Early Eocene Leptictida, Pantolesta, Creodonta, Carnivora, and Mesonychidae (Mammalia) from the Eureka Sound Group, Ellesmere Island, Nunavut

Jaelyn J. Eberle and Malcolm C. McKenna

Abstract: We describe the leptictid *Prodiacodon*; the pantolestids *Palaeosinopa* sp.nov., cf. *Palaeosinopa*, and Pantolestidae, gen. et sp. indet.; the creodonts *Palaeonictis* and *Prolimnocyon*; the carnivorans *Viverravus*, cf. *Vulpavus*, and *Miacis*; and the mesonychid *Pachyaena* from early Eocene (i.e., Wasatchian) strata of the Eureka Sound Group on central Ellesmere Island, Nunavut. *Palaeosinopa* and *Palaeonictis* may have originated in mid-latitude North America and subsequently migrated to Europe via a north Atlantic land bridge, while *Prolimnocyon* and *Pachyaena* probably originated in Asia. Additionally, the occurrence of *Pachyaena* in the Early Eocene of Europe probably is best explained by dispersal from high-latitude North America to Europe via a north Atlantic land bridge. We update the Eureka Sound Group mammalian faunal list.

Résumé : Nous décrivons le leptictidé *Prodiacondon*, les pantolestidés *Palaeosinopa* sp.nov. cf. *Palaeosinopa* et *Pantolestidae*, gen et sp. indét.; les Créodontes *Palaeonictis* et *Prolimnocyon*; les Carnivores *Viverravus*, cf. *Vulpavus* et *Miacis*; ainsi que le mésonychidé *Pachyaena* provenant des strates du Groupe de Eureka Sound, au centre de l'île Ellesmere, au Nunavut, et datant de l'Éocène précoce (c.-à-d. Wasatchien). *Palaeosinopa* et *Palaeonictis* peuvent provenir de latitudes moyennes de l'Amérique du Nord et avoir migré par la suite vers l'Europe par un pont continental nord-américain, alors que *Prolimnocyon* et *Pachyaena* peuvent être originaires de l'Asie. De plus, la venue de *Pachyaena* à l'Éocène précoce en Europe est probablement le mieux expliqué par une dispersion de l'Amérique du Nord vers l'Europe à des latitudes élevées par un pont continental nord-américain. Nous mettons à jour la liste de la faune mammifère du détroit d'Eureka.

[Traduit par la Rédaction]

Introduction

The northernmost record of early Tertiary mammals is from Eocene strata of the Eureka Sound Group in Canada's eastern Arctic archipelago, Nunavut. The first specimens were discovered in 1975 near Strathcona Fiord, on central Ellesmere Island (Dawson et al. 1976), with subsequent discoveries in the late 1970s and 1980s in similar-aged strata elsewhere on Ellesmere Island and near Mokka Fiord on the east coast of Axel Heiberg Island (Dawson 1990; Dawson et al. 1993). More recently, tooth fragments of a large, diplacodont brontothere were discovered in strata of middle to late Eocene age at the Geodetic Hills fossil forest site on eastern Axel Heiberg Island (Eberle and Storer 1999). In addition to fossil mammals, a diverse lower vertebrate fauna from the Eureka Sound Group, including land tortoises, monitor lizards, snakes, and crocodilians, strongly corroborates long-standing paleobotanical evidence for a mild, equable arctic climate during the Eocene (Estes and Hutchison 1980; McKenna 1980).

Although the Eureka Sound faunal assemblages slightly postdate the land connection between Europe and North America across the North Atlantic, they nevertheless support previous hypotheses relating to Eocene paleogeography of the North Atlantic region. Plate tectonics, and generic affinities between early Eocene mammalian faunas in Europe and mid-latitude North America, have long provided evidence for a corridor connecting Europe to North America sometime during early Eocene time (see McKenna 1975). There are two vertebrate faunal levels in the Eureka Sound Group, the lower of which corroborates the existence of such a dispersal route in that it contains several early Eocene genera that still persisted on both sides of the Atlantic (Marincovich et al. 1990). Additionally, the Eureka Sound fauna provides support for a North American origin for certain mammalian taxa, notably the microparamyine rodents (Dawson 2001), and their subsequent dispersal to Europe.

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J.J. Eberle.[1] Canadian Museum of Nature, P.O. Box 3443, Station D, Ottawa, ON K1P 6P4, Canada.
M.C. McKenna. American Museum of Natural History, New York, NY 10024, U.S.A.

[1] Corresponding author (e-mail: jeberle@mus-nature.ca).

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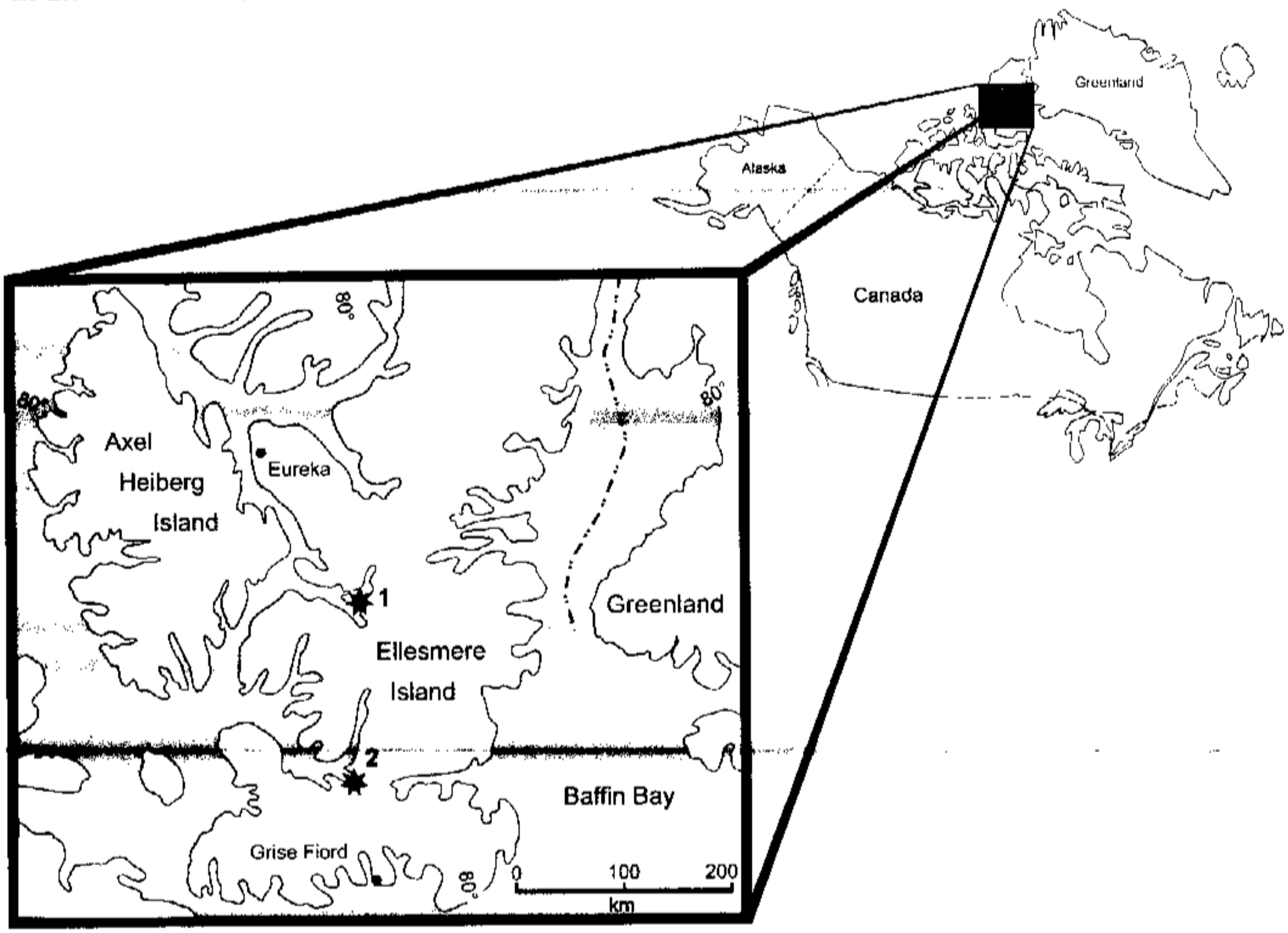
Fig. 1. Map of Axel Heiberg and Ellesmere islands, Nunavut. The stars indicate general locations of terrestrial vertebrate-bearing localities of the Eureka Sound Group discussed in the text. 1, Bay Fiord; 2, Stenkul Fiord.



Here we provide systematic description of several members of the Eureka Sound mammalian fauna, specifically the Carnivora, Creodonta, Cimolesta, Leptictida, and Mesonychidae, based on fossils recovered near Bay and Stenkul fiords on Ellesmere Island (Fig. 1), and we discuss their paleobiogeographic implications. We name a new species of the pantolestid *Palaeosinopa*. In light of more recent research, including this paper, we conclude with an updated list of the Eureka Sound mammalian fauna.

Geologic setting

Although its strata were recognized in the late 1800s (Greely 1888), the Eureka Sound Group was not named until 1950 by Troelson (1950). Subsequently, Tozer (1963) reduced the Eureka Sound Group to formational rank. Since then, three sets of names have been applied to strata of the Eureka Sound Group. Following their discovery of fossil vertebrates in the Bay Fiord area (West et al. 1975; Dawson et al. 1976), West et al. (1981) subdivided the Eureka Sound Formation into four informal members, the uppermost (i.e., Member IV) containing two levels of Eocene terrestrial vertebrates. Independent of one another, Miall (1986) and Ricketts (1986) raised the Eureka Sound Formation to group rank and subdivided it into formations. Consequently and quite confusingly, the terrestrial vertebrate-bearing strata near Bay Fiord fall under three different names: Member IV of West et al., Margaret Formation of Miall, and Iceberg Bay Formation of Ricketts. Based on more recent publications and maps (e.g., Okulitch 1991), the general consensus seems to be that the Eureka Sound is a group divisible into numerous formations. Consequently, the informal members of West et al. are best replaced by formational names. Although others follow the terminology of Miall in referring the Eocene vertebrate-bearing strata near Bay Fiord to the Margaret Formation, we believe the Mokka Fiord Formation on eastern Axel Heiberg Island is lithologically more similar to the Eocene strata at Bay Fiord. Work in progress, including fieldwork begun in 2001, may sort out this problem.

Eocene terrestrial vertebrates occur in two stratigraphic levels in upper parts of the Eureka Sound Group in the Bay Fiord area (West et al. 1981; Dawson 1990, 2001; Dawson et al. 1993). A diversity of vertebrates, including fish, amphibians, reptiles, birds, and over 20 mammalian taxa, is documented from the lower faunal level and indicates an early Eocene age, equivalent to the younger part of the Wasatchian North American Land Mammal "Age" (NALMA; Dawson et al. 1993; West et al. 1981). Eocene vertebrate-bearing strata near Stenkul Fiord which Miall (1986) provisionally assigned to the Margaret Formation are correlated to this faunal level (Dawson 2001, and references therein). Although the known sample of the upper faunal level is considerably less diverse, it is interpreted as early Middle Eocene in age, equivalent to the Bridgerian NALMA (Dawson et al. 1993; Dawson 1990; McKenna 1980; West et al. 1981). Palynology corroborates an early to middle Eocene age range for the terrestrial vertebrate-bearing strata 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 coal swamps (Miall 1986).

Materials and methods

Specimens described here were recovered in the 1970s and 1980s by field parties headed by the Carnegie Museum of Natural History and reside in fossil collections at the Canadian Museum of Nature in Ottawa. The specimens are from three localities in the Wasatchian-aged lower faunal level near Bay Fiord on central Ellesmere Island and from one locality farther south on Ellesmere Island at the head of Stenkul Fiord (Fig. 1). The majority of specimens come from locality 85, the most productive screening locality in the Eureka Sound Group south of Bay Fiord, discovered in 1976 (M.R. Dawson, personal communication, 2001). The specimen of *Prolimnocyon* described herein is from locality 44, and the single mesonychid fossil is from the D7 locality, also in the Bay Fiord area. Although stratigraphic relationships between the fossil vertebrate localities are not clear, partly due to effects of the Eurekan orogeny, locality 44 has been tied to stratigraphic sections and is approximately 110–115 ft (1 ft = 0.3048 m) above the base of section 77-71 of Miall (1986); locality 85 is probably stratigraphically higher than locality 44 (J.H. Hutchison, personal communication, 2001). Near Stenkul Fiord, the creodont *Palaeonictis* occurs with other mammalian taxa, as well as fossils of turtles, in correlative strata of the Eureka Sound Group (M.R. Dawson, personal communication, 2001). Riediger and Bustin (1987) reported a single tooth of *Coryphodon* from their Member 4 of the Eureka Sound Group at Stenkul Fiord which they correlated to Miall's uppermost Margaret Formation at Bay Fiord. 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 jaw fragments, teeth, or tooth fragments, we follow dental terminology outlined by Van Valen (1966), Novacek (1977), and Flynn and Galiano (1982). We follow McKenna et al. (2000) in assignment of loci of leptictid premolars (i.e., we use P4). Measurements were taken with a Wild/Censor microlength measuring attachment on a stereomicroscope. Measurements of the leptictid tooth follow Novacek, and measurements of carnivoran teeth are outlined by Gingerich and Winkler (1985) and Gingerich (1983). Classification follows McKenna and Bell (1997) and Flynn (1998).

Institutional abbreviations and dental terminology

AMNH, American Museum of Natural History, New York, N.Y.; CMN, Canadian Museum of Nature, Ottawa, Ont.; PU, Princeton University, Princeton, N.J.

C, I, M, and P designate canine, incisor, molar, and premolar, respectively. Lower-case letters (e.g., m1) designate teeth from lower jaws, and upper-case letters (e.g., M1) teeth from upper jaws. L, left tooth (e.g., Lm1); R, right tooth (e.g., Rm1).

Systematic paleontology

Leptictida McKenna, 1975
Leptictidae Gill, 1872
Leptictinae Gill, 1872
Prodiacodon sp.

Referred specimen

CMN 32385, RP4.

Locality

Locality 85, lower mammalian faunal level, upper part of Eureka Sound Group, south of Bay Fiord, central Ellesmere Island, Nunavut, Canada (Wasatchian).

Description and discussion

When compared with members of the Leptictidae, CMN 32385, a nearly complete RP4 missing its parastylar region (Pl. 1, fig. 1), is most similar to *Prodiacodon*. Although the closely allied genus *Palaeictops* is dentally very similar to *Prodiacodon* (see Bown and Schankler 1980), *Palaeictops* generally has lower, more bulbous cusps, conules that are more labially located, and short anterior cingula (Novacek 1977). In contrast to *Palaeictops*, but as in *Prodiacodon* (see Novacek 1977), CMN 32385 has sharp, piercing cusps, conules that are set lingually and not at the base of the paracone and metacone, and a long precingulum. As in *Prodiacodon tauricinerei* (see Jepsen 1930; Novacek 1977), CMN 32385 possesses a hypocone, and its stylar shelf is very narrow but present labial to the metacone. Both *P. tauricinerei* and CMN 32385 have a better developed hypocone than the larger species *P. puercensis*. As in *P. crustulum* (see Novacek 1977), the metacone on CMN 32385 is smaller and shorter than the paracone, and the paraconule is higher and larger than the metaconule. On CMN 32385, the paraconule is more bulbous and slightly more lingual than the metaconule, which is pyramid-shaped and bears a strong premetaconule wing.

Minimal estimates of length and anterior width of CMN 32385, respectively, are 2.18 and 2.45 mm, and its posterior width is 2.77 mm. Although the length of CMN 32385 is similar to that of P4 on PU 13104, the holotype of *P. tauricinerei* (see Novacek 1977, table 2), CMN 32385 is considerably less transverse than the latter. However, we suspect that Novacek's (1977, table 2) width measurements of the P4 on PU 13104 may be a misprint, as the anterior width listed is much greater than the posterior width. All other P4s of *Prodiacodon* measured by Novacek (table 2)

Plate 1. fig. 1. CMN 32385, RP4 of *Prodiacodon* sp. from locality 85. **fig. 2.** CMN 30810 (holotype), Rm2 of *Palaeosinopa nunavutensis*, sp.nov. from locality 85. **fig. 3.** CMN 30809, lingual half of LM1 or M2 of *Palaeosinopa* cf. *P. Nunavutensis* from locality 85. **fig. 4.** CMN 30947, left dentary fragment with trigonid of m2 or m3 of Pantolestidae, genus and species indeterminate from locality 85. **fig. 5.** CMN 51272, parts of the left (top photograph) and right (bottom photograph) maxillaries containing roots of P3–M2 of *Palaeonictis* sp. from locality 87H7-22-4. **fig. 6.** (*a*, *b*) Labial and occlusal views, respectively, of CMN 30846, a distorted, incomplete right dentary of *Prolimnocyon* sp. from locality 44.

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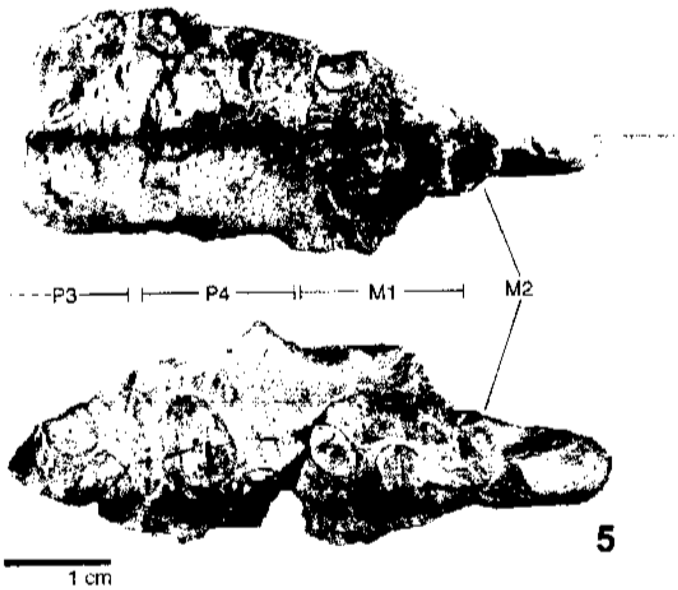

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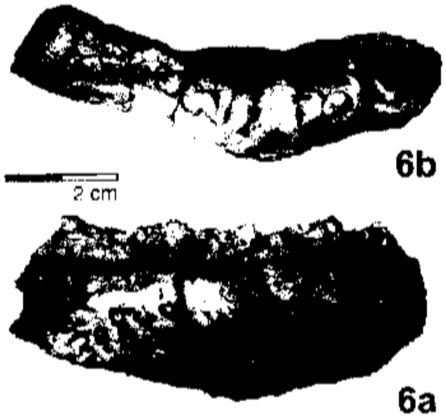


demonstrate the opposite (i.e., the posterior width is greater than the anterior width). Note that the leptictid P5 in Novacek equals P4 in this paper.

Prodiacodon is known from the early Paleocene (i.e., Puercan NALMA) through early Eocene (i.e., Wasatchian NALMA) of North America (Novacek 1977; Bown and Schankler 1980).

Cimolesta McKenna, 1975
Pantolesta McKenna, 1975
Pantolestidae Cope, 1884
Pantolestinae Cope, 1884
Palaeosinopa Matthew, 1901
Palaeosinopa nunavutensis, sp.nov.

Holotype

CMN 30810, Rm2.

Locality

Locality 85, lower mammalian faunal level, upper part of Eureka Sound Group, south of Bay Fiord, central Ellesmere Island, Nunavut, Canada (Wasatchian).

Diagnosis

Large species of *Palaeosinopa*, comparable in size to *Palaeosinopa veterrima* and larger than *Palaeosinopa didelphoides* and *Pantolestes longicaudus*; m2, particularly trigonid, more transverse than other species of *Palaeosinopa* and *P. longicaudus*; metaconid and protoconid of same height, but metaconid more inflated than protoconid; paraconid better developed than *Pantolestes*, but smaller than that of *P. veterrima* and *P. didelphoides*; talonid longer, although narrower, than trigonid, and open lingually; entocristid absent.

Etymology

In honour of Nunavut, Canada's newest territory, which includes Canada's eastern Arctic archipelago.

Description and discussion

CMN 30810 (Pl. 1, fig. 2) is larger than m2s of *P. didelphoides* and *P. longicaudus*, and is comparable in length to larger specimens of *P. veterrima* (see Bown and Schankler 1980). However, CMN 30810 is wider than m2s of other species of *Palaeosinopa*. Additionally, several morphologic characters (discussed herein) differentiate CMN 30810 from other species of *Palaeosinopa* and *P. longicaudus*.

As is characteristic of both *Palaeosinopa* and *Pantolestes* (see Matthew 1901, 1909), the metaconid and protoconid on CMN 30810 are subequal in height, although the metaconid is more inflated than the protoconid. In contrast, the paraconid on CMN 30810, whose apex has been removed by wear, is smaller and shorter than the protoconid and metaconid. In differentiating *Palaeosinopa* from *Pantolestes*, Matthew (1909) noted that the paraconid is well developed on *Palaeosinopa* but only vestigial on *Pantolestes*. Although the paraconid on CMN 30810 is relatively smaller than that of *P. veterrima* and *P. didelphoides*, it is well developed and could not be considered vestigial. As in *P. veterrima* and *P. didelphoides*, CMN 30810 bears a cingulid on its anterior margin, below and labial to the paraconid.

CMN 30810 possesses a talonid that is longer, although noticeably narrower, than the trigonid. Similarly, on m2s of *P. veterrima*, the trigonid is wider than the talonid, but is not so transverse as on CMN 30810. In contrast, on m2s of *P. longicaudus* with which CMN 30810 was compared (AMNH 12089 and AMNH 12086), the talonid was slightly wider than the trigonid. On CMN 30810, the talonid basin is open lingually, due to a deep talonid notch and absence of an entocristid. Although lack of an entocristid is unusual in *Palaeosinopa*, it is not unheard of, because Rose (1981) noted absence of an entocristid on a Clarkforkian specimen that he referred to *Palaeosinopa* cf. *P. lutreola*. In other characters of the talonid, including cusp arrangement, CMN 30810 is comparable to *P. veterrima*. The hypoconid is the largest talonid cusp, followed in size by the entoconid and a much smaller hypoconulid. On CMN 30810, the hypoconulid forms a diagonal ridge with two other tiny cusps which runs anterolingually towards the entoconid. A V-shaped notch separates the hypoconulid ridge from the entoconid. A hypoconulid ridge also occurs on some specimens of *P. veterrima* (AMNH 16822 and AMNH 15096), although tiny cusps additional to the hypoconulid are not so clearly differentiated as on CMN 30810. Labial and lingual cingulids are absent on CMN 30810.

Measurements of length, trigonid width, and talonid width are 6.0, 5.0, and 4.6 mm, respectively.

Although caution must be taken in naming a new species, particularly on the basis of one specimen, we are confident that the characters which differentiate CMN 30810 from other species of *Palaeosinopa*, notably its width, size of the paraconid, and absence of an entocristid, are enough to diagnose a new species. Moreover, a considerable geographic distance separates CMN 30810 from the nearest North American and European representatives of *Palaeosinopa*, so it is not surprising that a new species is represented in the Eureka Sound Group.

Palaeosinopa is known from late Paleocene through early Eocene aged strata of North America, and from early Eocene aged strata of Europe (McKenna and Bell 1997).

Palaeosinopa cf. *P. nunavutensis*

Referred specimen

CMN 30809, lingual half of LM1 or M2.

Locality

Locality 85, lower mammalian faunal level, upper part of Eureka Sound Group, south of Bay Fiord, central Ellesmere Island, Nunavut, Canada (Wasatchian).

Description and discussion

We tentatively identify CMN 30809 (Pl. 1, fig. 3) as *Palaeosinopa* cf. *P. nunavutensis*, based on size and on morphologic similarities to upper molars of *P. veterrima* and *P. didelphoides*. As in CMN 30810, the holotype of *P. nunavutensis*, CMN 30809 appears similar in size to *P. veterrima*. As is characteristic of upper molars of *Palaeosinopa* (see Matthew 1915), CMN 30809 bears a strong postero-internal cingular ledge, even wider than that of *P. veterrima* and *P. didelphoides*. Although crenulations are evident, a distinct hypocone cusp is absent on CMN 30809. The protocone on CMN 30809 is more rounded and inflated, and its apex more lingual in placement, compared to *P. veterrima* and *P. didelphoides*. The paraconule is larger than the metaconule. Although the anterior margin of the tooth has been broken away, a thin sliver anterior to and below the paraconule suggests the initial presence of a precingulum.

Based on its size, it seems plausible that CMN 30809 belongs to the new species of *Palaeosinopa* described here. We are reluctant, however, to identify it beyond *Palaeosinopa* cf. *P. nunavutensis* until more complete specimens are recovered.

Pantolestidae, gen. et sp. indet.

Referred specimen

CMN 30947, left dentary fragment with trigonid of m2 or m3.

Locality

Locality 85, lower mammalian faunal level, upper part of Eureka Sound Group, south of Bay Fiord, central Ellesmere Island, Nunavut, Canada (Wasatchian).

Description and discussion

CMN 30947 (Pl. 1, fig. 4), a left dentary fragment containing a nearly erupted trigonid of an m2 or m3, appears most similar to the pantolestids *P. longicaudus* and larger species of *Palaeosinopa*. On CMN 30947, the protoconid is slightly taller than the metaconid. The paraconid is smaller and shorter than the protoconid and metaconid, and is relatively smaller than that of *P. veterrima* and *P. didelphoides*, but larger than that of *P. longicaudus*. As in *P. longicaudus*, the paraconid on CMN 30947 is more medial in position than that of *Palaeosinopa*.

The estimated width of the trigonid on CMN 30947 is 3.7 mm, which falls within the ranges of trigonid widths for m2 and m3 of *P. longicaudus* and *P. didelphoides*, but is narrower than those of *P. veterrima* (see Bown and Schankler 1980, fig. 10) and the holotype of *P. nunavutensis* (described earlier).

Creodonta Cope, 1875
Oxyaenidae Cope, 1877
Palaeonictinae Denison, 1938
Palaeonictis sp.

Referred specimen

CMN 51272, numerous skull fragments, including parts of the left and right maxillae containing roots of P3–M2, bone-encased fragments of the roots of canines and ?anterior premolars, and fragments of the cranium.

Locality

Locality 87H7-22-4, upper part of Eureka Sound Group, head of Stenkul Fiord, southern Ellesmere Island, Nunavut, Canada (Wasatchian).

Description and discussion

CMN 51272 (Pl. 1, fig. 5) was initially identified as a mesonychid and was listed as Mesonychidae, genus and species unidentified, in previous faunal lists (e.g., Marincovich et al. 1990, table 4). Detailed examination of the pattern of the roots contained in the maxillary fragments, however, indicates its close similarity to members of the Oxyaenidae, specifically *Palaeonictis*.

Based on the size and arrangement of the roots in the maxillaries, CMN 51272 bore a large P4, followed by a smaller, less transverse M1 and a tiny, single-rooted M2. This arrangement is uncharacteristic of mesonychids but occurs within the Palaeonictinae. CMN 51272 had large canines.

The arrangement of the roots on CMN 51272 compares well with *Palaeonictis occidentalis* from the early Wasatchian Willwood Formation in the Big Horn Basin, Wyoming. The only noticeable difference is that CMN 51272 appears to have had a less transverse M1 than *P. occidentalis*. Like CMN 51272, P4 on *P. occidentalis* is a big tooth, and P3 is less transverse (i.e., a long, narrow tooth) and M1 is smaller than P4. P4 is the largest, most transverse tooth.

CMN 51272 is probably from an animal similar in size to that of *P. occidentalis*, which, according to Osborn and Wortman (1892), was one-fourth larger than the American puma (*Felis concolor*). Its postcranial anatomy, based on skeletal material from mid latitude North America, suggests that *Palaeonictis* was a generalized terrestrial quadruped (i.e., ambulatory). Members of the Palaeonictinae typically have heavy jaws and blunt-cusped teeth, seemingly adapted for heavy bone crushing (Gunnell 1998).

Palaeonictis is known from late Paleocene through early Eocene aged strata of North America, and from early Eocene aged strata of Europe (McKenna and Bell 1997). The oldest known representatives of the Creodonta are from the Tiffanian NALMA (= late Paleocene) of North America (Gingerich 1980; Gunnell 1998).

Hyaenodontidae Leidy, 1869
Limnocyoninae Wortman, 1902
Prolimnocyon Matthew, 1915
Prolimnocyon sp.

Referred specimen

CMN 30846, distorted, incomplete right dentary with heavily worn and damaged p4–m3, roots of p3, and posterior root of p2.

Locality

Locality 44, lower mammalian fauna level, upper part of Eureka Sound Group, south of Bay Fiord, central Ellesmere Island, Nunavut, Canada (Wasatchian).

Description and discussion

CMN 30846 (Pl. 1, fig. 6) is an incomplete right dentary that is distorted and bent in the region of m1–m2. A line between p4 and m1 indicates where the dentary was broken and subsequently glued back together. The specimen contains a damaged and worn p4–m3, roots of p3, and the posterior root of p2. Despite the heavy wear and incompleteness of the teeth (due to breakage), CMN 30846 possesses several characters which allow us to refer it confidently to *Prolimnocyon*. As is diagnostic of this genus (Matthew 1915; Gunnell 1998; Gingerich and Deutsch 1989), CMN 30846 possesses an m1 that is subequal in size to m2, an m2 whose trigonid is as wide as it is long, and a small, vestigial m3. In size and general outline of the teeth, CMN 30846 appears most similar to *Prolimnocyon antiquus*. Like *P. antiquus*, the m3 of CMN 30846 has only one root. Although Matthew (1915) considered a single-rooted m3 as diagnostic of *P. antiquus*, this character subsequently was found in *P. elisabethae* (see Gazin 1952) and at least one specimen of *P. atavus* (see Gingerich and Deutsch 1989). Moreover, Gingerich and Deutsch (1989) considered *P. elisabethae* a probable synonym of *P. antiquus*. Both species are late Wasatchian in age, and *P. atavus* is known from the Graybullian and Lysitean subages, middle and late Wasatchian NALMA.

Based on dentitions and postcranial material from mid-latitude North America, *Prolimnocyon* was a small, generalized carnivore and capable climber that probably lived in or near trees (Gunnell 1998; Gebo and Rose 1993).

Prolimnocyon is known from the early Eocene and very questionably from the Paleocene of North America (McKenna and Bell 1997; Rigby 1980). According to Gunnell (1998), the questionable "hyaenodontids" from the Paleocene of North America probably represent palaeoryctid or pantolestid insectivorans. Importantly, *Prolimnocyon* has recently been reported from the late Paleocene of Asia (Meng et al. 1998).

Carnivora Bowdich, 1821
Feliformia Kretzoi, 1945
Viverravidae Wortman and Matthew, 1899
Viverravus Marsh, 1872
Viverravus sp.

Referred specimen

CMN 30877, LP4.

Locality

Locality 85, lower mammalian faunal level, upper part of Eureka Sound Group, south of Bay Fiord, central Ellesmere Island, Nunavut, Canada (Wasatchian).

Description and discussion

CMN 30877 (Pl. 2, fig. 1) is most similar in size and morphology to P4s of an unpublished species of *Viverravus* from E. Alheit Pocket Quarry in the Wasatch Formation, Moffat County, Colorado, whose specimens are housed in AMNH collections. CMN 30877 is considerably smaller than *Viverravus sicarius* and *Viverravus politus* and possesses a better developed lingual cingulum than *V. sicarius*. CMN 30877 has a well-developed parastyle and deep, narrow carnassial notch, as is diagnostic for the Feliformia (see Flynn 1998).

Length and width measurements of CMN 30877 are 4.31 and 2.33 mm, respectively.

Viverravus is documented from late Paleocene through middle Eocene aged strata of North America, from late Eocene and questionably early Eocene aged strata of Europe (McKenna and Bell 1997), and tentatively from the late Paleocene of Asia (Meng et al. 1998).

Caniformia Kretzoi, 1943
Miacidae Cope, 1880
Vulpavus Marsh, 1871
cf. *Vulpavus* sp.

Referred specimen

CMN 30987, incomplete left dentary with basal part of canine, alveoli for p1–p3, complete p4, and alveoli for m1.

Locality

Locality 85, lower mammalian faunal level, upper part of Eureka Sound Group, south of Bay Fiord, central Ellesmere Island, Nunavut, Canada (Wasatchian).

Description and discussion

When compared with specimens of Early Eocene miacids *Vulpavus*, *Oödectes*, *Uintacyon*, *Vassacyon*, and *Miacis* housed in the collections at the AMNH, CMN 30987 (Pl. 2, fig. 2) is most similar in size and morphology to *Vulpavus australis*. As discussed later in the paper, however, minor differences are noted between CMN 30987 and *Vulpavus*. Consequently, CMN 30987 is only tentatively referred to this genus.

CMN 30987 is similar in length to dentaries of *V. australis*, but is not so deep as the latter. The two mental foramina on the labial side of the dentary are in the same positions as in other early miacids, including *Miacis*, *Uintacyon*, and *Vulpavus*: one foramen is below p1, and the other is below p3. The basal part of the canine preserved on CMN 30987 indicates a large tooth with an ovate cross section. Based on the pattern of alveoli, p1 of CMN 30987 bore a single root, and p2 and p3 each had two roots. The double-rooted p4 possesses a tall, acute, main cusp that is more keeled, but less inflated or robust, than that of *Vulpavus* and *Vassacyon*. Unlike *Uintacyon* and *Oödectes* (see Flynn 1998; Matthew 1915), but like *Vulpavus*, p4 on CMN 30987 possesses an anterior accessory cusp (AAC), located slightly lingual of the midline and of a medial ridge extending anteriorly from the main cusp. The AAC on p4 of CMN 30987, however, is larger and better developed than that of *V. australis*. A labial ridge runs posteriorly from the main cusp. As is characteristic of the Early Eocene miacids and considered primitive for Carnivora (see Flynn 1998; Flynn and Galiano 1982; Heinrich 1997), p4 on CMN 30987 possesses an elongate, well-developed talonid with two posterior accessory cusps (PAC). The more anterior PAC is a large, oblong cusp that in life would have joined the labial ridge extending posteriorly from the main cusp, had it not been for an extensive crack in the enamel between the two. The much smaller, circular, second PAC, whose apex is slightly anterior to the posterior cingulum, is separated from the first PAC by a notch. Minor damage, specifically a small chip in the enamel, separates the posterior cingulum from the second PAC. A lingual cingulid is absent.

Length and maximum width measurements of p4 of CMN 30987 are 4.98 and 2.24 mm, respectively.

Based on postcranial material from mid-latitude North America, *Vulpavus* was a small carnivore, comparable in size to the living coatimundi (*Nasua nasua*), which was well adapted for climbing (Heinrich and Rose 1997).

As *Vulpavus* is documented from the Wasatchian and Bridgerian NALMAs, Early and early Middle Eocene, respectively, (Heinrich and Rose 1997; Gingerich 1983), the occurrence of cf. *Vulpavus* in contemporaneous strata on Ellesmere Island is not surprising. *Vulpavus* is known only from North America (Heinrich and Rose 1997).

Miacis Cope, 1872
Miacis sp.

Referred specimen

CMN 30817, damaged RM1.

Locality

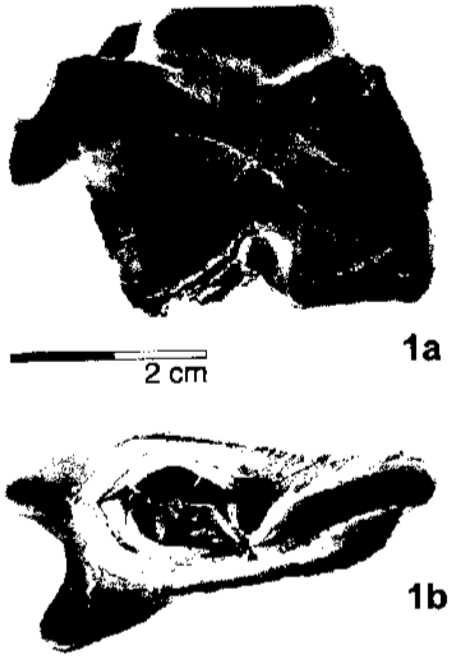
Locality 85, lower mammalian faunal level, upper part of Eureka Sound Group, south of Bay Fiord, central Ellesmere Island, Nunavut, Canada (Wasatchian).

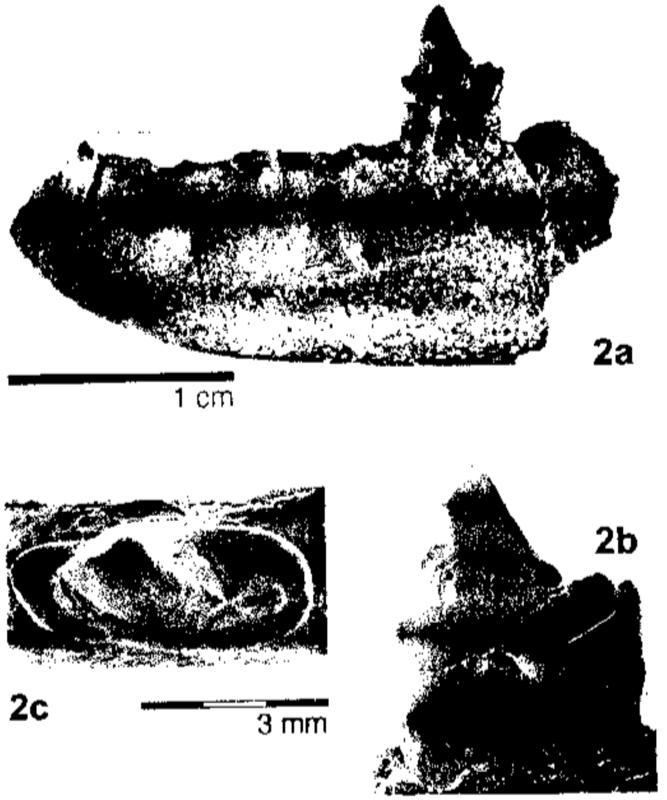
Description and discussion

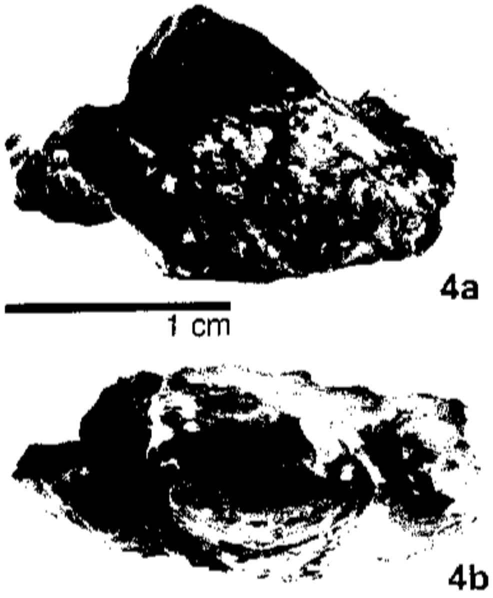
CMN 30817, a damaged RM1 (Pl. 2, fig. 3), is most similar in size and morphology to M1 of *Miacis exiguus*, and is considerably smaller than M1s of *Miacis gracilis*, *Miacis hargeri*, and *Miacis medius*. We are reluctant, however, to assign CMN 30817 to *M. exiguus*, due to its incompleteness. Although the characters preserved on CMN 30817 also occur on M1s of *M. exiguus*, they are not diagnostic for the species.

The entire protocone and most of the paracone on CMN 30817 are missing, as is the posterolabial corner of the tooth (i.e., the metastyle wing). Moreover, the base of the paracone indicates that this cusp was much larger than the metacone, and probably similar in size to that of *M. exiguus*. Similarly, the metacone on CMN 30817 is comparable in height and circumference to that of *M. exiguus*. CMN 30817 possesses a large, anterior-projecting parastyle wing and a well-developed paracrista, as in *M. exiguus*. Because the

Plate 2. fig. 1. (*a, b*) Labial and occlusal views, respectively, of CMN 30877, LP4 of *Viverravus* sp. from locality 85. **fig. 2.** (*a*) Labial view of CMN 30987, an incomplete left dentary of cf. *Vulpavus* from locality 85. (*b, c*). Labial and occlusal views, respectively, of p4 on CMN 30987; (*b*) and (*c*) share the scale bar. **fig. 3.** CMN 30817, a damaged and incomplete RM1 of *Miacis* sp., from locality 85. **fig. 4.** CMN 32519, an incomplete p4 or m1 of *Pachyaena* sp. from locality D7.







metastyle wing is not preserved, however, it is impossible to determine its size relative to the parastyle wing, an otherwise useful character in determining the phylogeny of early Eocene miacids (Heinrich 1997). An elongate cuspule occurs just posterior to the junction of the paracrista with the ectocingulum. Although difficult to discern due to damage, an inflated region of the ectocingulum, mesiolabial to the metacone, suggests that a mesostyle may have been present. A wear facet lingual to the metacone indicates the presence of a small, although distinct, metaconule. A tiny cuspule is next to, and posterolabial from, the metaconule. A precingulum and a small region of the postcingulum posterior to the metaconule are preserved on CMN 30817.

Minimum estimates of the length and width of CMN 30817 are 4.6 and 7.0 mm, respectively.

Postcranial material from Wyoming indicates that *Miacis* was a small carnivore whose body size probably overlapped that of *Vulpavus* (see Gingerich 1983, fig. 13).

Miacis is known from early through late Eocene aged strata of Europe, North America, and Asia (McKenna and Bell 1997; Ting 1998). Earliest representatives of the family Miacidae appear in the late Paleocene of North America and Europe (McKenna and Bell 1997), and questionably in the early Paleocene of Asia (Ting 1998). The Asian record, however, is based on *Pappictidops*, the only known carnivore genus from the Paleocene of China, that has been included in Miacidae (see Wang et al. 1998; Ting 1998), or alternatively in Viverravidae (see McKenna and Bell 1997; Gingerich and Winkler 1985).

Acreodi Matthew, 1909
Mesonychidae Cope, 1875
Pachyaena Cope, 1874
Pachyaena sp.

Referred specimen

CMN 32519, a worn, incomplete p4 or m1.

Locality

D7 locality, lower mammalian faunal level, upper part of Eureka Sound Group, south of Bay Fiord, central Ellesmere Island, Nunavut, Canada (Wasatchian).

Description and discussion

CMN 32519 (Pl. 2, fig. 4) is most similar to *Pachyaena*. CMN 32519 appears larger than *Dissacus* and *Pachyaena gracilis*, and is similar in size to *P. ossifraga*. As in p4–m1 of *Pachyaena* and p4 of some species of *Dissacus* (see Matthew 1909, 1915; Archibald 1998; O'Leary and Rose 1995), CMN 32519 lacks a metaconid. Despite its incompleteness, CMN 32519 appears wider than p4s of *Dissacus* and is more comparable in width to p4s and m1s of *P. ossifraga*. The protoconid on CMN 32519 is backwardly keeled, as is common in premolars and m1 of *Pachyaena*, but not in m2–m3. Although CMN 32519 bears a relatively smaller paraconid and lower protoconid than species of *Pachyaena*, this may be due, in part, to wear and postmortem damage to the tooth. Specifically, the enamel on CMN 32519 is heavily pitted and etched, probably indicating an acidic depositional environment. Despite the damage, a small portion of the lateral surface of the protoconid on CMN 32519 preserves a delicately rugose, almost fingerprint-like, enamel ornamentation, similar to that of *P. gigantea* (see O'Leary and Rose 1995).

Based on more complete specimens from mid-latitude North America, species of *Pachyaena* were among the largest known Eocene mammals, ranging from about wolf-sized (*P. gracilis*) to bear-sized (larger species). Its skeletal anatomy, which included hooves, indicates *Pachyaena* was a cursorial ungulate, having a combination of characters found in cursorial carnivores and more generalized ungulates, and was adapted more for power and endurance than for speed (O'Leary and Rose 1995). Both *Dissacus* and *Pachyaena* were probably carnivorous, although their teeth appear to be adapted for some kind of hard-object diet that involved little shearing like that of other mammalian carnivores (O'Leary and Tedford 1992).

Despite a general rarity of mesonychid fossils in Paleogene Holarctic faunas (O'Leary and Rose 1995), *Pachyaena* has been reported from Eocene strata in Asia, Europe, and North America.

Paleobiogeographic implications

Based on high generic affinities between North American Early Eocene (i.e., Wasatchian) faunas and contemporaneous, Sparnacian-aged faunas in Europe (McKenna 1975), mammalian dispersal between the two continents is inferred to have taken place as late as the Paleocene–Eocene boundary, across one or possibly two land bridges connecting their northern reaches (McKenna 1983). This high-latitude dispersal route broke when extensive rifting began in the North Atlantic in Chron C24r (Ritchie and Hitchen 1996), probably very soon after the Wasatchian–Sparnacian dispersal event (Beard and Dawson 1999). Like the microparamyine rodents (Dawson 2001), *Palaeosinopa* and *Palaeonictis* made their first appearance in the late Paleocene of the western United States. Their subsequent occurrence in the Wasatchian-aged lower faunal level at Bay Fiord and in contemporaneous faunas in Europe suggests that they may have originated in mid-latitude North America and subsequently dispersed northward into arctic Canada, and eastward into Europe across a North Atlantic land bridge. A North American origin for the Oxyaenid creodonts (of which *Palaeonictis* is a member) seems reasonable, as the group is first recognized in North America, and its principal radiation and diversification occurred in North America (Gunnell 1998). Although the carnivore *Viverravus* is first documented in mid-latitude North America during late Paleocene time and in high-latitude North America and Europe during the Eocene (McKenna and Bell 1997), an Asian origin cannot be ruled out. Meng et al. (1998) reported cf. *Viverravus* sp. from the late Paleocene aged Bayan Ulan fauna of Inner Mongolia, China. The carnivore *Miacis* is perplexing in that morphologically very similar forms seem to appear simultaneously in the early Eocene of North America, Europe, and Asia. *Miacis winkleri* appears in earliest Wasatchian strata of North America, *Miacis latouri* in the early Sparnacian of Europe, and *M. tenuis* in the Bumbanian Asian Land Mammal Age (ALMA; see Gingerich 1983). Earliest Sparnacian mammal faunas of western Europe are virtually synchronous with earliest Wasatchian faunas from the United States. Beard and Dawson (1999) correlated the Bumbanian ALMA to the uppermost Clarkforkian and Wasatchian NALMA, and one of us (MM) believes the Bumbanian ALMA correlates only to the Wasatchian NALMA (see McKenna and Bell 1997, fig. 1). The Asian species, *Miacis tenuis*, is from the Ningjiashan Member of the Xinyu Formation, which is thought to represent the third and youngest interval zone of the Bumbanian ALMA, the *Heptodon* Interval Zone. This interval zone, in turn, has been correlated with the late Wasatchian NALMA by Ting (1998), although others have considered the Ningjiashan Member to be older (Zheng et al. 1975).

Table 1. Wasatchian and Bridgerian aged mammalian taxa of the Eureka Sound Group.

- Class Mammalia
  - Infraclass Allotheria
    - Order Multituberculata
      - Family Neoplagiaulacidae
        - *Neoplagiaulax* sp. (Wasatchian)
  - Infraclass Holotheria
    - Superorder Leptictida
      - Family Leptictidae
        - Subfamily Leptictinae
          - *Prodiacodon* sp. (Wasatchian)
    - Superorder Preptotheria
      - Order Rodentia
        - Family Ischyromyidae
          - Subfamily Paramyinae
            - *Paramys hunti* (Wasatchian)
            - ?Paramyinae sp. (Wasatchian)
          - Subfamily Microparamyinae
            - *Microparamys bayi* (Wasatchian)
            - *Strathcona minor* (Wasatchian)
            - *Strathcona major* (Wasatchian)
      - Grandorder Ferae
        - Order Cimolesta
          - Suborder Pantolesta
            - Family Pantolestidae
              - Subfamily Pantolestinae
                - *Palaeosinopa nunavutensis* (Wasatchian)
                - *Palaeosinopa* cf. *P. nunavutensis* (Wasatchian)
                - Genus and species indeterminate (Wasatchian)
          - Suborder Taeniodonta
            - Family Stylinodontidae
              - Genus and species unidentified (Bridgerian)
          - Suborder Pantodonta
            - Family Coryphodontidae
              - *Coryphodon* sp. (Wasatchian)
        - Order Creodonta
          - Family Oxyaenidae
            - *Palaeonictis* sp. (Wasatchian)
          - Family Hyaenodontidae
            - *Prolimnocyon* sp. (Wasatchian)
        - Order Carnivora
          - Suborder Feliformia
            - Family Viverravidae
              - *Viverravus* sp. (Wasatchian)
          - Suborder Caniformia
            - Family Miacidae
              - *Miacis* sp. (Wasatchian)
              - cf. *Vulpavus* (Wasatchian)
      - Grandorder Archonta
        - Order Primates (sensu lato)
          - Suborder Dermoptera
            - Family Paromomyidae
              - Subfamily Phenacolemurinae
                - Genus and species unidentified (Wasatchian)
            - Family Plagiomenidae
              - Subfamily Plagiomeninae
                - *Ellesmene eureka* (Wasatchian)
                - Several undescribed species (Wasatchian)
      - Grandorder Ungulata
        - Order Procreodi
          - Family Arctocyonidae
            - Subfamily Arctocyoninae
              - *Anacodon* sp. (Wasatchian)
        - Order Perissodactyla
          - Suborder Hippomorpha
            - Family Equidae
              - ?*Hyracotherium* (Wasatchian)
          - Suborder Ceratomorpha
            - Family Brontotheriidae
              - Subfamily Lambdotheriinae
                - cf. *Lambdotherium* (Wasatchian)
              - Subfamily Brontotheriinae
                - cf. *Telmatherium* sp. (Bridgerian)
            - Family Hyracodontidae
              - Subfamily Hyrachyinae
                - ?*Hyrachyus* (Wasatchian)
        - Order Cete
          - Suborder Acreodi
            - Family Mesonychidae
              - *Pachyaena* sp. (Wasatchian)

The hyaenodontid *Prolimnocyon* and the mesonychid *Pachyaena* probably originated in Asia. Near the Paleocene–Eocene boundary in both North America and Europe, a marked mammalian faunal turnover is documented, notably the apparently simultaneous first appearances of artiodactyls, perissodactyls, primates, and hyaenodontid creodonts. Asia seems the most likely source for these immigrant taxa (Beard and Dawson 1999; Beard 1998), which would have crossed into North America via Beringia, an emergent land bridge through most of the Cenozoic (McKenna 1983; Woodburne and Swisher 1995; Beard and Dawson 1999). The earliest, undoubted appearance of *Prolimnocyon* in North America is from early Wasatchian aged strata in Wyoming (Gunnell 1998). Within the Eureka Sound Group, *Prolimnocyon* occurs in the late Wasatchian aged lower faunal level in the Bay Fiord area. Occurrence of *Prolimnocyon* in North American middle and high latitudes postdates its occurrence in Asia. Specifically, the Asian species *Prolimnocyon chowi* from the late Paleocene Bayan Ulan fauna of Inner Mongolia, China, appears to be the oldest, most primitive species of *Prolimnocyon* (see Meng et al. 1998). *Prolimnocyon chowi* also represents the oldest undoubted occurrence of the Hyaenodontidae, suggesting an Asian origin for this group (Beard and Dawson 1999). The mesonychid *Pachyaena* also is documented from the Bayan Ulan fauna of Asia (Meng et al. 1998), predating its early Eocene appearance in the Eureka Sound Group fauna, mid-latitude North America, and Europe, and suggesting an Asian origin. The occurrence of *Pachyaena* in the early Eocene of Europe probably is best explained by dispersal from high-latitude North America to Europe via a North Atlantic land bridge, as a direct interchange between Asia and Europe was probably hindered by the Turgai Straits (McKenna 1983; Beard and Dawson 1999). The pantodont *Coryphodon*, whose teeth are among the most common mammal fossils in Eureka Sound Group strata, is another probable immigrant from Asia (Tong and Wang 1998).

Concluding remarks

In light of more recent research and revisions to mammalian systematics (e.g., McKenna and Bell 1997), we provide an updated list of the Eureka Sound Group mammalian fauna (Table 1). As numerous members of the Eureka Sound Group fauna have not yet been formally described, Table 1, which is compiled from Marincovich et al. (1990), Dawson (2001), K.C. Beard (personal communication to MM), and data presented in this paper, is meant as a working list that will require periodic updating.

As noted by Dawson (2001), the Wasatchian element of the Eureka Sound Group mammalian fauna is most similar to contemporaneous mid-latitude North American faunas. Notably, the plagiomenids, the perissodactyl *Lambdotherium*, the leptictid *Prodiacodon*, the arctocyonid *Anacodon*, and the carnivore *Vulpavus* are documented only from North America. As is the case with mid-latitude North America, most Wasatchian genera in the Eureka Sound Group are known also from Europe, and these include *Neoplagiaulax*, *Paramys*, *Microparamys*, *Palaeosinopa*, *Coryphodon*, *Palaeonictis*, *Viverravus*, *Miacis*, ?*Hyracotherium*, cf. *Hyrachyus*, and *Pachyaena*. Several of these genera, however, are also shared with Asia, specifically *Paramys*, *Coryphodon*, *Miacis*, cf. *Hyrachyus*, *Pachyaena*, and possibly *Viverravus*. One genus in the Eureka Sound Group, *Prolimnocyon*, is known from North America and Asia, but not Europe.

Although mid- and high-latitude North American Wasatchian faunas share many genera with contemporaneous (i.e., Sparnacian) European faunas (McKenna 1975), affinities with Asia have only recently been recognized (Beard and Dawson 1999, and papers therein). Asia is thought to be the source of many important elements of North American Wasatchian and European Sparnacian faunas, notably artiodactyls, perissodactyls, primates, and hyaenodontid creodonts (Beard and Dawson 1999; Beard 1998). As the dispersal route between North America and Asia is inferred to have been at high latitudes, across Beringia (McKenna 1983; Beard and Dawson 1999) and including arctic Canada, it is surprising that artiodactyls and hyopsodontids are apparently absent from the Eureka Sound Group.

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