

Life at the top of the greenhouse Eocene world— A review of the Eocene flora and vertebrate fauna from Canada's High Arctic

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ABSTRACT

Early–middle Eocene (ca. 53–38 Ma) sediments of the Eureka Sound Group in Canada's Arctic Archipelago preserve evidence of lush mixed conifer–broadleaf rain forests, inhabited at times by alligators, turtles, and diverse mammals, including primates, tapirs, brontotheres, and hippo-like *Coryphodon*. This biota reflects a greenhouse world, offering a climatic and ecologic deep time analog of a mild ice-free Arctic that may be our best means to predict what is in store for the future Arctic if current climate change goes unchecked. In our review of the early–middle Eocene Arctic flora and vertebrate fauna, we place the Arctic fossil localities in historic, geographic, and stratigraphic context, and we provide an integrated synthesis and discussion of the paleobiology and paleoecology of these Eocene Arctic forests and their vertebrate inhabitants. The abundance and diversity of tapirs and plagiomenids (both rare elements in midlatitude faunas), and the absence of artiodactyls, early horses, and the hyopsodontid “condylarth” *Hyopsodus* (well represented at midlatitude localities) are peculiar to the Eocene Arctic. The Eocene Arctic macrofloras reveal a forested landscape analogous to the swamp-cypress and broadleaf floodplain forests of the modern southeastern United States. Multiple climate proxies indicate a mild temperate early–middle Eocene Arctic with winter temperatures at or just above freezing and summer temperatures of 20 °C (or higher), and high precipitation. At times, this high precipitation resulted in freshwater discharge into a nearly enclosed Arctic Ocean

basin, sufficient to cause surface freshening of the Arctic Ocean, supporting mats of the floating fern *Azolla*. Fluctuating Arctic Ocean sea level due to freshwater inputs as well as tectonics produced temporary land bridges, allowing land plants and animals to disperse between North America and both Europe and Asia.

INTRODUCTION

Today's High Arctic is a polar desert characterized by a cold, dry climate (annual precipitation <10 cm that comes mostly as snowfall) and an extreme photoperiod marked by continuous daylight in summer, intervals of twilight in spring and fall, and a long winter night that lasts from a day at the Arctic Circle to six months at the North Pole (Pielou, 1994; Aiken et al., 2007). The treeless tundra of Canada's Arctic Archipelago is home to ~357 species of vascular plant (Aiken et al., 2007), some 11 year-round bird species, and about a dozen terrestrial mammal species that are adapted in numerous ways to the short, cool growing season, cold dark winter, poor soil, and drought (Pielou, 1994).

There is mounting evidence, however, that the Arctic is changing, with temperatures rising at almost twice the rate of the rest of the world (ACIA, 2005; Bekryaev et al., 2010; Serreze and Barry, 2011). With warming predicted to continue well into the future, recent models project that the Arctic Ocean may be free of permanent ice within 30 yr, and significant changes have already been observed in both the marine and terrestrial environments (Barber et al., 2008; Wang and Overland, 2009). As the Arctic undergoes rapid warming, the impact on its biota is unclear. From a geologic perspective, climatic and ecologic deep time analogs of a mild, ice-free Arctic are among the best means to under-

stand and predict what is in store for today's Arctic region as climate continues to change.

Among the best deep time analogs, lower–middle Eocene (ca. 53–38 Ma) sediments of the Eureka Sound Group in Canada's Arctic Archipelago (Fig. 1) preserve fossil evidence of lush swamp forests of predominantly conifers such as redwoods and cedars (e.g., *Metasequoia*, *Chamaecyparis*), but also including the pine family (*Larix*, *Picea*, *Pinus*, *Pseudolarix*, and others), and a diverse dicot flora with alder or birch (*Alnus* and *Betula* spp.), walnut (*Juglans* spp.), and other deciduous broadleaf trees (Basinger, 1991; Greenwood and Basinger, 1994; McIver and Basinger, 1999; Greenwood et al., 2010; see Table 1). These swamps were inhabited at times by alligators, turtles, and fish (Estes and Hutchinson, 1980), in addition to a diversity of mammals that included primates, tapirs, brontotheres (rhinoceros-like perissodactyl ungulates), and hippo-like *Coryphodon* (Dawson et al., 1993; Eberle, 2005, 2006; Tables 2 and 3). The relevant fossil-bearing rocks of the Eureka Sound Group were just a few degrees farther south than their present-day latitudes and well above the Arctic Circle in the Eocene (McKenna, 1980; Irving and Wynne, 1991; Fig. 2); consequently, these forest communities experienced months of continuous sunlight, twilight, and darkness. Taken together, the spectacular paleontological discoveries in Canada's High Arctic (some of which date back well over a century; e.g., Greely, 1886) confirm beyond doubt that this region enjoyed a much warmer and wetter climate during the Eocene than at present. Multiple, independent climate proxies corroborate the paleontological evidence for a mild, ice-free Eocene Arctic and provide quantitative estimates for Eocene climatic conditions at northern high latitudes (Table 4), although global circulation models have been challenged to retro-predict Eocene

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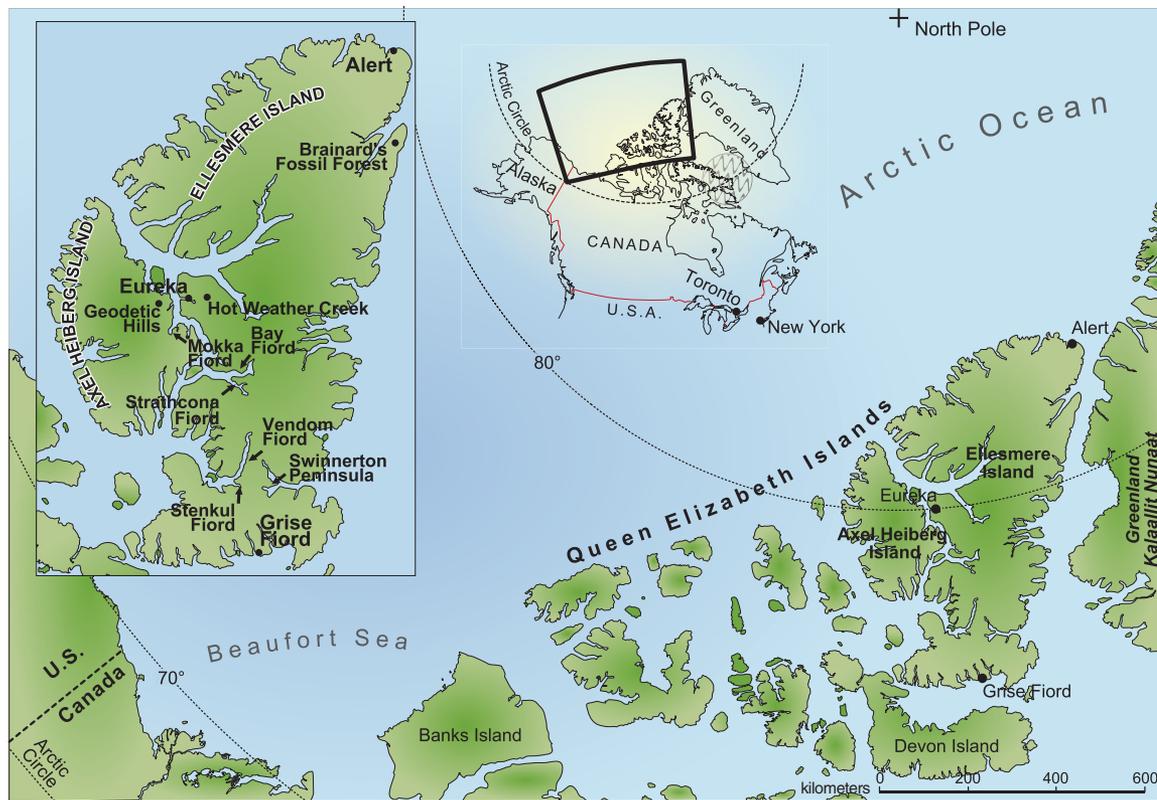


Figure 1. Map of northern Canada north of the Arctic Circle showing principal locations mentioned in the text. Artwork by L. McConnaughey.

climatic conditions inferred from the proxy data (Shellito and Sloan, 2005; Shellito et al., 2009; Huber and Caballero, 2011).

From a biogeographical perspective, the High Arctic was a major corridor for terrestrial organisms dispersing between North America and both Europe and Asia at various times throughout the Cenozoic Era (i.e., the past 65.5 Ma). Although the notion of dispersal across Holarctic land masses was proposed over half a century ago (Simpson, 1953), the rules changed with the discovery of seafloor spreading in the late 1960s and the acceptance of plate tectonics. The initial evidence for a North Atlantic land corridor came predominantly from paleontological data showing that early Eocene, mid-latitude mammalian faunas and floras from these two continents share over half of their genera (McKenna, 1975; Manchester, 1999; Tiffney, 2000). However, beginning in the 1970s, a wealth of geologic and geophysical data added tectonic foundations supporting the existence of at least one (Thulean) and perhaps a second (De Geer) land bridge across the North Atlantic Ocean (McKenna, 1975, 1983). More recently, Asia has been hypothesized as the source area for several mammalian orders, including artiodactyl and perissodactyl ungulates, as well as true primates,

which abruptly appeared in North America at the onset of the Eocene (Beard, 1998). The dispersal route between North America and Asia is inferred to have been at high latitudes, across the Bering Strait (Beringia) and including Arctic Canada (McKenna, 1983; Beard and Dawson, 1999). The Eocene Arctic vertebrate fauna strengthens the hypotheses for Eocene dispersal across polar land bridges, as it shares several genera with Europe and Asia (Eberle and McKenna, 2002). Moreover, there is evidence that large herbivores such as hippo-like *Coryphodon* were year-round inhabitants in the Eocene High Arctic, a probable prerequisite to dispersal across these Arctic land corridors (Eberle et al., 2009). The presence of giant formicine ants associated with tropical forests in both Europe and Wyoming in the Eocene is interpreted as demonstrating the presence of short-lived climatic-physiological gates opening during Eocene hyperthermals (e.g., the Paleocene-Eocene thermal maximum, ETM2 (Eocene Thermal Maximum 2), and EECO (Early Eocene Climatic Optimum), allowing dispersal of tropical (thermophilic) biota across the Arctic land corridor as well (Archibald et al., 2011).

Here, we provide an integrated look at the early–middle Eocene forest communities of

the Canadian Arctic and their ancient vertebrate inhabitants. The early–middle Eocene was the warmest interval in all of Cenozoic time and our most recent greenhouse world (Zachos et al., 2008). We begin our review by placing the Arctic fossil localities in historic, geographic, and stratigraphic context. We synthesize our knowledge of this extinct biota, including discussions of its taxonomic composition, diversity, and paleoecology. Where new names have been applied to previously published accounts of plant taxa described from the Eocene Arctic macrofloras (e.g., Hickey, 2001; LePage, 2001, 2007; Kotyk et al., 2003), these are noted in this review (e.g., Table 1), but we offer no new systematic interpretations of these fossil plants. The Eocene Arctic flora and fauna are powerful proxies for inferring Eocene climate, and we provide comparison with other climate proxies. From phylogenetic and biogeographical perspectives, we discuss the Canadian Arctic as a thoroughfare for Eocene plants and animals dispersing between North America and both Europe and Asia. We conclude with our take on the most interesting, outstanding questions concerning the Eocene Arctic, and avenues that future research on this unique polar biota may illuminate about our understanding of polar greenhouse worlds.

TABLE 1. LIST OF TAXA FROM THE BUCHANAN LAKE FORMATION, DIVIDED ACCORDING TO LITHOLOGICAL FACIES, AND NUMBER OF SITE-GROUPS* FROM WHICH A TAXON HAS BEEN RECORDED. ALL DATA ARE FROM McIVER AND BASINGER (1999), WITH NOMENCLATURAL UPDATES FROM RECENT LITERATURE (SEE FOOTNOTES)

Taxon	Swamp	Sandstones	Mudstones	Ironstones	Total sites
cf. Ericaceae	1				1
cf. Myricaceae	1				1
<i>Chamaecyparis eureka</i> [†]	2				2
<i>Sequoia</i>	1				1
<i>Taiwania</i>	1				1
Trigonobalanus	1				1
<i>Tsuga swedaeae</i> [§]	3				3
Unknown Cupressaceae-Taxodiaceae	1				1
<i>Picea palustris</i>	1				1
<i>Picea sverdrupii</i> , <i>P. nansenii</i> [#]	6	6			12
<i>Larix altoborealis</i> ^{**}	4	3			7
cf. <i>Keteleeria</i>	1	1			2
Dicot angiosperm unk.	4	1	3		8
Juglandaceae cf. <i>Juglans</i> ^{††}	2	1	2		5
<i>Metasequoia</i>	7	4	4	1	16
<i>Pinus</i>	7	3	1	1	12
Unknown 'Taxodiaceae'	2		1		3
<i>Osmunda</i>	2		4		6
<i>Glyptostrobus</i> /cf. <i>Glyptostrobus</i>	2		2		4
<i>Betula</i>	2		1	1	4
<i>Pseudolarix amabilis</i> or <i>P. wehrli</i> ^{§§}	6			1	7
<i>Trochodendroides</i>			5		5
cf. <i>Archeampelos</i> / <i>Archeampelos</i>			4		4
cf. <i>Sparganium</i>			4		4
cf. <i>Nyssa</i>			4		4
Menispermaceae			4		4
cf. <i>Ushia</i> / <i>Ushia</i>			3		3
<i>Equisetum</i>			3		3
Betulaceae			3		3
Unknown fern			3		3
<i>Ginkgo</i>			3	1	4
<i>Alnus</i>			3	1	4
<i>Quercus</i>			3		3
<i>Nyssidium arcticum</i>			2		2
cf. <i>Rhus</i>			2		2
<i>Platanus</i>			2		3
<i>Nordenskioldia borealis</i>			1		1
Monocot angiosperm unk.			1		1
cf. <i>Tilia</i>			1		1
<i>Onoclea</i>			1		1
cf. <i>Fraxinus</i>			1		1
No. taxa	23	7	29	6	43
No. of sites/lithology	11	7	6	1	25

*Site-groups are the pooled individual collection quarry sites (University of Saskatchewan paleontology collection or "US" numbered "localities") listed by McIver and Basinger (1999) in their appendices. In some cases, a site-group is a single collecting locality (e.g., US 588); in most cases, 2–6 individually numbered quarry sites were lumped together by McIver and Basinger (1999) as they constitute a single physical "locality" where multiple quarries were sampled.

[†]Kotyk et al. (2003).

[§]LePage (2003).

[#]LePage (2001).

^{**}LePage and Basinger (1991).

^{††}Listed as *Carya*/cf. *Carya* in McIver and Basinger (1999)

^{§§}LePage and Basinger (1995).

HISTORY OF COLLECTING FOSSIL PLANTS AND VERTEBRATES IN THE ARCTIC

Discovery of Paleogene floral assemblages dates back well over 130 yr to Captain Nares' Royal Navy expedition of 1875 (Fielden and De Rance, 1878), which resulted in a large collection of fossil leaves from northern Ellesmere Island described by Heer (1878). Sergeant D.L. Brainard, a survivor of the ill-fated Greely expedition of 1881–1883, discovered petrified logs on northeastern Ellesmere at a locality coined

"Brainard's Petrified Forest" (Greely, 1886; Fig. 1). In the early 1900s, a forest locality was discovered at Stenkul Fiord on southern Ellesmere Island by Per Schei, a member of Norwegian explorer Otto Sverdrup's expedition in the *Fram* (Nathorst, 1915). More recent discoveries include a stump field near the Eureka weather station (McMillan, 1963), the Strathcona Fiord Fossil Forest on central Ellesmere Island discovered by Dawson in 1973 (Francis, 1988), and the famous Geodetic Hills (GH) mummified fossil forest discovered by Geological Survey of Canada (GSC) geologist Brian Ricketts

in 1985 (Fig. 1). The exceptional preservation of the Geodetic Hills Fossil Forest has resulted in numerous studies, ranging from taxonomic analyses and forest paleoecology (e.g., Basinger, 1991; LePage, 2001, 2003, 2007; LePage and Basinger, 1995; Greenwood and Basinger, 1993, 1994; McIver and Basinger, 1999; Williams et al., 2003; Jahren et al., 2009), to estimates of paleoclimatic variables that include temperature (Basinger et al., 1994; Greenwood and Wing, 1995), relative humidity (Jahren and Sternberg, 2003, 2008), precipitation (Greenwood et al., 2010), and the isotopic composition of environmental water (Jahren et al., 2009), to the northernmost record of Paleogene mammals (Eberle and Storer, 1999). The Paleocene and Eocene floras of Axel Heiberg and Ellesmere Islands were reviewed by McIver and Basinger (1999), and an overview of the Geodetic Hills Fossil Forest that includes taxonomic lists from previous studies was presented by Jahren (2007). The Geodetic Hills Fossil Forest was also the focus of a special volume edited by Christie and McMillan (1991). Consequently, our perspective for this paper is broadened to the early and middle Eocene Arctic biota as a whole, and we integrate paleoecological studies that have appeared subsequently to these works, and additionally described fossil taxa.

Discovery of Paleogene Arctic terrestrial vertebrates, including the world's first Arctic alligators (*Allognathosuchus* is assigned to the Alligatorinae; Estes and Hutchison, 1980) and turtles, came in the summer of 1975 through field work by vertebrate paleontologists Mary Dawson (Carnegie Museum of Natural History) and Robert (Mac) West (Milwaukee Public Museum) on central Ellesmere Island, Nunavut (Dawson et al., 1976). Subsequent expeditions by Dawson and colleagues spanned nearly four decades (1973–2010; see review by Eberle and McKenna, 2007), with most field research focused on Canada's eastern Arctic Archipelago—Ellesmere and Axel Heiberg Islands (Fig. 1). The best-documented and most diverse vertebrate faunal assemblage was discovered near Bay Fiord on central Ellesmere Island, although vertebrate fossils also are known from temporally correlative strata near Stenkul Fiord and on Swinnerton Peninsula on southern Ellesmere Island (Fig. 1). Preliminary field work in Eureka Sound exposures on northern Banks Island (Canada's westernmost Arctic island) by Jaelyn Eberle and colleagues produced the first Paleogene terrestrial vertebrates on that island, including shell fragments of an emydid (pond) turtle that implies an early Eocene age (Hutchison, 2011, personal commun.). Additionally, several thousand shark teeth that represent predominantly sand tigers (*Striatolamia*

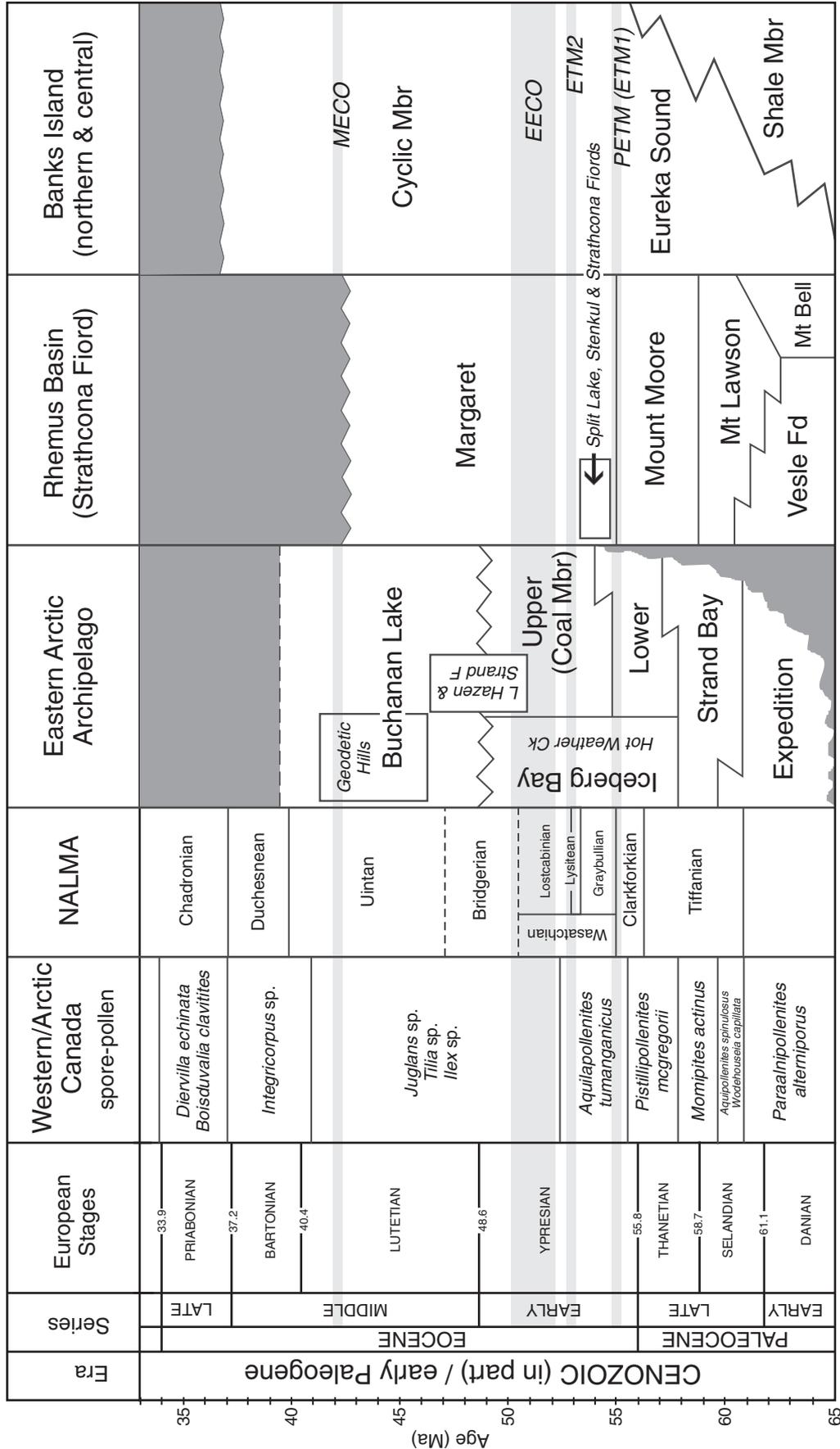


Figure 2. Schematic stratigraphic chart showing the principal geological formations and major macrofossil sites discussed in the text, based in part on a similar diagram in McIver and Basinger (1999) with Banks Island added, and updated based upon Harrison et al. (1999) and the geochronometric scale of Ogg et al. (2008). The chronological positions of the Eocene hyperthermals—Paleocene-Eocene thermal maximum (PETM), Eocene thermal maximum 2 (ETM2), and early Eocene climatic optimum (EECO)—are based upon Zachos et al. (2008).

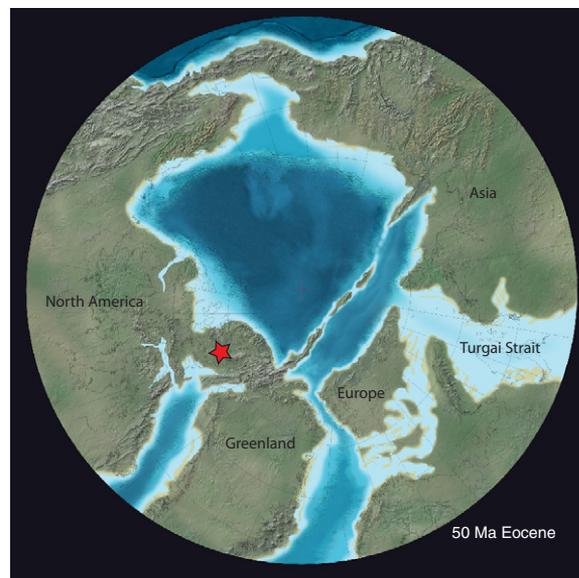
and *Carcharias*), a clade in which living representatives inhabit warm, shallow coastal waters worldwide (Padilla, 2008), were uncovered in unconsolidated sands of the Eureka Sound Formation on northern Banks Island (Fig. 2).

GEOLOGIC AND STRATIGRAPHIC FRAMEWORK

The formations comprising the Eureka Sound Group (Fig. 2) range in age from Late Cretaceous (Campanian or Maastrichtian) through middle or late Eocene, and they were deposited in the Sverdrup Basin—a long-lived basin (with roots in the Mississippian) that saw its eventual demise and breakup into several small sub-basins during the Eureka orogeny (Ricketts, 1994). The Eureka orogeny, in turn, was an Arctic-wide mountain-building event that began in the late Paleocene, as evidenced by the onset of thrusting on northern Ellesmere Island due to the north-directed indentation of this part of the North American plate by the ancestral Greenland plate (Harrison et al., 1999). The Eureka orogeny coincided with the emplacement of one or several mantle plumes from a hotspot that first manifested beneath West Greenland and then migrated eastward to eventually lie beneath the North Atlantic Oceanic plate and ancestral Iceland. Several factors associated with the eastward migration of the mantle plume head and the North Atlantic spreading ridge are hypothesized to have driven the Greenland plate northward and were the primary driving forces for the westward expansion of the Eureka orogen (Harrison et al., 1999). Synorogenic deposition of Eureka Sound Group strata, for which dates are constrained by the fossil vertebrates and floras, suggests that the Eureka orogeny continued through the late Eocene, although it may have been in decline after the middle Eocene (Harrison et al., 1999, and references therein). The nature of the tectonic contact between the North American and Greenland plates (beneath Nares Strait, the waterway east of Ellesmere Island) has long been debated, and the most recent discussion can be found in a volume edited by Mayr (2008).

From a paleogeographical perspective, the Eocene configuration of land masses within the Arctic Circle almost closed off the Arctic Ocean basin (Fig. 3). This isolation, combined with the large volume of freshwater runoff from the Holarctic land masses into the Arctic Ocean basin, is hypothesized to have considerably reduced the salinity of the Arctic Ocean (McKenna, 2003; Waddell and Moore, 2008), which has also been inferred from occurrence of the freshwater-brackish fern *Azolla* in middle Eocene-aged sediments of the Arctic Ocean

Figure 3. Paleogeographic reconstruction of polar region during the Eocene, courtesy of R. Blakey (Northern Arizona University), with the general location of the early Eocene fossil localities on central Ellesmere Island identified by the red star. During the early–middle Eocene, these sites were located at ~77°N paleolatitude (Irving and Wynne, 1991). The Turgai Strait is shown open. Some reconstructions show this closed in the early to middle Eocene (e.g., Brinkhuis et al., 2006; Barke et al., 2011).



(Brinkhuis et al., 2006; Barke et al., 2011). The Eocene paleogeography of North America (Fig. 3) was such that two high-latitude land corridors—one in the east extending from Ellesmere Island across Greenland, the newly forming North Atlantic Ocean, and proto-Iceland to western Europe (McKenna, 1975, 1983, 2003), and the other in the west across the Bering Strait (Beringia)—connected North America to Europe and Asia, respectively. The North Atlantic land corridor is hypothesized to have been in existence only during the earliest Eocene, as initially evidenced by high generic similarity (>50% shared genera) between earliest Eocene (Wasatchian) mammal faunas in midlatitude North America and the temporally correlative Sparnacian faunas of Europe (McKenna, 1975). This interval marked the highest generic similarity between the two continents in all of mammalian history (Savage and Russell, 1983) and floral history (Manchester, 1999; Tiffney, 2000). Tectonic data suggest that seafloor spreading in the North Atlantic began in magnetochron C24r (latest Paleocene–earliest Eocene), coincident with the eastward migration of the mantle plume head, which, by mid-early Eocene time, had moved off of East Greenland (Harrison et al., 1999). Late-early Eocene deposition of marine sediments otop of subaerially exposed volcanics on East Greenland (Harrison et al., 1999) probably saw the end of North Atlantic land continuity, and the bridge was most certainly broken by the middle Eocene, as evidenced by a significant drop in faunal resemblance between North American and European land mammal faunas (McKenna, 1975; Beard and Dawson, 1999). In contrast to the geologically short-lived North Atlantic land corridor, Beringia in the

western Arctic was intermittently a land bridge throughout the Cenozoic Era, and was the probable port of entry into North America for many major clades of mammals, including perissodactyls, artiodactyls, and true primates at the onset of the Eocene (Beard, 1998).

Although the Eocene fossil localities in Canada's eastern High Arctic occur today between 77°N and 82°N latitude (Fig. 1), paleomagnetic data suggest that during the Eocene, these forest ecosystems lived between 74°N and 80°N paleolatitude (Irving and Wynne, 1991; McKenna, 1980). Located well above the Arctic Circle, this environment experienced months of continuous daylight and darkness, the Arctic summer and winter, respectively. Inferences about paleobiology and paleoecology of the Eocene Arctic biota are discussed later herein.

Although Paleogene fossil-bearing rocks were first recognized in the Canadian Arctic over a century ago (Greely, 1886), the Eureka Sound Group was not named until 1950 by Troelson. 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 (Fig. 2). Following their discovery of Paleogene vertebrates on central Ellesmere Island (West et al., 1975; Dawson et al., 1976), West et al. (1981) subdivided the Eureka Sound Formation into four informal members, the uppermost member IV containing the Eocene terrestrial vertebrates. Independently, Miall (1986) and Ricketts (1986) raised the Eureka Sound Formation to group rank and subdivided it into formations. Consequently (and quite confusingly), Paleogene terrestrial vertebrate-bearing strata on central Ellesmere Island fall under three different names—member IV

of West et al. (1981), the Margaret Formation of Miall (1986), and the Iceberg Bay Formation of Ricketts (1986). At Stenkul Fiord on southern Ellesmere, the Eureka Sound Formation was initially subdivided into four informal members (Riediger and Bustin, 1987) independent of the subdivisions by West et al. (1981), although Riediger and Bustin (1987) correlated their members II, III, and IV with the Margaret Formation, and fossil vertebrate-bearing member IV at Stenkul appears to temporally correlate with member IV of West et al. (1981) at Bay Fiord. These strata were tentatively assigned to the Margaret Formation by Miall (1986) and the Iceberg Bay Formation by Kalkreuth et al. (1996). On northern Ellesmere Island, the fossil plant-bearing strata of the Eureka Sound Group in Lake Hazen and Judge Daly Basins have been mapped as Mokka Fiord Formation (Miall, 1986); the latter basin preserves Brainard's Fossil Forest on Judge Daly Promontory, i.e., the northeastern "finger" of Ellesmere Island where Nares Strait is narrowest. The age is tentatively assigned as Eocene–Oligocene (Miall, 1986); no fossil vertebrates are documented from Lake Hazen or Judge Daly Basins. On Axel Heiberg Island, Lower Eocene fossil-bearing strata have been assigned either to the Margaret Formation (western Axel Heiberg) or the Mokka Fiord Formation (eastern Axel Heiberg) by Miall (1986), whereas Ricketts (1986) maintained the name Iceberg Bay Formation for these strata. The middle–upper Eocene conglomeratic sediments that overlie the Lower Eocene strata on Axel Heiberg Island are mapped as either the Boulder Hills Formation by Miall (1986, 1991), or the Buchanan Lake Formation by Ricketts (1986, 1991). However, it should be noted that Miall's formational contacts do not line up precisely with those of Ricketts.

Today's general consensus is that the Eureka Sound is a group divisible into numerous formations, and generally Miall's formational names are applied to Ellesmere Island (e.g., Harrison et al., 2009; although see Kalkreuth et al., 1996), while Ricketts's nomenclature is most often used on Axel Heiberg Island (e.g., Jahren, 2007); we retain that usage here (Fig. 2). On Banks Island, the Eureka Sound initially retained formational rank and was divided into members (Thorsteinson and Tozer, 1962; Miall, 1979); the Cyclic Member contains the Paleogene fossil wood and vertebrates. Since then, Miall (1986, 1991) reassigned the Cyclic Member on Banks Island to the Margaret Formation. However, given the enormous distance from Miall's (1986) type section of the Margaret Formation (Strand Fiord on southern Axel Heiberg Island), the Paleogene wood- and vertebrate-bearing sediments on northern Banks Island are here left as the

Cyclic Member. There are also environmental differences; the Margaret Formation in the eastern Arctic is predominantly nonmarine, while the Cyclic Member on northern Banks Island contains abundant shark teeth, clams, and locally abundant *Ophiomorpha* (shrimp burrows; Eberle, 2010, personal observation), a trace fossil indicative of shallow-water, nearshore marine and intertidal environments. Marine microfossils (foraminiferans and radiolarians) also are known (though rare) from the Cyclic Member (Miall, 1979).

LITHOLOGY AND AGE

The Margaret Formation (= Iceberg Bay Formation) consists of coarsening-upward cycles of interbedded cross-bedded sandstone, siltstone, mudstone, and coal that have been interpreted as a proximal delta-front to delta-plain environment with abundant channels and coal swamps (Miall, 1986; Ricketts, 1986). Terrestrial vertebrates occur in two stratigraphic levels in the Margaret Formation near Bay Fiord on central Ellesmere Island (Dawson, 1990, 2001; Eberle and McKenna, 2002). A diverse fauna that includes fish, amphibians, alligators, turtles, a boid snake, and some 25 mammalian genera is documented from the lower faunal level (Tables 2 and 3) 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). Specifically, perissodactyls, hyaenodontid creodonts, *Pachyaena*, *Miacis*, and cf. *Vulpavus*, all of which first appear at midlatitudes in the Wasatchian, as well as Wasatchian index taxon *Pachyaena* and the archaic ungulate *Anacodon*, which last appears in the Wasatchian (Robinson et al., 2004), are known from the lower faunal level. A late Wasatchian age is further suggested by the presence of the tapiroid *Heptodon*, which first appears at midlatitudes in the late Wasatchian (Lysitean; Robinson et al., 2004), and the brontothere cf. *Eotitanops*, for which mid-latitude representatives first appear (albeit very rarely) in latest Wasatchian strata (Smith and Holroyd, 2003) or at the onset of the Bridgerian (Gunnell et al., 2009). Eocene vertebrate-bearing strata near Stenkul Fiord on southern Ellesmere Island appear to correlate to this faunal level (Dawson, 2001), and a zircon recovered from volcanic ash on the southern shore of Stenkul Fiord yielded a preliminary date of 52.6 ± 1.9 Ma (Reinhardt et al., 2010), consistent with the vertebrate biostratigraphy. The admittedly depauperate sample from the upper faunal level at Bay Fiord (Tables 2 and 3, taxa marked with *) is interpreted as early middle Eocene in age, equivalent to the Bridgerian NALMA (Dawson, 1990; Dawson

et al., 1993; McKenna, 1980; West et al., 1981); it contains a larger, more advanced brontothere than cf. *Eotitanops* from the lower faunal level and shell fragments of an anosteirine turtle, a clade for which earliest midlatitude North American records are from the early Bridgerian (Estes and Hutchison, 1980). Palynology supports an early–middle Eocene age range for the terrestrial vertebrate-bearing sediments near Bay Fiord (Norris and Miall, 1984), although others (e.g., Kalkreuth et al., 1996) have suggested a late Paleocene–early Eocene age for correlative strata at Stenkul Fiord.

At Mokka Fiord on eastern Axel Heiberg Island, the Iceberg Bay Formation (= type Mokka Fiord Formation of Miall, 1986) has produced a single fossil mammal—the plagiomenid *Ellesmene* (Dawson et al., 1993)—which, along with fossils of four families of turtle (Baenidae, Emydidae, Testudinidae, and Trionychidae), suggests an early Eocene age that is correlative to the lower faunal level at Bay Fiord. The exception, a shell fragment belonging to an anosteirine turtle, may suggest a slightly younger, middle Eocene (Bridgerian) age for some strata of the Iceberg Bay Formation at Mokka Fiord (Eberle, 1998).

The sediments on eastern Axel Heiberg Island containing the Geodetic Hills Fossil Forest comprise part of the upper coal member of the Buchanan Lake Formation (= Boulder Hills Conglomerate; Fig. 2). As the youngest stratigraphic unit of the Eureka Sound Group, the Buchanan Lake Formation is syntectonic, formed in response to late stages of the Eureka orogeny, specifically the uplift of Princess Margaret Arch (which forms the backbone of Axel Heiberg Island) and fragmentation of Sverdrup Basin (Ricketts, 1991, 1994). The Buchanan Lake Formation consists mostly of diabase pebble conglomerate and lithic sandstone (Ricketts, 1986), although the upper coal member (which preserves the mummified tree trunks, peat layers, and vertebrate fossils) consists of interbedded fine-grained sandstone, siltstone, mudstone, and prominent lignite seams, typically in fining-upward sequences (Ricketts, 1991). The depositional environment of the Buchanan Lake Formation is interpreted as an east/southeast-prograding alluvial-fan/meander plain system formed by debris shed off of the uplifting Princess Margaret Arch, and the upper coal member likely represents the distal-most, downslope component of this system deposited in sandy meandering river channels and adjacent crevasse splay–floodplain deposits (Ricketts, 1991, 1994). The fossil forest swamp facies, mudstone, and other facies from the Geodetic Hills on Axel Heiberg Island (e.g., site US 188 of Greenwood and Basinger, 1994; Basinger

et al., 1994; McIver and Basinger, 1999) from the upper coal member were palynologically dated as middle Eocene (McIntyre, 1991; Richter and LePage, 2005), while the occurrence of tooth fragments of brontotheres also suggests a middle Eocene age (Eberle and Storer, 1999). In North American midlatitudes, brontotheres range throughout the Eocene Epoch, although the fossils from Axel Heiberg Island are most similar to midlatitude genera documented from the Uintan and Duchesnean NALMA (correlative with the middle Eocene or ca. 38–46 Ma; Robinson et al., 2004). Farther east at Mokka Fiord, fossils of fish, crocodilians, and turtles were discovered weathering out of conglomerates and conglomeratic sandstones of the Buchanan Lake Formation (Eberle, 1998), and the occurrence of the large tortoise *Hadrianus* suggests an age no older than early Eocene (Hutchison, 2010, personal commun.). Oligocene-aged rocks are not known to exist in the Canadian Arctic Islands, although volcanic rocks of this age are known from West Greenland (Harrison et al., 1999).

Harrison et al. (1999) provided a comprehensive analysis and overview of High Arctic Paleogene stratigraphy that we have updated and refined here (Fig. 2). The sediment packets at individual High Arctic sites in some cases were correlated by Harrison et al. (1999) to the geochronologic scale of Berggren et al. (1995), North American Land Mammal Ages (NALMA), or the Western/Arctic Canada spore-pollen zonation (Fig. 2). This is updated here to the geochronologic scale of Ogg et al. (2008). A suite of macrofloral sites in the Expedition Formation (e.g., Fosheim anticline east and west, and Strathcona Fiord) is likely wholly early Paleocene in age, whereas sediments of the Strand Bay Formation (= Mount Lawson Formation of Miall, 1986) containing macrofloras (e.g., Split Lake and Strathcona Fiord) are considered early late Paleocene by Harrison et al. (1999). Sediments containing macrofloras in the lower Margaret Formation (e.g., Split Lake, Stenkul Fiord, and Strathcona Fiord) are considered equivalent to the Coal Member of the Iceberg Bay Formation (Fig. 2), as they contain pollen taxa that first appear in magnetochron C24r in the Arctic (Harrison et al., 1999). The Margaret Formation at Bay Fiord contains a mammalian fauna that appears correlative with late Wasatchian and early Bridgerian faunas from midlatitude North America (Ypresian and early Lutetian European stages), whereas isotopic and faunal evidence indicates that the underlying Mount Moore Formation was deposited during the Thanetian (Tripathi et al., 2001), further constraining stratigraphic relationships. The macrofloras from the Buchanan Lake For-

mation on Axel Heiberg Island (Basinger et al., 1994; Greenwood and Basinger, 1994; McIver and Basinger, 1999) are considered time equivalents of the Uintan or perhaps Duchesnean NALMA (late Lutetian and Bartonian), on the basis of pollen and vertebrate faunal evidence summarized by Harrison et al. (1999).

EOCENE VERTEBRATES OF THE ARCTIC

Eocene Arctic Mammal Fauna

At least 25 mammalian genera occur in lower Eocene (Wasatchian-aged) strata of the Margaret Formation on Ellesmere Island (Table 2; Fig. 4), while one genus (*Ellesmene*) is also documented from correlative strata near Mokka Fiord on eastern Axel Heiberg Island (Dawson et al., 1993). The faunal list in Table 2 is meant as a working list that will continue to grow, as formal descriptions of several species are not

yet completed. Approximately two-thirds of the Wasatchian Arctic genera are shared with North American midlatitude localities, and certain taxa such as the hippo-like pantodont *Coryphodon* are abundant at both midlatitudes and in the early Eocene Arctic (Dawson, 2012). However, there are peculiarities in the composition of the early Eocene Arctic fauna that deserve some discussion. Specifically, the plagiomenids—small, enigmatic herbivores or frugivores whose teeth suggest affinities to Dermoptera or flying lemurs (Rose, 2008)—are abundant and diverse in the early Eocene Arctic (Dawson et al., 1993), as are early members of the tapir lineage (Eberle, 2005), whereas at midlatitudes, the tapir lineage made its first appearance in the middle Eocene (Bridgerian NALMA) with *Helalestes*, and they tend to be very rare as fossils (Colbert and Schoch, 1998), as are midlatitude plagiomenids (Rose, 2008). Similar to the tapir lineage, brontotheres appeared at midlatitudes at the advent of middle Eocene time; specifically, the appearance of the

TABLE 2. MAMMALIAN FAUNAL LIST FROM THE MARGARET FORMATION, EUREKA SOUND GROUP, ELLESMERE ISLAND, NUNAVUT

Class Mammalia	Class Mammalia (<i>continued</i>)
Order Multituberculata	Order Carnivora
Family Neoplagiulacidae	Family Viverravidae
? <i>Neoplagiulax</i> sp.	<i>Viverravus</i> sp.
Superorder Leptictida	Family Miacidae
Family Leptictidae	<i>Miacis</i> sp.
<i>Prodiacodon</i> sp.	cf. <i>Vulpavus</i>
Order Rodentia	Order Primates (sensu lato)
Family Ischyromyidae	Family Paromomyidae
<i>Paramys hunti</i>	<i>Ignacius</i> spp.*
? <i>Paramyinae</i> sp.	Order Dermoptera
<i>Microparamys bayi</i>	Family Plagiomenidae
<i>Strathcona minor</i>	<i>Ellesmene eureka</i>
<i>Strathcona major</i>	<i>Ellesmene</i> n. spp.*
Order Cimolesta	Plagiomenidae, n. gen. 1*
Family Pantolestidae	Plagiomenidae, n. gen. 2*
<i>Palaeosinopa nunavutensis</i>	Plagiomenidae, n. gen. 3*
<i>Palaeosinopa</i> cf. <i>P. nunavutensis</i>	Order Procreodi
Pantolestidae, gen. et. sp. indet.	Family Arctocyoniidae
Family Stylinodontidae	<i>Anacodon</i> sp.
Genus and species unidentified	Order Perissodactyla
(Bridgerian)	Family Isectolophidae
Order Pantodontia	<i>Homogalax</i> sp.
Family Coryphodontidae	Ceratomorpha
<i>Coryphodon</i> n. sp.*	<i>Heptodon</i> sp.
?Order Pholidota	Superfamily Tapiroidea
Suborder Palaeanodonta	<i>Thuliadanta mayri</i>
<i>Arcticanodon dawsonae</i>	<i>Thuliadanta</i> n. spp.*
Order Creodontia	Tapiroidea, n. gen.*
Family Oxyaenidae	Family Brontotheriidae
<i>Palaeonictis</i> sp.	cf. <i>Eotitanops</i>
Family Hyaenodontidae	cf. <i>Palaeosyops</i> (Bridgerian)
<i>Prolimnocyon</i> sp.	Order Cete
	Family Mesonychidae
	<i>Pachyaena</i> sp.

Note: All taxa occur in early Eocene (Wasatchian) strata unless otherwise noted.
 *Indicates taxa that are currently being described. List compiled from: Dawson (2001); Dawson et al. (1993); Eberle (2005, 2006); Eberle and McKenna (2002, 2007); Eberle and Storer (1999); McKenna (1980); and Rose et al. (2004).

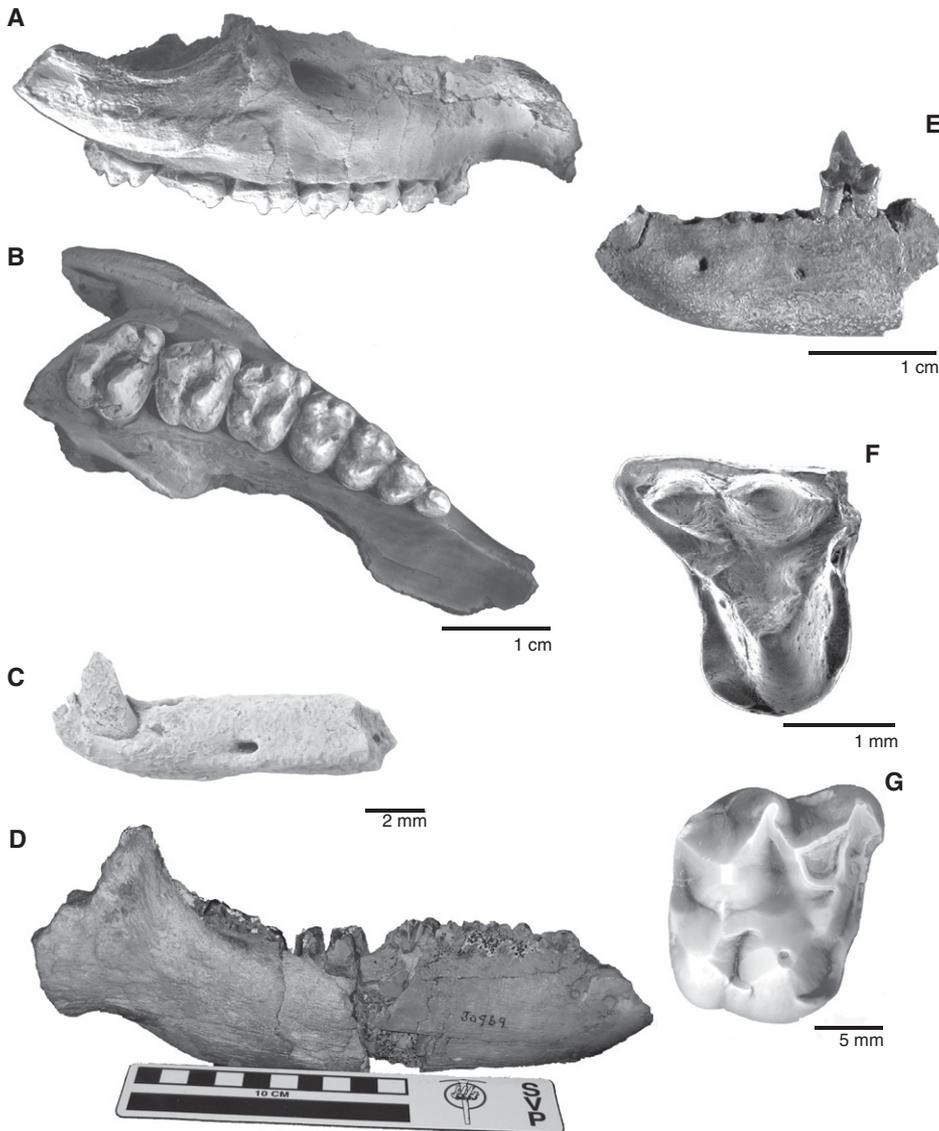


Figure 4. Representative mammalian fossils from early Eocene (late Wasatchian) localities at Bay Fiord, central Ellesmere Island, Nunavut. (A, B) Lateral and occlusal views of CMN 30804, holotype of the Arctic tapir *Thuliadanta mayri* Eberle, 2005; (C) lateral view of NUFV 10, holotype of the palaeonodont *Articanodon dawsonae* Rose et al. (2004); (D) lateral view of CMN 30969, right dentary of *Coryphodon* n. sp. (image courtesy of M. Dawson); (E) lateral view of CMN 30987, incomplete left dentary of the squirrel-sized carnivoran cf. *Vulpavus*; (F) occlusal view of CMN 32395, right P4 of the leptictid *Prodiacodon* sp.; and (G) occlusal view of CMN 32279, right M1 of the brontothere cf. *Eotitanops* described by Eberle (2006). Fossils are stored in the paleontology collection at the Canadian Museum of Nature (CMN) in Ottawa, Canada.

earliest, most primitive brontotheriid *Eotitanops borealis* (a sheep-sized, hornless form) defines onset of the Bridgerian NALMA (Gunnell et al., 2009; but see Smith and Holroyd, 2003). In the Arctic, however, a brontothere identified as cf. *Eotitanops* (but which may represent a new genus; Muhlbachler, 2010, personal commun.) is known from several late Wasatchian localities on Ellesmere Island (Eberle, 2006). Its early ap-

pearance in the Arctic is consistent with either an Asian origin for brontotheres as suggested by some (Beard, 1998), or a North American origin as recently suggested by Muhlbachler (2008). In midlatitude North America, the small dog-sized horse *Eohippus* and the rat-sized hyopsodontid *Hyopsodus* are the most abundant faunal elements in most late Wasatchian faunal assemblages, where *Hyopsodus* may account for up to

50% of the mammalian fossils from individual localities (Bown et al., 1994); neither genus is known from the Eocene Arctic. The absence of early horses in the Eocene Arctic is particularly puzzling because they are known from the early Eocene of both North America and Europe and are hypothesized to have dispersed across a North Atlantic land bridge (Hooker, 2005). Also absent from the Eocene Arctic are artiodactyls (even-toed or cloven-hoofed ungulates), yet this clade shows modest diversity and abundance at early Eocene midlatitude localities and is a probable immigrant from Asia (Theodor et al., 2005) that presumably would have dispersed across Beringia. In today's Arctic, artiodactyls are the only ungulates.

There are multiple explanations for the absence in the Eocene Arctic of artiodactyls, horses, and *Hyopsodus*, not the least of which is sampling bias. Despite over three decades of collecting vertebrate fossils in the Canadian Arctic, the number of mammalian fossils that are identifiable to genus is quite small ($N \sim 230$), and the most productive Eocene Arctic site—locality 85 on central Ellesmere Island—has produced only roughly 80 diagnostic mammalian specimens. In contrast, in midlatitude basins such as the Wind River Basin, where field collecting efforts date back to the late 1800s, late Wasatchian collections contain thousands of specimens (L. Ivy, 2011, personal commun.), while individual localities contain hundreds of specimens (Stucky, 1984). Consequently, the absence of *Hyopsodus*, early horses, and artiodactyls in the early Eocene Arctic could be a function of small sample size and perhaps limitations on the kinds of collecting techniques. For Arctic localities, the majority of vertebrate fossils were surface-collected, as the permafrost precluded any quarrying at depth. However, it should be noted that tiny mammal fossils (e.g., rodent and insectivoran teeth) have been recovered from Arctic localities; consequently, if *Hyopsodus*, early horses, and artiodactyls were of high abundance in the Eocene Arctic (as in midlatitude localities), we would expect to find some evidence for them on Ellesmere Island. Further, the sampling bias cannot explain the unusual diversity of plagiomenids and tapiroids, nor the early appearance of brontotheres, in the Eocene Arctic. We suggest that the unusual character of the early Eocene Arctic fauna is more likely the result of its unique environment and/or geography, although sampling bias probably also plays a role.

Stratigraphically above the lower Eocene localities on central Ellesmere Island, early middle Eocene (Bridgerian-aged) localities in the Margaret Formation have produced only two mammalian taxa thus far—a brontothere

that is larger than the Wasatchian brontothere and a tooth fragment questionably identified as belonging to a taeniodont (a rare, enigmatic order of eutherian mammal having midlatitude representatives that are interpreted as rooters and grubbers; Schoch, 1986). In younger, stratigraphically higher strata on eastern Axel Heiberg Island, tooth fragments of an even larger brontothere were recovered from the middle Eocene Buchanan Lake Formation that preserves the Geodetic Hills Fossil Forest; these fossils represent the northernmost known record of Paleogene mammals, and they are the only documented vertebrate fossils from the Geodetic Hills Fossil Forest (Eberle and Storer, 1999). Although the tooth fragments probably represent a new genus of diplacodont brontothere, their size and morphology are comparable to middle Eocene (Uintan or perhaps Duchesnean NALMA), midlatitude North American brontothers.

Nonmammalian Vertebrate Fauna from the Eocene Arctic

The early Eocene nonmammalian vertebrate fauna is based primarily on dissociated and fragmentary fossils from Ellesmere Island (Table 3). Although this fauna is not yet formally described, short preliminary descriptions of some members of the Arctic lower vertebrate fauna were given by Estes and Hutchison (1980), and a more detailed description is in progress (Hutchison, 2011, personal commun.). Therefore, only brief notes for each major clade are given here. According to Estes and Hutchison (1980), the closest ecologic analog to the Eocene Arctic nonmammalian vertebrate assemblage is the vertebrate community that inhabits today's Austroriparian zone (the conifer forests in the southeastern United States).

Fish fossils representing three families—the Amiidae (bowfins), Lepisosteidae (gars), and Esocidae (pike)—are documented from early Eocene nonmarine sediments on Ellesmere Island (Estes and Hutchison, 1980). In the underlying Mount Moore Formation, fish otoliths were described as the first evidence of marine sediments in the Eureka Sound Group (West et al., 1975), but they are rare and will not be discussed here. Of the three nonmarine families, the bowfins are the best represented in the Eocene Arctic, and analyses of their vertebrae by M. Newbrey (University of Alberta) indicate that like their living relatives, the Eocene Arctic bowfins grew year-round, although more bone was deposited during the summer months (Eberle et al., 2010). In addition to fishes, a single amphibian genus—the giant salamander *Piceoerpeton* (up to 100 cm long)—is known from bones and bone fragments from Elles-

TABLE 3. NONMAMMALIAN, NONMARINE VERTEBRATE TAXA FROM THE MARGARET FORMATION, EUREKA SOUND GROUP (COURTESY OF J.H. HUTCHISON, MAY 2011)

Class Osteichthyes	Class Reptilia (<i>continued</i>)
Order Lepisosteiformes	Order Testudines (<i>continued</i>)
Family Lepisosteidae (gars)	Family Testudinidae
cf. <i>Lepisosteus</i> sp.	<i>Hadrianus</i> sp.
Order Amiiformes	Family Kinosternidae
Family Amiidae (bowfins)	Kinosternidae genus indet.
<i>Cyclurus fragosa</i>	Family Carettochelyidae
<i>Amia</i> cf. <i>A. pattersoni</i>	Anosterinae genus indet.
Order Esociformes	(Bridgerian)
Family Esocidae (pikes)	Family Trionychidae
cf. <i>Esox</i>	<i>Apalone</i> sp.
Class Amphibia	Order Crocodylia
Order Urodela	Family Alligatoridae
Family Scapherpetontidae	<i>Allognathosuchus</i> sp.
<i>Piceoerpeton</i> cf. <i>P. willwoodense</i>	Order Squamata
Class Reptilia	Family Anguidae
Order Testudines	Glyptosaurinae indet.
Family Baenidae	Anguidae indet.
<i>Baena</i> cf. <i>B. arenosa</i>	Family Varanidae
Family "Macrobaenidae"	Varanidae indet.
cf. Macrobaenidae gen. indet.	Family Boidae
Family Chelydridae	Erycinae indet.
<i>Protochelydra</i> sp.	Class Aves
Family Platysternidae	Order Gastornithiformes
Platysternidae, n. gen.	Family Gastornithidae
Family Bataguridae	<i>Gastornis</i> sp.
<i>Echmatemys</i> cf. <i>E. testudinea</i>	Order Anseriformes
Family Emydidae	Family Presbyornithidae
Emydidae, n. gen.	<i>Presbyornis</i> sp.
Genus indet. (Bridgerian)	

Note: All occur in early Eocene (Wasatchian) strata unless otherwise noted. The fishes *Amia* and *Esox*, as well as the trionychid, "macrobaenid," chelydrid, and emydid turtles, the alligatorid *Allognathosuchus*, and the shorebird *Presbyornis* range into the early middle Eocene (Bridgerian North American Land Mammal Age).

mere Island (Estes and Hutchison, 1980). The genus also occurs in midlatitude North America, where body fossils are known from upper Paleocene strata of the Western Interior (Naylor and Krause, 1981), and where tracks of a *Piceoerpeton*-sized salamander occur in lower Eocene lacustrine deposits in Wyoming (Foster, 2001).

The most famous of the nonmammalian vertebrate fossils from the Eocene Arctic, the Paleogene alligator *Allognathosuchus*, is relatively abundant at Arctic localities, known from dozens of teeth and osteoscutes as well as jaws and an incomplete skull from Ellesmere Island. *Allognathosuchus* was a small-bodied alligator (the Arctic skull was estimated to have been no more than 15 cm long; Estes and Hutchison, 1980) that was also abundant in midlatitude faunas. Alligator fossils have long been used as paleoclimate proxies based upon the assumption that fossil taxa occupied essentially the same climatic window as their extant relatives (Markwick, 1994). Recent oxygen isotope-based paleotemperature estimates for the early Eocene Arctic suggest that *Allognathosuchus* had a somewhat greater climatic window than that implied by today's distribution of crocodylians, although their occurrence in the fossil record is a reliable proxy for above-freezing tempera-

tures (Eberle et al., 2010). Incidentally, observational and experimental data from zoo animals indicate that alligators are hardier than other crocodylians and can survive short intervals of subfreezing temperatures by submerging themselves in water. Access to water is the most important element of an alligator's habitat, acting as a buffer to cooler air temperatures (Asa et al., 1998). Abundance of alligator fossils at Eocene localities on Ellesmere Island, in the absence of other crocodylian taxa (which are known from early Eocene midlatitude localities), implies that ancient populations of alligators probably were hardier and inhabited seasonally cooler environments than other crocodylians. Its small body size also probably afforded Eocene Arctic *Allognathosuchus* more opportunities for protection from winter exposure than its larger-bodied, midlatitude relatives.

Nine families of turtle, ranging from giant land tortoises (*Hadrianus*) to soft-shelled turtles (Trionychidae) to pond turtles (Emydidae, the most common turtle fossils on Ellesmere Island) are represented by bones, nearly complete shells, shell casts in ironstone concretions, and shell fragments in lower Eocene strata on Ellesmere Island (Estes and Hutchison, 1980; Table 3). Most of the Eocene Arctic turtles are aquatic, and their living representatives survive

cool (even freezing) winter temperatures by submerging themselves in water or burrowing. The exception is the large land tortoise *Hadrianus*, whose living relatives inhabit areas such as the Galápagos Islands, where winter temperatures are generally above 10 °C (Hutchison, 1982). With an estimated shell length of up to 64 cm, Eocene Arctic *Hadrianus* was probably too large to burrow (Estes and Hutchison, 1980), although it probably could avoid exposure during cold spells by pulling its arms and legs into its shell and pushing under the leaf litter, a behavior known to occur in extant tortoises (Ernst and Barbour, 1989). Given that their late Pleistocene range extended northward into Pennsylvania and Illinois (Holman, 1995), the giant tortoises' current distribution probably does not represent their fullest geographic range allowed by climate.

Two families of lizard as well as a boid snake are known from the early Eocene fossil record on Ellesmere Island (Estes and Hutchison, 1980). Anguid lizards are an entirely Northern Hemisphere family that includes today's alligator lizards, while varanid lizards are primarily top predators that include the monitor lizards. During the Paleogene, varanids inhabited both North America and Europe, but extant varanid lizards are Old World, inhabiting Africa, Asia, Southeast Asia, and Australia (Pianka and King, 2004). The presence of a varanid on Ellesmere Island was considered among the best proxies for a warm, equable climate during early Eocene time (Estes and Hutchison, 1980). However, it should also be noted that among extant species, the northernmost *Varanus griseus* has a distribution that extends as far north as 46°N in Asia, and it hibernates underground during the winter months (Stanner, 2004). So, despite cooler (near freezing) winter temperatures in the Eocene Arctic (discussed later herein), hibernation could allow a varanid lizard to escape exposure during an Arctic winter.

Bird fossils are rare in the Eocene Arctic, with just two genera—the giant, flightless bird *Gastornis* (= *Diatryma*) and the aquatic bird *Presbyornis* (a shorebird and close relative to extant ducks; Ericson, 1997)—known from fossils from Ellesmere Island. Both *Gastornis* and *Presbyornis* are known from midlatitude, Paleocene–Eocene strata (Carroll, 1987).

Several of the nonmammalian vertebrate taxa—including the fishes *Amia* and *Esox*, trionychid, macrobaenid, chelydrid, and emydid turtles, the alligatorid *Allognathosuchus*, and the shorebird *Presbyornis*—extend into middle Eocene (Bridgerian) parts of the Margaret Formation at Bay Fiord. The unique occurrence in these strata of an anosteirine turtle supports a middle Eocene age, as this clade of turtles does

not appear in North America until the Bridgerian NALMA (Estes and Hutchison, 1980).

Although not as explored for fossil vertebrates as the eastern Arctic, Paleogene sediments of the Cyclic Member of the Eureka Sound Formation on northern Banks Island have produced thousands of sharks' teeth representing three genera—the sand tigers *Striatolamia* and *Carcharias* and an extinct sharpnose shark *Physogaleus*—in addition to rare fossils of bony fishes and a warm-water ray (Padilla, 2008). Additionally, the first fossils of Paleogene terrestrial vertebrates—rare shell fragments of a pond turtle (Emydidae)—were found on northern Banks Island in 2004, implying a probable early Eocene age (Hutchison, 2010, personal commun.), which is consistent with the palynology (Miall, 1979) and the occurrence of the shark genus *Physogaleus* (limited elsewhere to the Eocene; Padilla, 2008).

EOCENE FLORAS OF THE ARCTIC

The floristic composition of the Canadian Eocene Arctic macrofloras is fairly consistent within particular lithologies (e.g., swamp forest-floor or “litter” facies and channel sands versus overbank mudstones in the Buchanan Lake Formation sites; Table 1), as the different facies sample different parts of the landscape via taphonomic sorting (Greenwood and Basinger, 1993, 1994; Basinger et al., 1994; McIver and Basinger, 1999; Greenwood et al., 2010). Particular genera of conifers and angiosperms are commonly present in most Eocene sites (e.g., *Metasequoia*, *Betula*, and *Ulmus*/Ulmaceae); however, the actual list of taxa for each site may be quite different, reflecting either floral evolution over time in response to climate change during the early to middle Eocene (e.g., hyperthermals), or locations where in the landscape is being sampled (Fig. 5). The early Eocene localities are mostly found on Ellesmere Island (e.g., Hot Weather Creek, Split Lake, and Stenkul Fiord; Figs. 1 and 2) and typically include taxa found in common with the middle Eocene sites (e.g., *Ginkgo*, *Metasequoia*, *Juglans*, *Nordenskiöldia borealis*, and *Trochodendroides*; Fig. 5). However, there is a small suite of taxa that is restricted to Lower Eocene strata (e.g., *Azolla*, *Thuja polaris*, *Comptonia*, and *Quereuxia*; the latter listed as *Trapago* in McIver and Basinger, 1999, but synonymized as *Quereuxia* by Hickey, 2001). Hot Weather Creek (Iceberg Bay Formation) and Split Lake and Stenkul Fiord (both Margaret Formation) (Figs. 1, 2, and 6) have macrofloras typical for the early Eocene sites, including between them: *Equisetum*, the fern *Osmunda*, *Metasequoia*, *Archeampelos*, *N. borealis*, *Nyssidium*

arcticum, *Trochodendroides*, *Ulmus*, *Ushia* (cf. Fagaceae), and *Juglans* (listed as *Carya* in McIver and Basinger, 1999), as well as leaves comparable to *Grewia*, cf. *Nelumbo*, cf. *Rhus*, cf. *Smilax*, cf. *Trema*, and cf. *Tilia* (McIver and Basinger, 1999). Macrofloras in the Coal Member (Iceberg Bay Formation) are known from Strand Fiord on Axel Heiberg Island and near Lake Hazen on northern Ellesmere Island, and they contain many of the previously listed taxa, but also *Ginkgo*, *Glyptostrobus*, *Comptonia*, and cf. *Viburnum* (Fig. 5).

The middle Eocene mudstone localities (e.g., US 188 at Geodetic Hills) are dominated by broadleaf taxa (e.g., *Ginkgo*, *Archeampelos acerifolia*, Betulaceae [*Alnus* and *Betula*], Cercidiphyllaceae, *Quercus*, Menispermaceae, Platanaceae, and Ulmaceae), and they contain various pteridophytes such as *Equisetum*, *Onoclea*, and *Osmunda*, as well as the conifers *Glyptostrobus* and *Metasequoia* (Basinger et al., 1994; Greenwood and Basinger, 1994; McIver and Basinger, 1999; Greenwood et al., 2010). The macrofloral assemblages in the channel sands are not diverse and include various seeds (e.g., Juglandaceae, cf. *Juglans* listed as *Carya* in McIver and Basinger, 1999) and Pinaceae (e.g., *Larix altoborealis*, *Picea sverdrupii*, and *Picea nansonii*, *Pinus* spp.) and *Metasequoia* seed cones and foliage (including rare dicot leaves), whereas the litter layers of the middle Eocene fossil forests are species rich but dominated by foliage, wood, and cones of *Metasequoia* and *Glyptostrobus*, with locally important contributions by *Chamaecyparis eureka*, *Pseudolarix* (mostly *Pseudolarix amabilis* but rarely *Pseudolarix wehrii*) and other Pinaceae (e.g., cf. *Keteleeria*, *Picea palustris*, *P. sverdrupii*, *P. nansonii*, *Pinus*, and *Tsuga swedaeae*), and rarely so by dicots such as *Alnus* or *Betula* as well as ferns (Greenwood and Basinger, 1993, 1994; LePage and Basinger, 1991, 1995; McIver and Basinger, 1999; LePage, 2001; Kotyk et al., 2003; Table 3). In addition, the conifers *Sequoia* and *Taiwania* are recorded from the forest-floor litters. Identification of the conifers is based primarily on seed cones, or rarely from isolated seeds or diagnostic foliage (McIver and Basinger, 1999; LePage, 2003). No taxa are restricted to the sandstone facies, so this assemblage is likely a taphonomically sorted subset of the forest-floor litter facies (Table 3).

Palynofloras from Axel Heiberg and Ellesmere Islands indicate the presence of vegetation in these areas that was floristically quite consistent among sites, and of quite low species number (McIntyre, 1991; McIver and Basinger, 1999; Kalkreuth et al., 1993). Pinaceae, Cupressaceae (*Glyptostrobus*, *Metasequoia*, and *Sequoia*), and Betulaceae (*Alnus* and *Betula*) appear to have

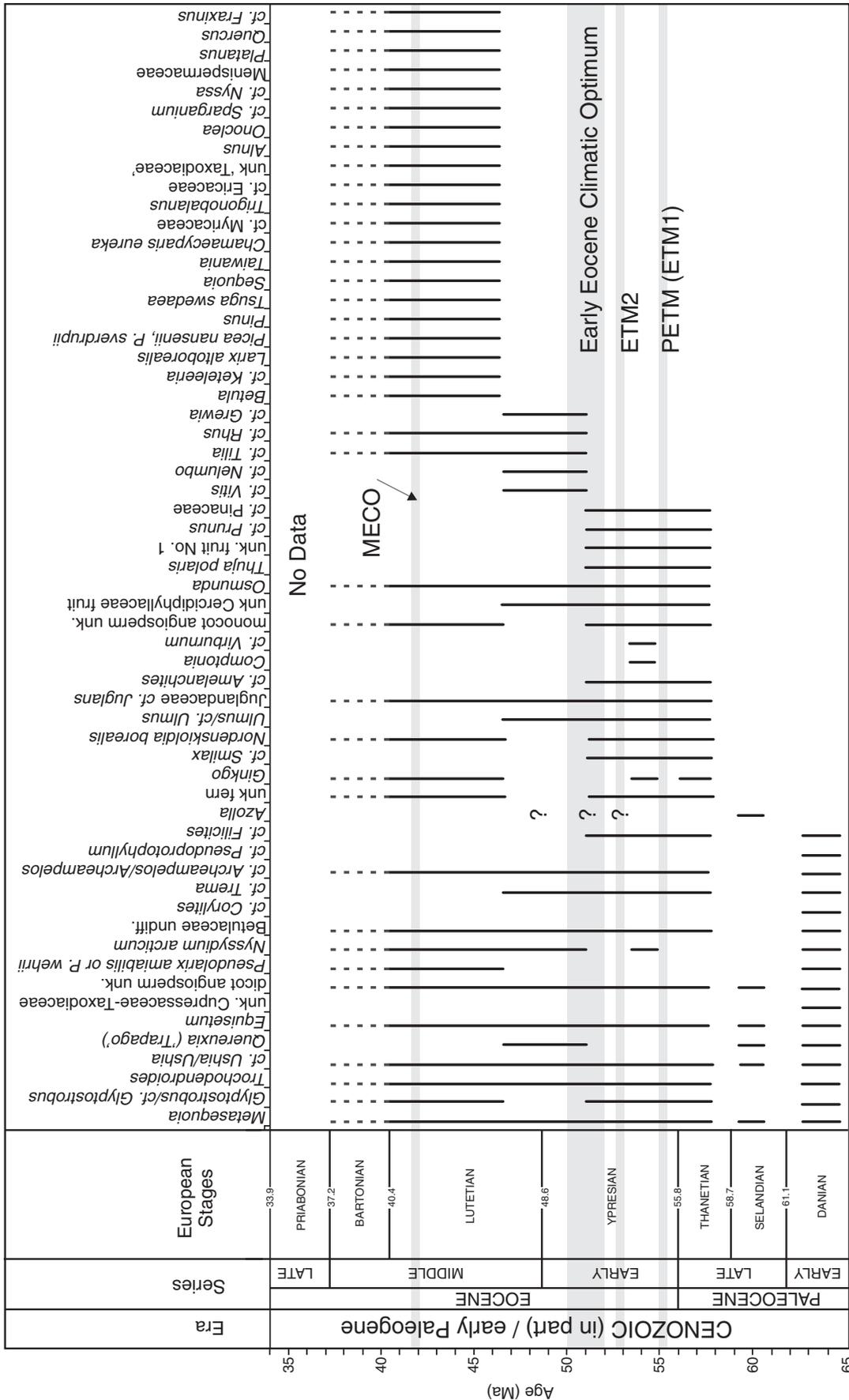


Figure 5. Chart showing the stratigraphic range of plant genera across the Paleocene to Eocene localities listed in McIver and Basinger (1999), including recent nomenclatural updates. Eocene hyperthermals—Paleocene-Eocene thermal maximum (PETM), Eocene thermal maximum 2 (ETM2), and middle Eocene climatic optimum (MECO).

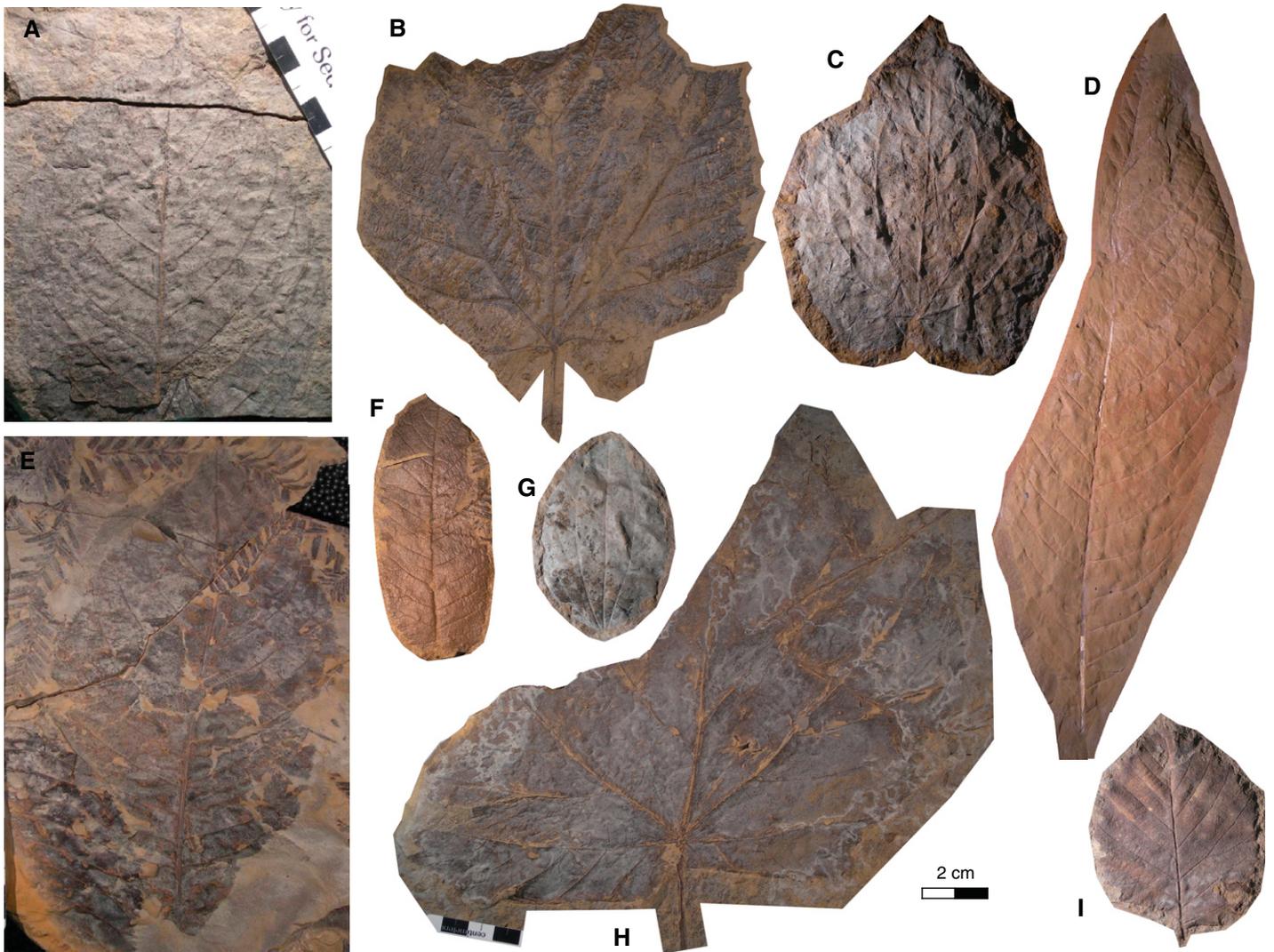


Figure 6. Representative leaf fossils from Strathcona Fiord (A, C–E, H), Stenkul Fiord (B, F), and Split Lake (I), all from the Margaret Formation. Leaf fossils A–E and H display the large size (length >10 cm) typical of these Arctic floras (Greenwood et al., 2010). Leaf fossils B and H are *Platanites* (Platanaceae); leaf fossil C is comparable to extant *Tilia* (Tiliaceae); and *Metasequoia* shoots are visible on the edges of the block with specimen E and lying across leaf fossil F. All specimens shown are from the University of Saskatchewan paleontology collection of J.F. Basinger. Photos are by Greenwood.

figured prominently in the regional vegetation (McIntyre, 1991), consistent with macrofloral evidence (McIver and Basinger, 1999). Similar patterns have been observed for Eocene microfloras from both Axel Heiberg and Ellesmere Islands, although overall diversity is higher than for Paleocene floras (Harrington, 2004; Richter and LePage, 2005). The microfloras in coals from the Margaret Formation (= Iceberg Bay Formation) in the Strathcona Fiord area (Figs. 1 and 2) include pollen representing extant genera recognized in the macroflora, viz. *Picea*, *Pinus*, *Metasequoia*, *Glyptostrobus*, cf. *Sequoia*, *Cercidiphyllum*, *Ulmus*, *Carya*, *Quercus*, *Alnus*, *Betula*, *Tilia*, *Nyssa*, *Fraxinus*, and *Viburnum*, as well as taxa not yet recognized in the macro-

floras, such as *Taxodium*, *Acer*, *Corylus*, *Liquidambar*, and *Pterocarya* (Kalkreuth et al., 1993; McIver and Basinger, 1999). Presence of taxa such as *Quercus*, *Tilia*, *Fraxinus*, and *Viburnum* in the Strathcona Fiord coals is consistent with an early Eocene age. Marine sediments from the Lomonosov Ridge record terrestrial vegetation on the Arctic Ocean margins at 50 Ma (Barke et al., 2011). Barke et al. (2011) recorded microfloras rich in angiosperm pollen, mainly *Carya*, Fagaceae, *Liquidambar*, and *Ulmus*, but also including *Alnus* and abundant gymnosperm pollen, such as *Larix*, *Picea*, *Pinus*, and Cupressaceae (e.g., *Metasequoia* and/or *Glyptostrobus*), matching comparable-aged micro- and macrofloras from the Arctic Archipelago. McIver and

Basinger (1999) noted comparable suites of taxa and diversity within families between the macroflora and microflora from sediments of the middle Eocene Buchanan Lake Formation.

EOCENE ARCTIC PALEOENVIRONMENT

Eocene Arctic Paleoclimates

Table 4 provides a summary of early and middle Eocene paleotemperature estimates using a variety of proxies, ranging from oxygen isotope analyses ($\delta^{18}\text{O}$) of biogenic apatite in vertebrate bones and teeth (specifically, mammal, turtle, and fish fossils; Eberle et al., 2010) to the

TABLE 4. EOCENE HIGH ARCTIC CONTINENTAL TEMPERATURE ESTIMATES

Location	Paleolat.	Age	MAT	MART	WMMT	CMMT	Proxy
Ellesmere Island (Bay Fiord)	~76°N	Lower Eocene	8 °C	16.5–19 °C	19–20 °C	0–3.5 °C	Oxygen isotope analyses of vertebrate fossils*
Lomonosov Ridge	~75°N	Lower Eocene	18–20 °C	—	—	—	Bacterial membrane lipids†
Ellesmere and Axel Heiberg Island	76–77°N	Upper Paleocene–Middle Eocene	12–15 °C	20–25 °C	>25 °C	0–4 °C	Paleofloral analyses NLR§
Ellesmere Island	~76°N	Lower Eocene	8.2 °C	14 °C	—	–2 °C	Paleofloral analyses MR†
Axel Heiberg Island (US Site 188)	~77°N	Middle Eocene	9.3 °C	—	—	–1 °C	Paleofloral analyses MR§
Axel Heiberg Island (US Site 188)	~77°N	Middle Eocene	14.7 °C	—	—	3.7 °C	Paleofloral analyses NLR**
Axel Heiberg Island (US Site 188)	~77°N	Middle Eocene	12.8 °C	—	—	—	Paleofloral analyses LMA**
Axel Heiberg Island	~77°N	Middle Eocene	13.2 °C	—	—	—	Isotopic equilibrium between carbonate and environ. water††
Norwegian–Greenland Sea	~75°N	Middle Eocene	14 °C	—	18–24 °C	>5 °C	Palynology NLR§§

Notes: MAT—mean annual temperature; CMMT—cold month mean temperature; WMMT—warm month mean temperature; MART—mean annual range of temperature; MR—multiple regression leaf physiognomic analyses; LMA—leaf-margin analysis; and NLR—nearest living relatives method (see Basinger et al., 1994; Greenwood, 2005; Greenwood et al., 2010). MAT estimated from soil-derived bacterial membrane lipids has standard error of approximately ±5 °C (Weijers et al., 2007); MAT estimated from spore and pollen assemblages has an error of ±3 °C; climate parameters estimated from paleofloral analyses, and specifically multiple regression (MR) models of physiognomic characters in paleoflora, have standard errors of: MAT ±0.7–2.0 °C; CMMT ±3.6 °C; and MART ±5.1 °C (Basinger et al., 1994; Greenwood and Wing, 1995; Greenwood et al., 2010); MAT estimated from leaf-margin analysis has an error of ±4.3 °C (Greenwood et al., 2010); MAT estimated from isotopic equilibrium between carbonate and environmental water has an error of ±2.0 °C (Jahren and Sternberg, 2003); and MAT and CMMT estimated from δ¹⁸O_{carb} values determined from δ¹⁸O analyses of mammalian fossils incorporated into a physiological model have a range of uncertainty of approximately ±7 °C. Turtle-derived WMMT has an estimated error of ±2.5 °C (Eberle et al., 2010; see discussion).

*Eberle et al. (2010).
 †Weijers et al. (2007).
 ‡Basinger et al. (1994).
 §Greenwood and Wing (1995).
 **Greenwood et al. (2010).
 ††Jahren and Sternberg (2003).
 §§Eldrett et al. (2009).

distribution of soil-derived bacterial membrane lipids (Weijers et al., 2007), to paleofloral analyses that include nearest living relative (NLR) methods (Basinger, 1991; Greenwood et al., 2010) and leaf physiognomic analyses (Basinger et al., 1994; Greenwood and Wing, 1995; Greenwood et al., 2010). In terms of timing, the early Eocene vertebrate and paleofloral assemblages from the Canadian Arctic appear to post-date the Paleocene-Eocene thermal maximum. The early Eocene Arctic vertebrate assemblage most closely correlates with late Wasatchian (ca. 52–53 Ma) midlatitude North American faunas, whereas the Paleocene-Eocene thermal maximum (ca. 55 Ma) is defined by a dramatic negative carbon isotope excursion (CIE) at the transition between the Clarkforkian and Wasatchian land mammal ages (Gingerich, 2003). Arctic paleotemperature at the Paleocene-Eocene thermal maximum is recorded from a single locality—a marine sediment core from the Lomonosov Ridge in the central Arctic Ocean—where a sea-surface temperature (SST) exceeding 23 °C was estimated from the distribution of isoprenoid tetraether lipids in the abundant marine prokaryotes Crenarchaeota, although this SST probably exhibits a summer season bias (TEX₈₆ proxy; Sluijs et al., 2006, 2009).

With regard to the early Eocene Arctic, oxygen isotope analyses of co-occurring vertebrates and paleofloral analyses produce broadly similar paleotemperature estimates that overlap when standard errors associated with the proxies are taken into consideration (see Table 4 note). All proxies converge on a mild, temperate early Eocene Arctic where winter temperatures remained at or just above freezing and summer temperatures extended to 20 °C or even higher. The early Eocene temperatures are a far cry from today's High Arctic, where Eureka on central Ellesmere Island experiences mean annual temperature (MAT) of –19 °C, a warm month mean temperature (WMMT) of –6 °C, and cold month mean temperature (CMMT) of –38 °C or colder (Environment Canada, 2004). The anomalously high MAT (18–20 °C) estimated from early Eocene soil-derived bacterial membrane lipids from the Lomonosov Ridge in the central Arctic Ocean probably reflects a summer season bias (Weijers et al., 2007; Eberle et al., 2010). The early Eocene Arctic temperature estimates have proven to be problematic for climate modelers, whose early Eocene general circulation models predicted temperatures that are 10–20 °C colder than those estimated from the early Eocene Arctic proxies (Shellito et al., 2003). Although more recent models that quadruple greenhouse gases (Shellito et al., 2009; Huber and Caballero, 2011) are beginning to narrow the gap, they may still be missing

fundamental mechanisms for heat transport (Shellito et al., 2003).

The early Eocene temperature estimates imply that Eocene Arctic alligators and giant tortoises had somewhat greater climatic tolerances than is suggested by their present-day distribution (Markwick [1994] for alligators; Hutchison [1982] for giant tortoises), although the basic assumption that alligators and large land tortoises correlate with above-freezing, year-round temperatures holds true. Along similar lines, extant members of the plant genera *Metasequoia*, *Ginkgo*, *Cercidiphyllum*, and *Glyptostrobus* are restricted to subtropical–warm temperate areas of Asia. However, it has been argued that Paleogene members of these monotypic genera likely occupied a wider ecological range than their modern counterparts, including wider thermal tolerances (e.g., Wolfe, 1985; Basinger et al., 1994). Nevertheless, the common modern preference of these genera and other “Taxodiaceae” for areas of moderate frost/winter freezing (CMMT >0 °C) or mostly frost-free areas today (CMMT >5 °C) has been presented as evidence that Paleogene species had similar limitations (Schweitzer, 1980; Hickey et al., 1988). A better approach is to consider the climatic limits of the whole assemblage of taxa (e.g., Hickey et al., 1988; Basinger et al., 1994; Eldrett et al., 2009; Greenwood et al., 2010).

Middle Eocene Arctic temperature estimates are based on paleofloral analyses (Basinger et al., 1994; Greenwood et al., 2010) as well as carbonate analyses from the Geodetic Hills locality on eastern Axel Heiberg Island (Jahren and Sternberg, 2003), and they are comparable to the early Eocene Arctic paleotemperature estimates. Again, when standard errors are considered (see Table 4 note), there is overlap in the early and middle Eocene temperature estimates. Small discrepancies may reflect the different methodologies used, as well as changes in climate over time. The middle Eocene localities at Geodetic Hills on Axel Heiberg Island (ca. 41–46 Ma) are several million years younger than the early Eocene localities on central Ellesmere Island, as are the middle Eocene pollen and spore assemblages from Greenland (ca. 49 Ma; Eldrett et al., 2009).

Using a whole-assemblage approach using the modern relatives of the bulk of the macroflora from middle Eocene sites on Axel Heiberg Island and microfloras from adjoining Greenland, mean annual precipitation was estimated at >120 cm/yr (Eldrett et al., 2009; Greenwood et al., 2010). From leaf area analysis—a leaf physiognomic approach—of leaf floras from High Arctic late Paleocene to middle Eocene shales, mean annual precipitation for Hot Weather Creek and US 111 (Fosheim anticline west/Lower Member,

Iceberg Bay Formation) on Ellesmere Island and a site near the Geodetic Hills on Axel Heiberg Island was estimated in the range of 133–153 cm/yr (errors in the range ±40–66 cm), implying the presence of an Arctic Eocene coastal rain forest (Greenwood et al., 2010). Leaf floras from Stenkul Fiord and Split Lake are also dominated by large leaves (Fig. 5), consistent with high precipitation. The paleofloral-based precipitation estimates are consistent with isotopic values for relative humidity of ~67% (with a summer peak of 90%–100%) derived from cellulose from the middle Eocene woods at Geodetic Hills Fossil Forest (Jahren and Sternberg, 2003, 2008), but they are considerably wetter than climate modeling estimates predict for the region in the Eocene (Shellito et al., 2009). Paleobotanical proxy estimates from Greenland and Spitsbergen (Eldrett et al., 2009; Uhl et al., 2007) indicate that high precipitation extended beyond the region of Axel Heiberg and Ellesmere Islands during the Eocene.

Overlapping $\delta^{18}\text{O}$ values among Arctic *Coryphodon* and perissodactyls also suggest a humid early Eocene High Arctic, consistent with sedimentology (e.g., abundant coal seams and absence of red beds; Miall, 1986) and the floral analyses noted already. Humidity controls the degree to which leaves are enriched in ^{18}O over surface water, due to preferential evaporation of ^{16}O . In dry climates, $\delta^{18}\text{O}$ of vegetation is higher and more variable, and because different browsers consume different plant species, there is less likelihood of overlap in their $\delta^{18}\text{O}$ values (Eberle et al., 2009).

Eocene Arctic Paleobiology and Ecosystems

Traditionally, the paleobiology and paleoecology of the Eocene Arctic mammals have been inferred by comparison with nearest living relatives (NLR) and presumed ecologic analogs. For example, by analogy with living mountain tapirs that are active during daylight and nocturnal hours (Downer, 1991), the Eocene Arctic tapir *Thuliadanta* seems quite well suited to an environment that experienced extensive periods of sunlight and darkness (Eberle, 2005). However, NLR-based inferences are not without critique (especially when it comes to extinct organisms with no living descendants), and the assumption that fossil organisms had the same paleobiology as their living descendants is challenging to prove. More recently, research tools such as stable isotope analyses have been adopted by paleontologists and are being used in tandem with NLR-based inferences to provide a more comprehensive reconstruction of the lifestyle of extinct species (e.g., Thewissen et al., 2007). With regard to the Eocene Arctic, among

the more compelling questions concerning their ecology and behavior is whether the large herbivores such as *Coryphodon* lived year-round in the Arctic. Today’s most abundant large mammals in the Arctic are caribou, who survive primarily by migrating south up to 1000 km to overwinter below the Arctic Circle, and this scenario was initially speculated for the large Eocene Arctic herbivores such as *Coryphodon* (Dawson, 1990). Alternatively, it has been postulated that Eocene brontotheres and tapirs were year-round residents above the Arctic Circle (Eberle and Storer, 1999; Eberle, 2005), primarily because the energy expenditures of migrating great distances over land would be too costly, an obstacle that precludes today’s High Arctic Peary’s caribou (*Rangifer tarandus pearyi*) from migrating south to subarctic forests (Pielou, 1994). As independent means to test this hypothesis, seasonal variations in the oxygen and carbon isotope compositions ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$, respectively) measured from the enamel of *Coryphodon* teeth suggest that these large herbivores were year-round residents in the Eocene Arctic (Eberle et al., 2009). Specifically, intratooth ranges in $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ are similar to those from trees that lived above the Arctic Circle during the Eocene (Jahren and Sternberg, 2008), and the seasonal range of $\delta^{18}\text{O}$ in Arctic *Coryphodon* is greater than would be expected if these large herbivores had migrated south (Eberle et al., 2009). The isotope data are bolstered by the paleontological data in that occurrence of baby and juvenile *Coryphodon* and tapiroids (as evidenced by jaws with partly and entirely deciduous dentitions) seems consistent with year-round residency.

If the large herbivores were year-round residents in the Eocene Arctic, the question that follows is: What did they eat? Studies of tooth morphology, NLR-based inferences, and carbon isotope analyses provide considerable insight into paleodiet. Its teeth suggest that *Coryphodon* was an herbivore, and its postcranial anatomy (known from complete skeletons at North American midlatitude localities) most closely resembles that of the living pygmy hippopotamus, *Hexaprotodon* (see Lucas, 1998), a forest dweller that spends its days in the water and nights on land (MacDonald, 1987). Refinement of *Coryphodon*’s niche and diet is inferred from stable isotope analyses. Specifically, lower $\delta^{13}\text{C}$ values in both midlatitude (Secord et al., 2008) and Arctic *Coryphodon* (Eberle et al., 2009), compared with other herbivores, when considered alongside lower variability in $\delta^{18}\text{O}$ than other taxa, probably reflect a semi-aquatic niche (Secord et al., 2008), consistent with its morphology. Further, seasonal variations in $\delta^{13}\text{C}$ measured from Arctic *Coryphodon* suggest a

summer diet similar to midlatitude *Coryphodon* composed mostly of angiosperm plants, although gymnosperms may have also been eaten by Arctic *Coryphodon*, as evidenced by slightly higher summer $\delta^{13}\text{C}$ values (Eberle et al., 2009). However, unusual winter $\delta^{13}\text{C}$ values indicate that Arctic *Coryphodon* had a different and varied diet during the dark winter months that included food items with high $\delta^{13}\text{C}$ values (consistent with wood and leaf litter, evergreen conifers, and fungi) as well as food items with anomalously low $\delta^{13}\text{C}$, which may suggest ingestion of phytoplankton and freshwater vascular plants (Eberle et al., 2009, and references therein). Anecdotally, the implication of a seasonal preference for angiosperm (and perhaps some deciduous conifer) versus evergreen gymnosperm foliage in *Coryphodon*'s diet supports a model where the dicot flora was predominantly deciduous, removing these plants as a winter food source.

Because *Coryphodon* is the most abundant large mammal in the Eocene Arctic fauna ($N \sim 75$), isotope analyses have necessarily focused on this genus. However, the diets of other large herbivores—in particular, the brontotheres and tapirs—have been interpreted through study of their tooth morphology and comparison with living perissodactyls. With regard to brontotheres, the distinct W-shaped arrangement of cusps and lophs (i.e., bumps and ridges) on their upper molars, combined with tooth microwear studies, suggests that they were browsers that fed on leaves and other fibrous woody material, somewhat akin to today's black rhinoceros (*Diceros bicornis*) and moose (*Alces alces*; Muhlbachler and Solounias, 2002). Similar to living tapirs, Eocene tapirs had low-crowned teeth with transverse lophs (or ridges), suggesting they were also browsers that could probably feed on a variety of food items, including trees, shrubs, branches, fruits, and seeds (Eberle, 2005; Colbert and Schoch, 1998). Based upon high-resolution X-ray computed tomography (C-T) scans of a juvenile skull of the Eocene Arctic tapir *Thuliadanta* (Colbert, 2010, personal commun.), the Arctic tapir had a short proboscis (or trunk), which, like modern tapirs, could be used for browsing selectively on leaves, sprouts, and aquatic plants (Janis, 1984), a plant community type that is well represented in the fossil macrofloras.

Given the presence of dense, swamp forests in the Eocene Arctic (e.g., Greenwood and Basinger, 1993, 1994; Williams et al., 2003; and discussed here), perhaps it is not too surprising that the Eocene Arctic vertebrate fauna included larger-bodied browsers (e.g., *Coryphodon*, tapirs, and brontotheres), semi-aquatic and aquatic vertebrates (e.g., *Coryphodon*, alli-

gators, fishes, a giant salamander, and several kinds of turtle), and several arboreal mammals (e.g., primates and small carnivorans). Morphologic comparison with Eocene midlatitude species and NLR-based inferences in progress by Eberle and colleagues should provide a more comprehensive picture of the paleobiology and ecologic niches occupied by the vertebrate inhabitants of the Eocene Arctic community.

Extensive, well-preserved Paleogene macrofloras from localities in Arctic Canada, as well as northern Europe and Asia, testify to the presence of extensive forests throughout the high paleolatitudes, including areas within the paleo-Arctic circle (e.g., Wolfe, 1985; Boyd, 1990; Basinger, 1991; Francis, 1991; Greenwood and Basinger, 1993, 1994; Basinger et al., 1994; Kvacek et al., 1994; McIver and Basinger, 1999; Williams et al., 2003; Eldrett et al., 2009; Greenwood et al., 2010; Barke et al., 2011). These forests are generally interpreted as a mixture of deciduous (e.g., *Larix*, *Pseudolarix*, and *Metasequoia*) and evergreen conifers (e.g., *Chamaecyparis*, *Picea*, and *Pinus*; see Kotyk et al., 2003), and deciduous broadleaved angiosperms (e.g., Betulaceae, Juglandaceae, and Ulmaceae). The deciduous character of these polar forests was initially considered an adaptation to polar-winter darkness (e.g., Basinger et al., 1994; Read and Francis, 1992); however, Royer et al. (2003, 2005) rejected this assumption experimentally. The hypothesis that these forests were dominated by trees that were deciduous, however, is supported by the fossil woods exhibiting a deciduous isotopic signature (Jahren and Sternberg, 2008), and the physiognomic character of the broadleaf assemblages is also consistent with modern temperate deciduous forests and not broadleaf evergreen forests (Basinger et al., 1994). As noted previously, isotopic inferences of herbivore diets implying a summer preference for angiosperm foliage versus a winter dependence on evergreen conifer foliage and other foods by *Coryphodon* (Eberle et al., 2009) are consistent with a seasonally available deciduous flora.

In their analysis of microstratigraphic variation in the forest-floor litters at the Geodetic Hills, Greenwood and Basinger (1993, 1994) demonstrated successional changes within these swamp forests over vertical depths of 10 cm to 1 m, likely reflecting ecological time scales of 1000–2000 yr. Early succession levels on mineral substrates (i.e., layers sitting atop clays) were rich in dicots, especially *Alnus*, together with the fern *Osmunda*, with mixed conifer associations sometimes alternating with a *Metasequoia*-dominated (or *Metasequoia*-*Glyptostrobus*, rarely also including *Pseudolarix* and/or *Pinus*) community in later successional stages. This pat-

tern was repeated in lateral transects over both tens of meters and over a 2 km transect, suggesting a dynamic swamp forest community, similar to present-day swamp cypress (*Taxodium* spp.) forests of the southeastern United States, where local community composition reflects spatial and temporal variation in local water depths (Willard et al., 2001). Williams et al. (2003) calculated closed canopies for the swamp forests between 40 and 25 m in height, and biomass and productivity values similar to those of modern old-growth coniferous rain forests of western North America and southern Chile. Richter and LePage (2005) demonstrated a dynamic landscape where the spore and pollen flora demonstrated shifts in dominance and presence-absence of key taxa through 238 m of vertical section at the Geodetic Hills fossil forest site. Changes in taxonomic composition in the microflora reflected changes in the hydrological regime within the floodplain resulting from decadal- to millennial-scale shifts in precipitation regimes and the courses of local rivers and the resulting locations of swamps and local lacustrine environments (e.g., Willard et al., 2001), matching the finer-scale (shorter temporal scale) changes demonstrated by the macroflora (Greenwood and Basinger, 1993, 1994).

The considerable discharge of freshwater into an enclosed Eocene Arctic Ocean from rivers resulting from the high precipitation estimated for the High Arctic region (e.g., Greenwood et al., 2010; Zacke et al., 2009) would have contributed to significant surface freshening of the Arctic Ocean, similar to what occurred during the Holocene in the Baltic Sea (Widerlund and Andersson, 2011), also a semi-enclosed sea. This surface freshening at times during the middle Eocene caused a cap on the Arctic Ocean of sufficiently low salinity that mats of the aquatic floating fern *Azolla* produced significant concentrations of microspore massulae in marine sediments around the Arctic coast, including along the Lomonosov Ridge (Brinkhuis et al., 2006; Greenwood et al., 2010; Barke et al., 2011). Barke et al. (2011) interpreted pulses of taxodiaceous swamps (*Metasequoia* and/or *Glyptostrobus*) and antiphase dicot assemblages as being due to a fluctuating Eocene Arctic hydrological regime tied to orbital obliquity (~40 k.y. cyclicity) where coastal lowlands expanded and contracted, alternately restricting and expanding coastal-margin habitats for *Azolla*. A strong correlation among swamp plant pollen, freshwater dinoflagellates, and *Azolla* peaks was interpreted as indicating periods of enhanced rainfall and runoff during *Azolla* blooms, linked to increased local summer temperatures during obliquity maxima. No *Azolla* remains have been reported, however, from early or middle Eocene shale or other

facies from Axel Heiberg or Ellesmere Island (Fig. 4; Table 4), since this taxon is restricted in the Canadian High Arctic to prodeltaic or muddy shelf sediments from the middle Paleocene Strand Bay Formation (Sverdrup Basin) on Ellesmere Island (Fig. 2), in association with *Equisetum*, *Metasequoia* and the aquatic plant *Quereuxia* (Sweet and Hills, 1976; McIver and Basinger, 1999). Its absence from the terrestrial aquatic facies (e.g., the mudstones) is puzzling, because *Azolla* remains are common in early middle Eocene (ca. 50 Ma) nearshore marine deposits throughout the Arctic Basin, including sites to the west and south of Axel Heiberg and Ellesmere Islands (Brinkhuis et al., 2006), as well as in lacustrine shales in western North America at the same time (Sweet and Hills, 1976; Greenwood et al., 2005).

PALEOBIOGEOGRAPHY

Although the biogeographic affinities of the Eocene Arctic vertebrate fauna are predominantly with midlatitude North America (Dawson, 2001), several mammalian genera are shared with early Eocene European faunas, including *Coryphodon*, *Paramys*, *Microparamys*, *Palaeosinopa*, *Palaeoictis*, *Viverravus*, *Miacis*, and *Pachyaena*, supporting the existence of a North Atlantic land corridor (although probably slightly postdating it; Marinovich et al., 1990). The microparamyine rodents are hypothesized to have originated in midlatitude North America and subsequently dispersed across a North Atlantic corridor to colonize western Europe (Dawson, 2001). The discovery of a primitive palaeonodont (an extinct, fossorial group of mammals related to today's pangolins or scaly anteaters) at an early Eocene locality on Ellesmere Island revives the hypothesis of a North American source for European palaeonodonts as well (Rose et al., 2004). Oxyaenid creodonts (of which *Palaeoictis* is a member) are another family that probably originated in midlatitude North America and subsequently dispersed across Arctic land corridors into both Europe and Asia, although hyaenodontid creodonts (to which *Prolimnocyon* belongs) most likely originated in Africa, followed by trans-Tethyan dispersal into both Asia and Europe, and eventual immigration from Asia into North America (across Beringia) at the onset of the Eocene (Gheerbrant et al., 2006).

As knowledge of the Paleogene mammal record expands in Asia, affinities with this continent have only recently been recognized, and several Eocene mammalian genera co-occurring in midlatitude North America and the Arctic (*Paramys*, *Coryphodon*, *Miacis*, *Pachyaena*, and *Prolimnocyon*) also are known from Asia

(Eberle and McKenna, 2002). Beard (1998) hypothesized that many (if not most) major mammal clades, including rodents, perissodactyl and artiodactyl ungulates, hyaenodontid creodonts, and true primates, originated in Asia and subsequently dispersed into North America via Beringia. Although some elements of the Eocene Arctic vertebrate fauna are consistent with Beard's East of Eden model (e.g., anosteirine turtles; Estes and Hutchison, 1980), other genera in the Eocene Arctic provide examples that are contrary. For example, a phylogenetically derived paleobiogeographic reconstruction of early members of the tapir lineage hypothesizes that this clade originated in North America, perhaps at high latitudes (given the earlier occurrence and abundance of tapirs in the early Eocene of Ellesmere Island), and subsequently dispersed to Asia (Eberle, 2005). Brontotheres also are hypothesized to have a North American origin with midlatitude *Lambdaotherium* as the sister group (Mihlbachler, 2008), and the occurrence of cf. *Eotitanops* at early Eocene Arctic localities (which predates the occurrence of *Eotitanops* in midlatitude North America) raises the possibility of a northern origin for this clade as well (Eberle, 2006). Consequently, and contrary to the idea that dispersal should occur primarily from the larger land mass (in this case, Asia) to the smaller land mass (North America) (Beard, 1998), the Eocene Arctic fauna sheds light on rare examples of counterflow in which exotic North American taxa successfully invaded Asia.

It has been noted for over a century that the extant floras of North America, Europe, and Asia share a number of plant genera, such as *Acer*, *Juglans*, and *Quercus*, amongst many others. The Paleogene fossil record significantly expands this list, adding taxa such as *Metasequoia*, *Pseudolarix* and several other conifers, *Ginkgo*, and several genera of angiosperms, including *Cercidiphyllum* (Manchester, 1987, 1999; Tiffney, 2000). Many of these tree genera are known, if not ubiquitous in the circumpolar Eocene macrofloras, including the extensive shale-floras and forest-floor litters of Axel Heiberg and Ellesmere Islands (McIver and Basinger, 1999). The fact that the Arctic through the warmer global climates of the latest Cretaceous through to the late Eocene provided a series of corridors through which plant taxa could be exchanged between these landmasses is clear from the fossil record, with Eocene Arctic fossil taxa showing affinities to living species in Asia, Europe, Japan, or North America (e.g., LePage and Basinger, 1995; Manchester, 1999; Kotyk et al., 2003; LePage, 2003). As-yet unpublished work is extending these connections to additional angiosperm taxa from the

Canadian Arctic Eocene floras, such as the walnuts, *Juglans* (J.F. Basinger, 2011, personal commun.), a group that, along with *Carya* (hickories), appears first in the New World and then in the Old World (Manchester, 1987). Unlike animals, this transcontinental exchange would not have occurred via migrations or discrete dispersal events, but rather through range extensions of the biomes that supported these taxa, during which times continuous populations of the taxa extended across the Arctic, or were exchanged through long-distance dispersal via island hopping (e.g., Lomonosov Ridge). A continuous circum-Arctic Ocean coastline around an enclosed Arctic ocean (Fig. 3) would have provided linked coastal populations with few geographic barriers for dispersal across a more-or-less homogeneous forest biome analogous in geographic extent to the modern boreal forest (e.g., Wolfe, 1985), but with a taxonomic composition and ecology more akin to the *Taxodium*-swamp-dryland forest mosaics of the southeastern United States.

Cooler upland habitats in the Eocene Arctic may have afforded opportunities for specialization and speciation in groups such as spruces and pines (*Picea* and *Pinus*), two genera well represented as both foliage and seed cones in the middle Eocene swamp forest and sandstone facies of the Geodetic Hills on Axel Heiberg Island, as are other Pinaceae (McIver and Basinger, 1999; LePage, 2003). The Pinaceae, including *Keteleeria*, *Picea*, *Pinus*, and *Tsuga* however, appear to have radiated much sooner than the middle Eocene (Lutetian), as these taxa are known from early Eocene (Ypresian) upland floras from western North America and Eurasia (LePage and Basinger, 1995; LePage, 2003; Greenwood et al., 2005). The High Arctic may therefore have acted as a mixing zone where populations ebbed and flowed across the Arctic with the vicissitudes of Paleogene climate change, forcing speciation as populations became isolated and later remixed. Species differ in their response to climate change, both currently and in the geological past. Pleistocene climate shifts from glacial to interglacial climates resulted in repeated changes in both the location and overall size of species' geographic ranges, and often rapid fluctuations in the sizes of local and regional populations, including extinctions and speciation (Dawson et al., 2011). Plant and animal populations in the Eocene Arctic could then have expanded rapidly during hyperthermal events (Paleocene-Eocene thermal maximum, ETM2 (Eocene Thermal Maximum 2) and MECO (Middle Eocene Climatic Optimum); see Fig. 4), permitting temporary (millennial scale) extensions northward linking North American, European, and Asian biomes

and their component species (e.g., the apparent exchange of giant [>5 cm] formicine ants between Europe and North America; Archibald et al., 2011). Subsequent cooling intervals would have seen range contractions (e.g., Barke et al., 2011), in some cases isolating populations of plants and animals in protected localized areas, offering opportunities for both allopatric and parapatric speciation when renewed warming restored connectivity between populations.

CONCLUSIONS AND FUTURE RESEARCH QUESTIONS

Taken together, the Eocene vertebrate and plant records from Canada's Arctic illuminate a lush rain forest community on a coastal delta plain teeming with life. Hippo-like *Coryphodon* spent its time browsing on vegetation in (or near) rivers that teemed with fishes, alligators, and turtles, while small primates and carnivorans inhabited the forest canopy, and tapirs roamed the forest floor (Fig. 7). The Eocene climate was mild, with above-freezing winters and summer

temperatures that approached 20 °C or higher, and very humid. With so much water running off of the land into a semi-enclosed basin, the Arctic Ocean was, at times, freshwater (at least at its surface layer) and covered in mats of the floating fern *Azolla*, much like today's Baltic Sea, which freshens with distance from the North Atlantic (Widerlund and Andersson, 2011). Sea level in the Arctic Ocean would have fluctuated due to the relative inputs of freshwater from the land as well as tectonics, allowing temporary land bridges along island arcs such as Lomonosov Ridge and other places (e.g., proto-Iceland), across which land animals and plants dispersed between Europe and North America when the climatic conditions suited their ecology. Beringia also saw the dispersal of land mammals from Asia to North America (and vice versa).

The diversity of fossil plants and vertebrates in the Eocene High Arctic begs the question of how did these organisms thrive in an environment where darkness prevails for several months each year? Although some of the mammals, such as *Coryphodon* and probably the other large herbi-

vores, had flexible and unusual diets that allowed them to live year-round in the High Arctic (Eberle et al., 2009), there are many questions yet to be answered concerning the paleobiology and paleoecology of most of the Eocene Arctic vertebrates and plants. Were these polar forests deciduous, as dominates most of the present-day northern temperate zone and the fossil record implies (Basinger et al., 1994), or were evergreen broadleaf trees and conifers significant components of the landscape as suggested by both taxa (e.g., *Chamaecyparis*; Kotyk et al., 2003) and experimental evidence (Royer et al., 2003, 2005)? The application of techniques for "looking inside" these Eocene organisms, such as X-ray computed tomography (CT-scans) and isotope analyses of their bones, teeth, wood, and leaves to interpret paleodiet and paleobehavior as well as phenology should shed more light on our understanding of the Eocene Arctic fauna and flora. From a biogeographical perspective, during the Eocene, the Arctic was en route for terrestrial organisms dispersing between North America and both Europe and Asia and the



Figure 7. Reconstruction of Eocene High Arctic rain forest environment with hippo-like *Coryphodon* in the foreground; inset shows detail of Eocene Arctic tapir *Thuliadanta*. Both images are courtesy of the American Museum of Natural History (© AMNH/D. Finnin).

probable port of entry for the earliest members of major clades of mammals. However, phylogenetic analyses of the Eocene Arctic taxa (e.g., Eberle, 2005) underscore the need to evaluate the Arctic as a source area for exotic species appearing in midlatitudes during the early Eocene. It is also clear that significant commonality in the floras of the northern continents reflects Eocene and pre-Eocene exchanges across the Arctic, perhaps reflecting shifts in biome extent and re-assortment accompanying climatic fluctuations (Manchester, 1999; Tiffney, 2000; Barke et al., 2011).

Unlike Eocene North American midlatitude localities, the Arctic fossils are very rare and hard won; in the nearly four decades of exploration of the Eureka Sound Group by vertebrate paleontologists, the number of diagnostic mammalian fossils is ~230, and many of the mammalian taxa are known from single specimens. With nearly every expedition to the High Arctic, a new species is discovered (e.g., Rose et al., 2004), and consequently a fundamental goal is to simply explore the vast expanses of Eocene rocks that stretch across the Canadian Arctic, many of which are largely untouched by vertebrate paleontologists. Fundamental questions remain unanswered from the paleofloral record too, with research questions concerning the phylogenetic relationships of nonconifer lineages nascent in comparison to the body of work on conifers in the Arctic (e.g., LePage, 2003) and midlatitude Eocene floras across all plant groups (McIver and Basinger, 1999). Across the U.S.-Canada border, Alaska preserves lower Eocene strata that are rich with fossil plants (e.g., Williams et al., 2010) but that have received little attention by vertebrate paleontologists. The happenstance discovery of a Paleogene turtle in the Chickaloon Formation by Anchorage high school students represents the first Cenozoic record of this order (Hutchison and Pasch, 2004) and builds promise for future discoveries of Paleogene vertebrates in Alaska. The Arctic was, and still is, among the last frontiers for paleontological exploration.

The fact that many of the paleoclimate proxies converge and overlap in their estimates of paleotemperature (Table 4) lends confidence that we are nearing the mark in our understanding of many (though not all) aspects of Eocene Arctic climate. Although, most proxies focus on mean annual temperature (MAT), factors far more important to the survival of many organisms are the seasonal range in temperature and warm and cold month means. In addition, our proxy-based paleotemperature estimates are still a puzzle to climate modelers, whose early Eocene general circulation models are unable to retro-predict the climate and environment of the Eocene Arctic

indicated by the paleontology (e.g., Shellito et al., 2003). Initial forays into reconstructing the hydrological regime (e.g., precipitation and humidity) are posing new questions, and may be fundamental in understanding Arctic Eocene warmth (e.g., Greenwood et al., 2010; Huber and Caballero, 2011). Nevertheless, the Eocene stands out as arguably our best deep time analog for a mild, ice-free Arctic. From a paleontological perspective, the study of the ways in which the ancient Arctic biota responded to past global warming is a key to understanding and being able to predict what is in store for today's Arctic biota and environment as Earth's climate continues to warm.

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