for several other mammalian members of the fauna. For example, the mustelid *Arctomeles sotnikovae* was described as "the most distinctive of these [species of *Arctomeles*] in both morphology and its geographic occurrence," and more primitive than other described species of *Arctomeles* (Tedford and Harington 2003, p. 388). The hipparionine horse, represented only by the maxilla of an immature individual with all deciduous teeth in place, has morphological differences from the usual equid condition, including having dual openings of the infraorbital foramen (Hulbert and Harington 1999). In the cricetid cf. *Baranomys* (possibly a new taxon), one of the folds of m1 is more strongly developed than in *Baranomys* from the Pliocene of Poland (Zakrzewski and Harington 2001). Even more remarkable is *Arctisorex*, which "does not fit the definition of any group of soricine shrew" (Hutchison and Harington 2002, p. 442). Most unusual in this shrew is the m3 with an elongated entoconid, a morphology suggesting that this animal was specialized for frugivory, the only known soricid showing this adaptation. It is not yet apparent (because they have not been completely analyzed) whether or not the more typically North American elements of the fauna— *Hypolagus*, *Dipoides*, and *Eucyon*—are also unusual, or whether only the Eurasian elements of the fauna suggest a prolonged period of endemic development.

Until the Early Pliocene opening of the Bering Strait, postulated to be between 5.5 and 4.8 Ma on the basis of the record of marine invertebrates (Marincovich 2000), the Holarctic was one vast biogeographic province, with floral and faunal interchange limited primarily by environmental conditions at high latitudes. The known Pliocene vertebrate fossil record north of about 55° is limited to the Beaver Pond locality. Although Tedford and Harington (2003, p. 388) regard 5–4 Ma as "an active period of interchange between Asia and North America" it would seem, based on the evidence from marine invertebrates, that most interchange, and subsequent differentiation, occurred earlier.

The concept of ruminant immigrations into North America from a northern Eurasian center is not a new one. Matthew (1926, p. 7) speculated "that the American deer were derived by a succession of invasions from a northern center of dispersal, and that certain common peculiarities in their succession were due to their being derived from the American side of this Boreal center." The northern aspect of this distribution was emphasized by Matthew to be an intermediate region comprising "northeastern Europe, northern Asia, Alaska and Canada, and of its Tertiary faunal history we have no record."

From the little that is currently known, it can be speculated that the striking apomorphies of *Boreameryx* developed from a relatively primitive cervoid stem. Further, the known record lends support for the postulate that this development occurred at high northern latitudes. Weak support may also come from the occurrences of *Orygotherium*, a possible sister taxon to *Boreameryx*, which is known to occur either in localities that are interpreted to be swampy (Rössner and Mörs 2001) or that are relatively far north (Vislobokova 1994, 2005).

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