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The Arctic Forest of the Middle Eocene

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Key Words

Metasequoia, Fossil Forest, paleoenvironment, paleosol, relative humidity, biomarker

Abstract

Lush forests, dominated by deciduous conifers, existed well north of the Arctic Circle during the middle Eocene (~45 Ma). The Fossil Forest site, located on Axel Heiberg Island, Canada, has yielded a particularly rich assemblage of plant macro- and microfossils, as well as paleosols—all exquisitely preserved. Methods ranging from classical paleobotany, to stable-isotope geochemistry, have been applied to materials excavated from the Fossil Forest and have revealed layers of diverse conifer forests with a rich angiosperm understory that successfully endured three months of continuous light and three months of continuous darkness. Paleoenvironmental reconstructions suggest a warm, ice-free environment, with high growing-season-relative humidity, and high rates of soil methanogenesis. Methods to evaluate intraseasonal variability highlight the switchover from stored to actively fixed carbon during the short annual growing season.

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INTRODUCTION

Between the dramatic warming events of the Paleocene-Eocene transition (~55 Ma) (Higgins & Schrag 2006, Maclennan & Jones 2006, Moran 2006, Sluijs et al. 2006) and the large-scale cooling at the Eocene-Oligocene transition (~24 Ma) (Dalai et al. 2006, DeConto & Pollard 2003, Grimes et al. 2005, Ivany et al. 2006), there spanned an ~21-million-year-long epoch known as the Eocene. The middle Eocene (~49 to ~37 Ma) is notable for the extensive landmasses that were located above the Arctic Circle for millions of years. **Figure 1** illustrates the large expanses of continental lithosphere located at high latitudes, during the middle Eocene and compared with the present. In addition, vast expanses of what now constitutes Siberia were located far north of the Arctic Circle. The major tectonic forces of the middle Eocene that are relevant to Arctic regions are illustrated by **Figure 2**, which shows the inception of spreading ridges near what is now Greenland, as well as the continuing opening of the Atlantic Ocean.

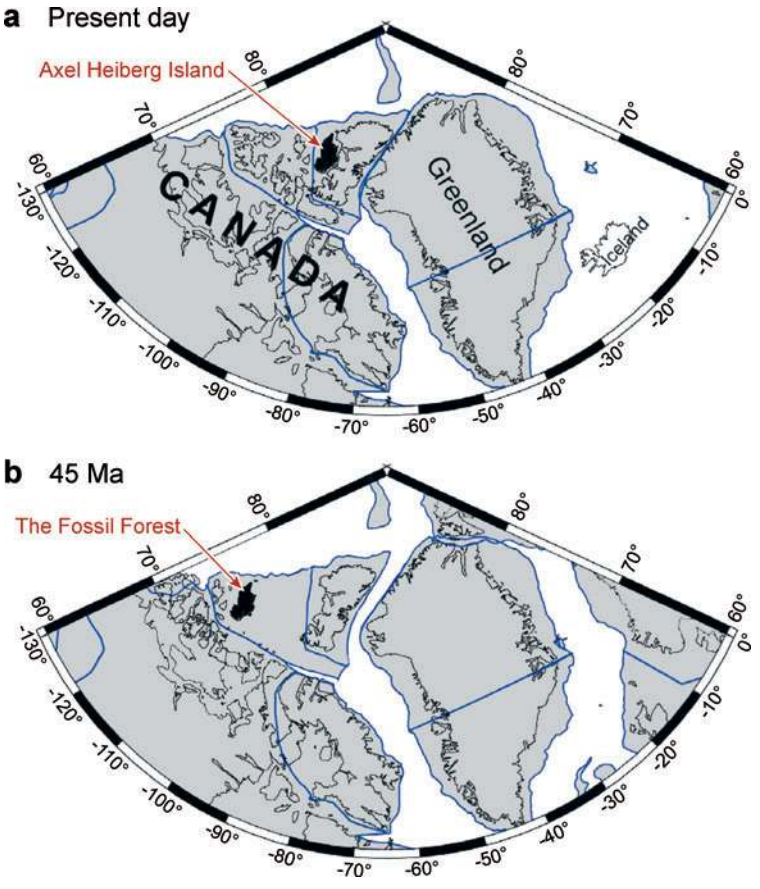

Figure 1

Position of tectonic plates at present (*a*) and during the middle Eocene (*b*). Tree wood, leaves, cones, and other fossils excavated from the Axel Heiberg site are the remnants of extensive deciduous conifer forests that were located well above the Arctic Circle (66°33′N), covering what are now Siberia, Greenland, and northern Canada. Plate boundaries are shown in blue; modern shorelines are indicated by black lines. This image was generated using the Plate Tectonic Reconstruction Service made public by the Ocean Drilling Stratigraphic Network (GEOMAR).

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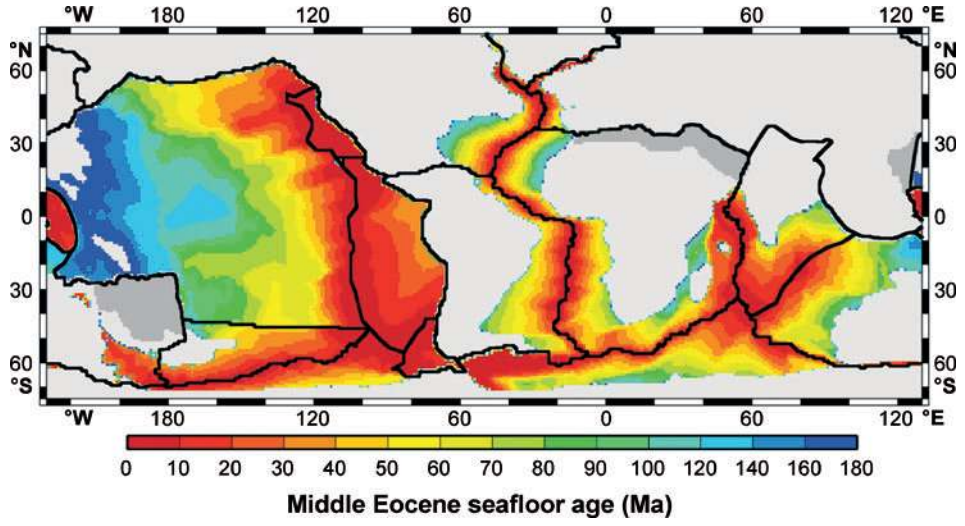

Figure 2

Continental locations and age of the seafloor during the middle Eocene (~45 Ma). The continental lithosphere (*light gray*) is contrasted with the color-coded seafloor; extensive landmasses existed at extreme latitudes. The initiation of spreading ridges defining what would become Greenland, the violent subduction of the remainder of the Farallon plate, and the rapid northward subduction of the Pacific plate beneath Alaska constitute the most important tectonic forces of the time, relative to the Axel Heiberg Island site. Seafloor age was determined from the reconstructions of Xu et al. (2006), which are based on an extrapolation of present-day ages (Müller et al. 1997) backward in time using the history of plate motions defined for the globe by Gordon & Jurdy (1986) and for the western Pacific by Hall (2002). Age could not be determined for regions indicated in dark gray.

THE HISTORY OF THE FOSSIL FOREST

The most important terrestrial fossil locality for the Arctic middle Eocene was found, like most rich fossil sites, purely serendipitously. In 1985, B. Ricketts of the Geological Survey of Canada found mummified Eocene-age plant deposits on Axel Heiberg Island while surveying the area. He informed J.F. Basinger of the site, who made a field excursion that same year to find well-preserved mummified plant remains, including cones, leaves, and wood fragments. The site established by Basinger was a few kilometers from the Fossil Forest locality, which was discovered in 1986 by a helicopter pilot named P. Tudge. Tudge noticed a large concentration of logs and in situ stumps from the air and landed to take a closer look and to take photographs. J. MacMillan of the Geological Survey of Canada told J.F. Basinger of this new site, and in 1986, the first research expedition by paleobotanists to the Fossil Forest was undertaken by J.F. Basinger, J.E. Francis, and J. MacMillan (Basinger et al. 1988).

At present, the Fossil Forest is located on Axel Heiberg Island, which is part of the Arctic Canadian Archipelago in the Nunavut territory of Canada. It is located at 79°55′N, 89°02′W (Geological Society of Canada Map 1301A), far above the Arctic

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Figure 3

Satellite image of Axel Heiberg Island, showing the location of the Fossil Forest. Figure courtesy of 2005 Geographic Data Technology Canada, Inc.

Circle (66°33′39″N). Axel Heiberg Island is 43,178 km^2 in size and is positioned directly west of Ellesmere Island (**Figure 3**). The Fossil Forest lies on the eastern side of Axel Heiberg Island between the Eureka Sound and the Princess Margaret Mountain Range (**Figure 4**). For reference, the site is located approximately 1500 km

Figure 4

Panoramic photograph of the Fossil Forest field site. The dark sedimentary layers are rich with abundant plant fossils representing all components of the middle Eocene Arctic deciduous conifer forest.

north of the Arctic Circle and is approximately 1000 km north of the most northern part of Alaska.

The modern climate of the Fossil Forest site (also known as Napartulik) is characterized as an arctic climate with long, cold winters and short, cool summers. The mean annual temperature (MAT) is estimated to be −20°C, and the site receives an annual precipitation of 65 mm, 70% of which falls as snow (Tarnocai & Smith 1991). Permafrost underlies the whole region. The Fossil Forest is preserved within the lignitic strata of the Upper Block Coal Member of the Buchanan Lake Formation. This Member consists of repeating fining-upward sequences of sandstones, mudstones, siltstones, and lignites (Ricketts 1991). The strata have likely been exposed by incision in response to isostatic rebound since the major Pleistocene glaciations (Ricketts 1987). The modern rate of surface erosion from these unconsolidated sediments is high, averaging a minimum of 3 mm per year (Bigras et al. 1995).

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THE GEOLOGICAL CONTEXT OF THE FOSSIL FOREST

Axel Heiberg Island, where the Fossil Forest is located, has been reconstructed to be located at 78.6°N (±1.6°N) during the period of 55 to 40 Ma (Irving & Wynne 1991, McKenna 1980). This position, north of the Arctic Circle, implies a winter of continuous darkness lasting 115 days, a summer of continuous light lasting 130 days, and very short transitional seasons (spring and fall), each lasting only approximately 60 days (**Figure 5**). Despite the extreme nature of the light environment, the middle Eocene Fossil Forest was teeming with diverse photosynthetic organisms, including abundant trees. The exquisite preservation of these mummified plant remains is stunning and has allowed for a wide range of approaches to paleoenvironmental reconstruction, ranging from the use of classical paleontological techniques to involved stable-isotope geochemistry.

Jahren & Sternberg (2002) documented 33 fossil-bearing layers within ∼150 vertical stratigraphic meters of sediment. Layers ranged from a few centimeters to several meters in thickness and contained a mixture of wood and leaf macrofossils from both conifer and angiosperm organisms. Greenwood & Basinger (1993) proposed that the accumulation rates of peat at the site were approximately 1–2 mm year^{-1} based on accumulation rates of modern *Taxodiaceous* swamps. However, the remnants of these peats (now expressed as lignite layers) have been variably compacted over time. Therefore, determining the original peat thickness and calculating time intervals of deposition proves elusive, given the obvious diagenesis. Kojima et al. (1998) estimated minimum accumulation rates of lignites by assuming (*a*) a constant leaf-area index and (*b*) that at least half the mass of *Metasequoia* leaves had been preserved. This approach resulted in a minimum accumulation rate of 0.8 mm year^{-1}. Comparing this calculated value to modern rates of peat accumulation using the ^{14}C method is difficult because of uncertainties associated with compaction ratios within lignites. Most workers do agree, however, that the Axel Heiberg middle Eocene forest was highly productive (e.g., Williams et al. 2003b).

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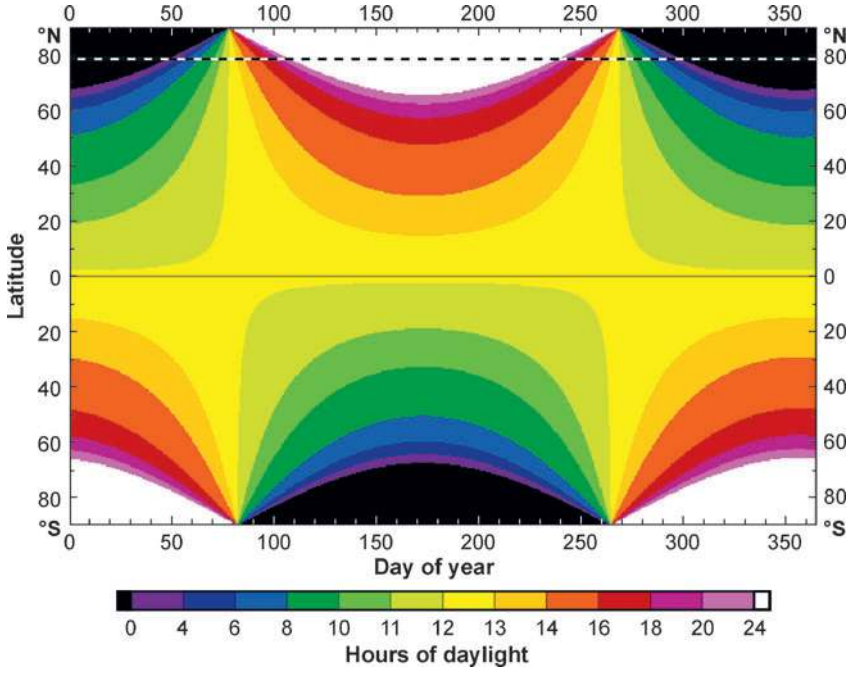

Figure 5

Hours of daylight shown as a function of calendar day of the year, calculated using Forsythe et al.'s (1995) CMB model. White and black represent periods of constant daylight and constant night, respectively. The black-and-white dashed line is located at 78.6°N, the reconstructed location of the Fossil Forest during the middle Eocene (Irving & Wynne 1991, McKenna 1980). The timing of sunrise and sunset are defined by the instant when the top of the sun appears even with the horizon for zero elevation and nonsloping ground, consistent with the U.S. government definition. Because this definition of daylight includes the time during which the sun crosses the horizon, day length at the equator exceeds 12 h. On the basis of these data, we estimate that the Fossil Forest of the Eocene Arctic experienced seasons as following: winter (continuous darkness) = 115 days, spring = 60 days, summer (continuous light) = 130 days, and fall = 60 days.

THE AGE OF THE SITE

The geologic age of the Fossil Forest is generally accepted to be middle Eocene (~45 Ma). This determination arises from several lines of evidence. The earliest observations concerned the Eurekan orogeny that formed the Princess Margaret Range, which still forms the central ridge of Axel Heiberg Island (**Figure 3**). Ricketts (1987) described the Buchanan Lake Formation as the strata containing extensive tree fossils and noted that it unconformably overlies rocks as old as Early Triassic in age and as young as middle Eocene in age. From this, Ricketts concluded that the Fossil Forest was derived from sediment shed during the orogeny, which he placed during the middle Eocene.

Although the Fossil Forest is rich with plant fossils of all types, limited age determination may be made on the basis of these assemblages. After an extensive examination of the palynomorphs that could be recovered from Fossil Forest strata, McIntyre (1991) concluded that the pollen flora was most similar to middle Eocene assemblages, but did not discount a late Eocene age. This study was later repeated by Richter & LePage (2005), and resulted in the same conclusions. It is also worth noting that the assemblage of paleobotanical macrofossils is not specific within the Phanerozoic (Jahren & Sternberg 2002).

The strongest evidence that the Fossil Forest formed during the middle Eocene can be found within work by Eberle & Storer (1999); these researchers recovered three tooth fossils from float on a sandstone that directly overlies one fossiliferous stratum. The tooth fragments were identified as from the brontothere, a quadrapedal herbivore, which became extinct in the late Eocene (**Figure 6**). The fossils themselves are most similar to genera found elsewhere in the Arctic that correlate with the middle Eocene, thus cementing the ~45 Ma age for the Fossil Forest.

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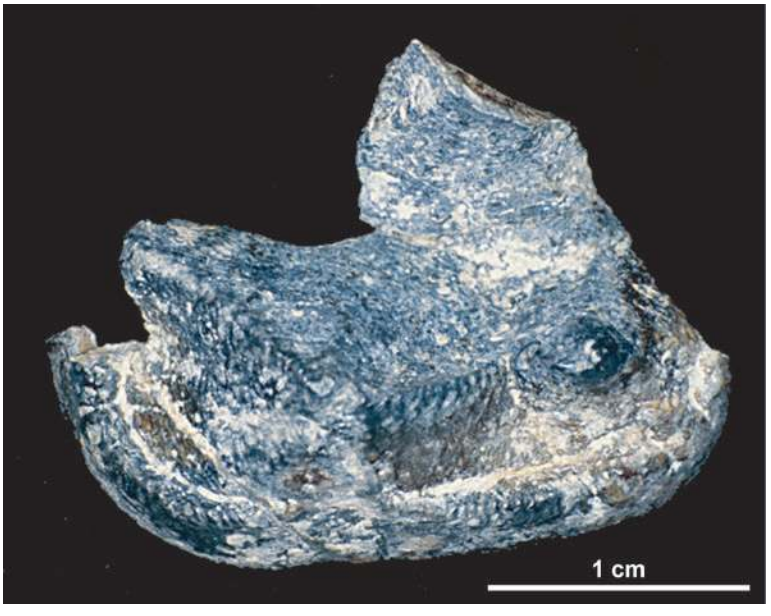

Figure 6

Cenozoic mammals, represented primarily by their teeth, are excellent index fossils for dating terrestrial strata because they are highly diagnostic, relatively abundant, and they evolved rapidly after the Cretaceous-Tertiary boundary. Teeth of large, rhinoceros-like brontotheres, including this incomplete premolar (CMN 51091) from the Fossil Forest, provide a time control for the Axel Heiberg Fossil Forest sediments. Specifically, the size and morphology of CMN 51091 and other brontothere fossils are most comparable to midlatitude brontotheres from the Uintan and Duchesnean North American Land Mammal Ages, correlative with middle Eocene time. Photo courtesy of J.J. Eberle.

FOSSIL ORGANISMS FOUND AT THE SITE

Metasequoia wood is, by far and away, the most abundant fossil within Fossil Forest strata (**Figure 7**); it is striking not only in its abundance, but also with respect to its exquisite preservation. The major anatomical features used to identify *Metasequoia* (at low resolution) include the presence of smooth-end walls of parenchyma (both ray and vertical) and the absence of resin canals, ray tracheids, and spiral thickenings (Obst et al. 1991). Extant *Metasequoia* can be found as moderate plantations within China and Japan (Williams et al. 2003a) and as single examples within botanical gardens and arboreta on many continents.

Excavations of macrofossils and palynomorphs within Fossil Forest strata revealed a lush and diverse Arctic ecosystem (**Figure 8**). **Table 1** catalogs the conifers (and the *Ginko* sp.) recovered from the site. Axel Heiberg Island was forested with fir, cypress,

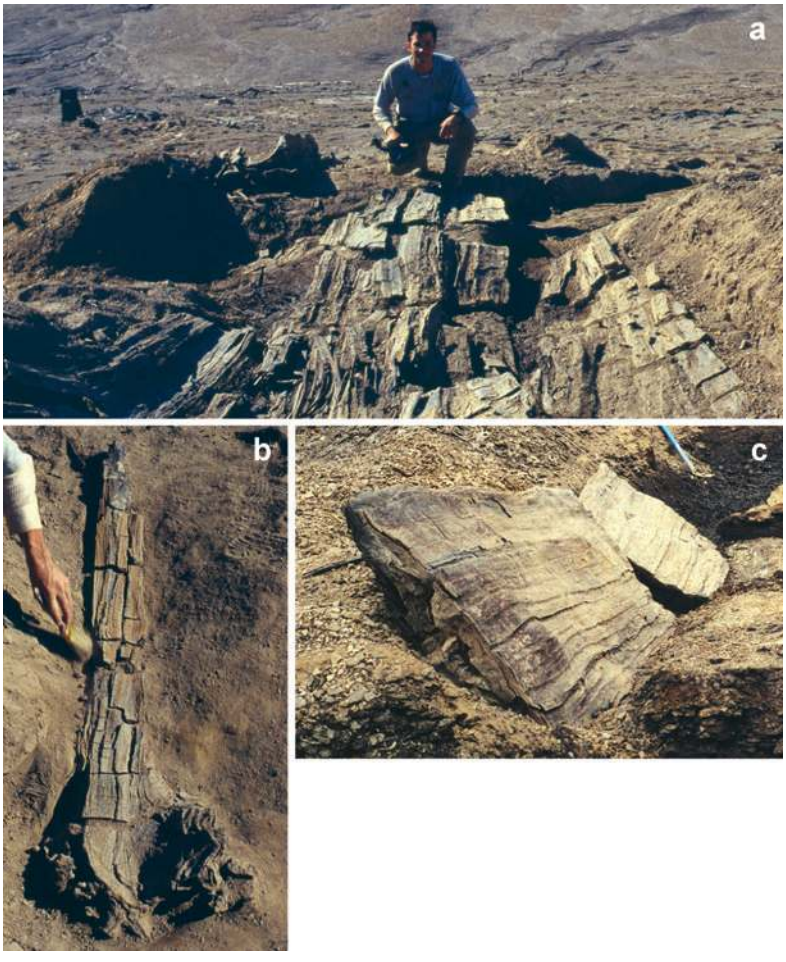

Figure 7

Wood excavated from the Fossil Forest site, showing the exceptional preservation. (*a*) The largest trees found measured close to 3 m in diameter. (*b*) Juvenile trees were also found, sometimes still attached to the root bole. (*c*) Continuous lengths, sometimes several meters in length, were often found.

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Figure 8

(*a*) The thick litter layer that blanketed the floor of the Fossil Forest, within which leaf, stem, cones, spores, and pollen are abundantly preserved. (*b*) Fossilized *Metasequoia* leaves. (*c*) Fossilized *Betula* leaves.

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larch, redwood, spruce, pine, and hemlock trees. A survey of angiosperms (**Table 2**) reveals an understory and/or fringe vegetation containing maple, alder, birch, hickory, chestnut, beech, ash, holly, walnut, sweetgum, sycamore, oak, willow, and elm trees. As for small plants, honeysuckle and sumac were present, as were various reeds (**Table 3**).

Several species of ferns and mosses have been recovered (**Table 4**), either as palynomorphs or as preserved fronds. Based on the above, the Fossil Forest is envisioned as a mosaic of angiosperm, conifer, and fern communities in a continually changing floodplain environment (Liu & Basinger 2000, McIntyre 1991, Richter & LePage 2005).

Day (1991) extensively surveyed both fossil spores and propagules from the Buchanan Lake strata and identified at least three families of ascospores and at least five families of conidia; also present were nonsporic propagules. As part of a novel study, Labandeira et al. (2001) identified engravings in *Larix altoborealis* (larch) fossil wood as the work of *Dendroctonus*, a bark beetle.

The Fossil Forests of Axel Heiberg Island have allowed for several significant reinterpretations of plant and animal evolution. Most importantly, it was using these

Table 1 Conifer and Ginkoaceae organisms found within middle Eocene sediments of the Fossil Forest of Axel Heiberg Island

Latin name	Common name	Fossil material	Reference
***Phylum Spermatophyta* Gymnospermae and Coniferae**			
?Abies sp.	Fir	Palynomorph	McIntyre (1991)
Cathaya sp.	—[a]	Palynomorph	Liu & Basinger (2000)
Chamaecyparis sp.	False cypress	Leaf, plant fragment, twig	Basinger (1991), Greenwood & Basinger (1993), McIver & Basinger (1999)
?Cupressaceae[b]		Palynomorph	McIntyre (1991)
Ginkgo sp.[c]	Maidenhair	Leaf	Basinger (1991), McIver & Basinger (1999)
Glyptostrobus sp.	Swamp cypress	Leaf, plant fragment, palynomorph	Greenwood & Basinger (1993), McIntyre (1991), McIver & Basinger (1999), Richter & LePage (2005)
Glyptostrobus nordenskioldii	Swamp cypress	Leaf, twigs, cone	Basinger (1991)
Larix sp.	Larch	Cone, needle, palynomorph, twig	Basinger (1991), LePage & Basinger (1991), McIntyre (1991), McIver & Basinger (1999), Richter & LePage (2005)
Larix altoborealis sp. nov.[d]	Larch	Cone, needle, twig, wood	LePage & Basinger (1991)
Metasequoia sp.	Dawn redwood	Cone, leaf, stem, palynomorph, wood	Basinger (1991), Greenwood & Basinger (1993), McIntyre (1991), McIver & Basinger (1999), Richter & LePage (2005), Williams, et al. (2003)
Metasequoia occidentallis	Dawn redwood	Leaf, twigs, cone	Basinger (1991)
Picea spp.	Spruce	Cone, palynomorph, twig	Basinger (1991), Jagels et. al. (2001), McIntyre (1991), McIver & Basinger (1999)
Picea beibergii sp. nov.	Spruce	Cone	LePage (2001)
Picea nansenii sp. nov.	Spruce	Cone	LePage (2001)
Picea palustris sp. nov.	Spruce	Cone, leaf, twig	LePage (2001)
Family Pinaceae[b]		Palynomorphs	Richter & LePage (2005)
Pinus sp.	Pine	Cone, leaf fascicle, palynomorphs	Basinger (1991), McIntyre (1991), McIver & Basinger (1999)
Pseudolarix	Golden larch	Scale	Greenwood & Basinger (1993), McIver & Basinger (1999)
Taiwania sp.	—	Cone	McIver & Basinger (1999)
Family Taxodiaceae[b]		Leaf, stump, twig	Basinger (1991), Greenwood & Basinger (1993), McIver & Basinger (1999)
Tsuga sp.	Hemlock	Cone, palynomorph	McIntyre (1991), McIver & Basinger (1999), Richter & LePage (2005)
Tsuga swedaea sp. nov.	Hemlock	Cone, twig	LePage (2002)

[a]No common name exists.
[b]Not identified to genus.
[c]Not a conifer.
[d]"sp. nov." indicates a new species.

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Table 2 Dicot angiosperms found within middle Eocene sediments of the Fossil Forest of Axel Heiberg Island

Latin name	Common name	Fossil material	Reference
***Phylum Spermatophyta* Angiospermae (Dicotyledonae)**			
Acer sp.	Maple	Palynomorph	McIntyre (1991)
Alnus sp.	Alder	Fruit, leaf, palynomorph	Basinger (1991), Greenwood & Basinger (1993), McIntyre (1991), McIver & Basinger (1999), Richter & LePage (2005)
Anacolosidites sp. (cf. *A. reklawensis* Elsik)	—[a]	Palynomorph	McIntyre (1991)
Archeampelos sp.	N.E.[b]	Leaf	McIver & Basinger (1999)
Betula spp.	Birch	Fruit, palynomorph	Basinger (1991), McIntyre (1991), McIver & Basinger (1999)
Family Betulaceae		Leaf	Basinger (1991), Greenwood & Basinger (1993), McIver & Basinger (1999)
Carya spp.	Hickory	Leaf, fruit, palynomorph	Basinger (1991), McIntyre (1991), McIver & Basinger (1991)
Carya veripites	Hickory	Palynomorph	McIntyre (1991)
Carya viridifluminipites	Hickory	Palynomorph	McIntyre (1991)
Castanea sp.	Chestnut	Palynomorph	McIntyre (1991)
Cercidiphyllum sp.	Katsura	Fruit, leaf, palynomorph	Basinger (1991), McIntyre (1991)
Family Cercidiphyllaceae		Fruit	McIver & Basinger (1999)
Corylus sp.	Hazel	Palynomorph	McIntyre (1991)
Diervilla sp.	—	Palynomorph	McIntyre (1991)
Engelhardtia sp. (cf. *E. chrysolepis*)	Chinquapin	Palynomorph	McIntyre (1991)
Family Ericaceae (*Ericipites* spp.)	N.E.	Palynomorph	McIntyre (1991)
Fagus sp.	Beech	Palynomorph	McIntyre (1991)
Fraxinus sp.	Ash	Palynomorph	McIntyre (1991)
Gothanipollis sp.	N.E.	Palynomorph	McIntyre (1991)
Ilex sp.	Holly	Palynomorph	McIntyre (1991)
Intratriporopollenites sp. (cf. Reevesia)	No extant	Palynomorph	McIntyre (1991)
Juglans spp.	Walnut	Nut, palynomorph	McIntyre (1991), McIver & Basinger (1999)
Family Juglandaceae		Leaf	McIver & Basinger (1999)
Liquidambar sp.	Sweetgum	Palynomorph	McIntyre (1991)
Lonicera sp.	Honeysuckle	Palynomorph	McIntyre (1991)
Family Menispermaceae		Leaf	McIver & Basinger (1999)
Myrica sp.	Sweetgale	Palynomorph	McIntyre (1991)
Nordenskioldia borealis	N.E.	Fruit, leaf	McIver & Basinger (1999)
Nyssa sp.	Tupelo	Fruit, palynomorph	McIntyre (1991), McIver & Basinger (1999)

(*Continued*)

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Table 2 (*Continued*)

Latin name	Common name	Fossil material	Reference
Nyssidium arcticum	N.E.	Fruit, leaf	McIver & Basinger (1999)
Pachysandra sp.	—	Palynomorph	McIntyre (1991)
Pistillipollenites mcgregorii Rouse	N.E.	Palynomorph	McIntyre (1991)
?*Planera* sp.	—	Palynomorph	McIntyre (1991)
Platanus	Sycamore	Leaf	Basinger (1991), McIver & Basinger (1999)
Pterocarya spp.	—	Palynomorph	McIntyre (1991)
Quercus spp.	Oak	Leaf, palynomorph	Basinger (1991), McIntyre (1991), McIver & Basinger(1999)
Rhus sp.	Sumac	Leaf, palynomorph	McIntyre (1991), McIver & Basinger (1999)
Family Rosaceae		Palynomorph	McIntyre (1991)
Salix sp.	Willow	Palynomorph	McIntyre (1991)
Tilia sp. (*T. vescipites* Wodehouse)	Linden	Palynomorph	McIntyre (1991)
Treigonobalanus sp.	—	Fruit	McIver & Basinger (1999)
Tricolporopollenites kruschii	N.E.	Palynomorph	McIntyre (1991)
Ulmus sp.	Elm	Leaf, palynomorph	McIntyre (1991), McIver & Basinger (1999)
Ushia sp.	—	Leaf	McIver & Basinger (1999)
?*Viburnum* sp. (cf. *V. cassinoides* L.)	—	Palynomorph	McIntyre (1991)

[a]No common name exists.
[b]None extant.

sediments that LePage & Basinger (1991b) described the earliest known occurrence of *Larix* (larch), which had previously been ambiguous prior to the Oligocene (LePage & Basinger 1995). Later, Jagels et al. (2001) provided the first definitive identification of fossil *Larix* wood through the identification of ray-tracheid bordered pits. The brontothere fragments (discussed above) discovered by Eberle & Storer (1999) constituted the northernmost record of Tertiary mammals (Eberle 2006).

Table 3 Monocot Angiosperms found within middle Eocene sediments of the Fossil Forest of Axel Heiberg Island

Latin name	Common name	Fossil material	Reference
***Phylum Spermatophyta* Angiospermae (Monocotyledonae)**			
Liliacidites sp.	N.E.[a]	Palynomorph	McIntyre (1991)
Monocolpopollenites sp.	N.E.	Palynomorph	McIntyre (1991)
Sparganium sp.	Reed	Fruiting head, palynomorph	McIntyre (1991), McIver & Basinger (1999)

[a]None extant.

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Table 4 Fern and fern-like organisms found within middle Eocene sediments of the Fossil Forest of Axel Heiberg Island

Latin name	Common name	Fossil material	Reference
Phylum Pteridophyta			
Cryptogramma sp.	Fern	Palynomorph	McIntyre (1991)
Deltoidospora spp.	N.E.[a]	Palynomorph	McIntyre (1991)
Gleichenia sp.	Fern	Palynomorph	McIntyre (1991)
Laevigatosporites spp.	N.E.	Palynomorph	McIntyre (1991)
Lycopodium spp.	Club moss	Palynomorph	McIntyre (1991)
Family Onoclea	Fern	Fronds, whole plant	Greenwood & Basinger (1993)
Osmunda spp.	Royal fern	Fronds, palynomorph	Greenwood & Basinger (1993), McIntyre (1991), McIver & Basinger (1999)
?*Polypodium* sp.	Fern	Palynomorph	McIntyre (1991)
Radialisporis radiatus	N.E.	Palynomorph	McIntyre (1991)

[a]None extant.

PALEOENVIRONMENT RECONSTRUCTIONS USING FOSSIL FOREST MATERIALS

Paleotemperature

Using disparate methods (**Table 5**), most workers have agreed that the middle Eocene forest of Axel Heiberg Island was subject to warm conditions, including MATs in excess of 12°C. The same studies have estimated mean cold-month temperatures in excess of 0°C, arguing against hard freeze events during the long, dark winters. Nearest-living-relative arguments (e.g., Basinger 1991, Francis 1991, McIntyre 1991) have emphasized a moist environment and lack of frost. The one exception to this interpretation resulted from Greenwood & Wing's (1995) multiple-regression model, which yielded significantly lower mean annual and cold-month mean temperatures for the Fossil Forest. Under this vision, mean temperatures were up to 5°C cooler than those suggested by other methods, including a climate-leaf analysis multivariate program (Wolfe 1994). The most recent paleotemperature determined for the site, based on the oxygen-isotope equilibration between environmental water and pedogenic carbonate, favors the warmer interpretation of the site (MAT $= 13.2 \pm 2.0$°C) (Jahren & Sternberg 2003).

Atmospheric Carbon Dioxide Levels

No consensus exists as to the probable CO_2 content of the middle Eocene atmosphere (Royer 2006). Pearson & Palmer (2000) used the boron-isotope ratio of foraminifera to estimate the pH of surface-layer seawater, which was then used to reconstruct middle Eocene pCO_2 ≈2400 ppm ($R \approx 6.5\times$). Although boron isotopes have implied the highest levels of middle Eocene pCO_2, work by Lowenstein & Demicco (2006) estimated high pCO_2 levels (2200 ppm; $R \approx 6\times$) by examining assemblages of middle Eocene Na-carbonates and assuming that they had precipitated in contact with the

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Table 5 Quantitative and qualitative estimates of paleotemperature made for the Eocene Arctic Fossil Forest

Temperature estimate (°C)					
MAT[a]	MART[b]	CCM[c]	Qualitative description	Method	Reference
13.2 ± 2.0				Oxygen isotope equilibration between environmental water and pedogenic carbonate	Jahren & Sternberg (2003)
13.7–17.2	—	3.3–8.6		CLAMP[d]	Wolfe (1994)
12–15	—	0–4		NLR[e]	Basinger et al. (1994)
			Mesothermal, moist, without severe winter frosts at low elevations	"based on current data" (probably informal NLR)	McIver & Basinger (1999)
			Warm and moist environment	NLR	Francis (1991)
			Warm and equable, without appreciable winter frost	NLR	Basinger (1991)
			Temperate to warm-temperate	NLR using pollen assemblages	McIntyre (1991)
			Temperate to warm-temperate with mild, wet winters and warm, moist summers	Analysis of paleosol features	Tarnocai & Smith(1991)
9.3 ± 2.0	13.8 ± 5.1	−0.8 ± 3.6		MRM[f]	Greenwood & Wing (1995)

[a]Mean annual temperature.
[b]Mean annual range of temperature (only reported within Greenwood & Wing 1995).
[c]Cold-month mean.
[d]Climate-leaf analysis multivariate program.
[e]Nearest-living-relative comparison.
[f]Multiple-regression model.

paleoatmosphere. Studies invoking the isotopic composition of pedogenic carbonate through time as a paleobarometer of CO_2 have yielded the relatively high estimates of middle Eocene pCO_2 ≈1,950 ppm (R ≈ 2.6×) (Ekart et al. 1999). Studies of the carbon stable isotope composition of alkenones in deep sea cores implied a middle Eocene range in pCO_2 ≈1000–1500 ppm (R ≈ 2.7× to 4×) (Pagani et al. 2005). In contrast, the GEOCARB carbon-cycling model estimates middle Eocene pCO_2 to have been ≈700 ppm (R ≈ 2×; figure 13 of Berner & Kothavala 2001). Stomatal density measurements have resulted in yet more disparate estimates: Retallack (2001) determined a pCO_2 ≈ 1,000 ppm (R ≈ 2.7×; five-point running average based on **Figure 4*b***), whereas Royer et al. (2001) used dissimilar methods to infer Eocene CO_2 levels to be near the same as that of today (R ≈ 1×). Owing to the myriad effects of elevated pCO_2 upon plant communities (and vice versa) (Schlesinger et al. 2006), the extent and composition of terrestrial forests during a given geological period cannot

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reliably be used to speculate as to the level of CO_2 in the paleoatmosphere. For these reasons, the ambient CO_2 level of the middle Eocene Arctic forests remains a topic of active controversy.

Soil Methanogenesis

Another striking feature of the Axel Heiberg Fossil Forest is the exceptionally well-preserved paleosols, which exhibit distinct organic and mineral horizons as well as preserved litter layers and root mass (**Figure 9**). Tarnocai & Smith (1991) described podzolic, gleyed-podzolic, gleysolic, and organic paleosols, emphasizing the water-saturated, acidic, and chemically reducing organic soil environment that existed within the Fossil Forest during the middle Eocene. They emphasized the integration of these soils into a floodplain environment with mild, wet winters and warm, moist summers. Some Fossil Forest paleosols exhibit enigmatic white layers that Tarnocai et al. (1991) investigated via X-ray diffraction and particle-size analyses. Much of the white material was revealed to be quartz with platy morphology; Tarnocai et al. (1991) proposed that this comprised the concentrated remains of opal phytoliths.

Within some of these paleosols is tree fossil material that has been diagenetically replaced with pedogenic carbonate. This replacement is notable, not only because it resulted soon after burial, given the lack of physical deformation of the macrofossil, but also because organic matter has been replaced at the cellular scale, preserving the tracheid morphology of the original tissue (**Figure 10*c***). These unusual secondary mineral deposits led Jahren et al. (2004) to use the carbon-isotope composition of organic carbon compared to carbonate to investigate carbon-cycling processes within the soils of the Fossil Forest. The fossil carbonate exhibited strikingly high $\delta^{13}C$

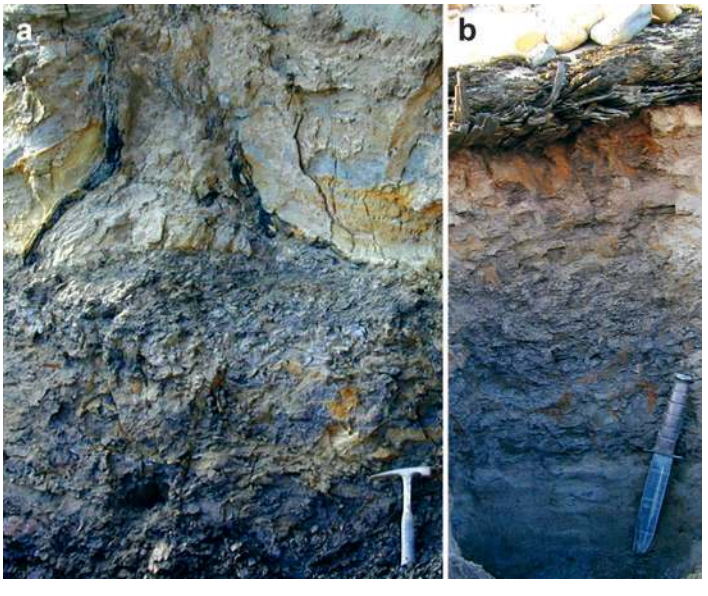

Figure 9

Exquisite paleosols are preserved within the Fossil Forest, some still bearing the outline of trees that grew within the soil (*a*), others exhibiting clear O, A, and B horizons (*b*).

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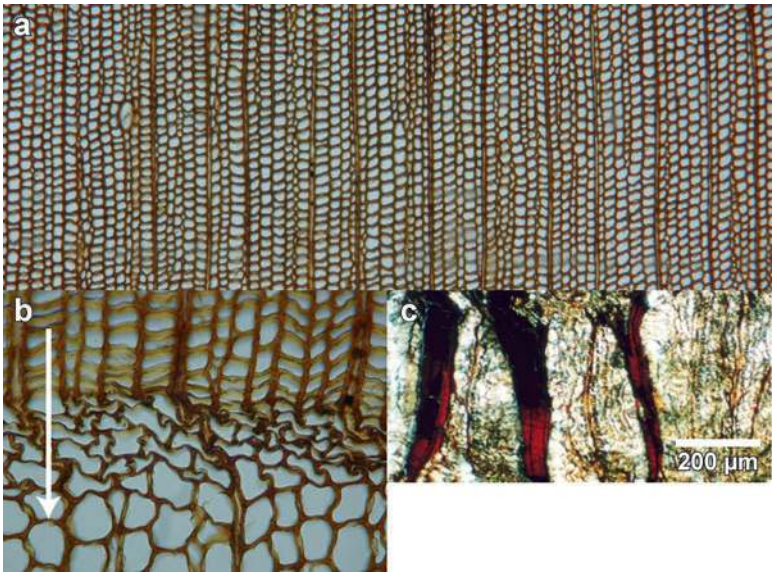

Figure 10

Light-microscope images of the cellular structure of fossil wood excavated from Axel Heiberg Island. (*a*) Late wood, with individual cells ~25 μm in diameter and abundant ray cells. (*b*) The transition of late wood into early wood, with arrow indicating the direction of growth. Early wood cells measure ~40 μm in diameter and are often compacted owing to burial. (*c*) Wood samples within which organic carbon (*dark areas*) has been partially replaced by carbonate (*light areas*) while preserving the wood microstructure.

values (+4.0‰ to +7.4‰), consistent with the idea that methanogenesis resulted in a ^{13}C-enriched CO_2 pool that equilibrated with soil water and gave rise to unusually ^{13}C-enriched pedogenic carbonate $\delta^{13}C$ values.

Other workers have reported conspicuously high $\delta^{13}C$ values within Mesozoic pedogenic carbonate and linked them with methanogenesis (e.g., Ludvigson et al. 1998; Ufnar et al. 2002, 2004). The gray colors, silty textures, and coarse mottling observed in Fossil Forest paleosols (**Figure 9**) are features associated with hydromorphic soils featuring low pH, low O_2 levels, and generally reducing conditions (Fastovsky & McSweeny 1987). Microsites within these soils may have alternately favored both the precipitation of carbonate and carbon cycling within microbial communities (Rask & Schoenau 1993). Biogenic methane production occurs in generally reducing terrestrial environments via two primary pathways: acetate fermentation:

$$CH_3COO^- + H^+ \rightarrow CH_4 + CO_2,$$

and the reduction of CO_2:

$$CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O.$$

Consideration of the fractionation factors (α) previously determined for these pathways (Gelwicks et al. 1994, Sugimoto & Wada 1993) and the isotopic difference between organic carbon and carbonate in the samples revealed that >80% of the carbon precipitated as carbonate resulted from the equilibration of CO_2 produced via acetate fermentation, in accordance with values observed for modern ecosystems (Hornibrook et al. 2000, Whiticar et al. 1986). The abundant preservation and partial decomposition of deciduous plant tissue would comprise a huge pool of acetate available for reduction within the Eocene Arctic forests: Annual leaf contributions have been estimated to be 320 g m^{-2} $year^{-1}$ within the Fossil Forest (Williams et al. 2003a,b). Given the carbon-cycling budgets of modern acetate-rich ecosystems (Küsel & Drake 1999), these values suggest that the maximum CH_4 release to the atmosphere due to these processes would have been $\approx$24 g C_{CH_4} m^{-2} $year^{-1}$ (Jahren et al. 2004). Because it is a powerful greenhouse gas (Lashof & Ahuja 1990), methane might have been an especially important component of the middle Eocene atmosphere, helping to maintain the elevated temperatures described above, particularly under a scenario featuring modest CO_2 levels (e.g., Royer et al. 2001).

Lack of Arctic Ice

Obst et al. (1991) performed the first chemical characterization of the organic component of Axel Heiberg fossils, which showed fossil wood to be rich in lignin (up to 80% lignin by mass). However, the same study postulated that fossilized gymnosperms had undergone extensive carbohydrate degradation with near complete removal of hemicelluloses. This was later refuted by multiple studies that identified, purified, and isolated both hemicellulose and α-cellulose (Jahren & Sternberg 2002, 2003, 2007). Yang et al. (2005) investigated the biomolecular preservational status of *Metasequoia* leaves and wood in Tertiary fossils using a comparative pyrolysis approach. They found that pyrolysates from middle Eocene Axel Heiberg *Metasequoia* wood were dominated by lignin-derived phenol compounds and proposed that the presence of structural polyphenolic compounds as initial decay products, such as tannins, provided resistance to further microbial and fungal degradation by binding to cellulose and other biomolecules. This may be a possible explanation for the exceptional preservation of the Fossil Forest paleovegetation.

A large amount of fossilized resin can be found within the sediments and the litter layers of the Fossil Forest (**Figure 11**), perhaps copiously produced by *Pseudolarix* as a defense compound (Anderson & LePage 1995). In addition, the abundance of higher-plant waxes gives rise to high concentrations of lipids, particularly odd-carbon-numbered *n*-alkanes. In particular, Yang et al. (2005) stated that the C_{29} predominance within Fossil Forest litter layers reflects the whole-leaf signature of *Metasequoia* spp., as opposed to leaf surfaces alone where C_{25} predominates. Jahren et al. (2007) isolated lipids from 19 lignite layers of the Buchanan Lake Formation and analyzed *n*-alkane biomarkers for hydrogen-stable isotopes to reconstruct the hydrogen-isotope composition (δD) of the precipitation value of paleoenvironmental water above the Arctic Circle during the middle Eocene. Comparatively few *n*-alkanes with a chain length $<C_{20}$ were found, indicating that diagenetic and catagenetic alteration was minimal,

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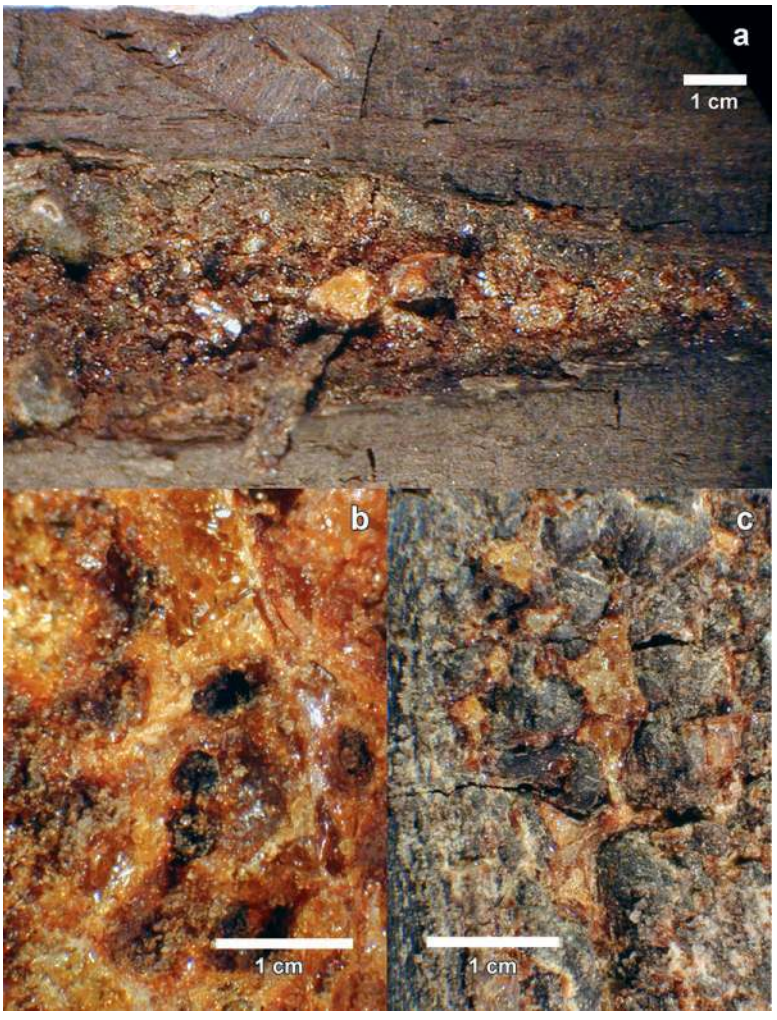
Figure 11

Fossilized resin preserved within sediment (*a*), wood (*b*), and litter (*c*) from the Fossil Forest.



consistent with the exceedingly mild thermal history of the formation (Ricketts 1991). Using the methods detailed within Byrne (2005), the average δD value of *n*-alkanes in each stratigraphic layer ranged from −284.6‰ to −252.5‰.

During the synthesis of lipids, most hydrogen is ultimately derived from cell water (Chikaraishi & Naraoka 2003, Sessions et al. 2002). The most applicable fractionation factor for the Fossil Forest ecosystem is found within Chikaraishi et al.'s (2004) work, which gives

$$\alpha = \frac{R_{n-\text{alkane}}}{R_{\text{environmental water}}} = 0.884 \left(R = {}^{D}/_{H}\right),$$

specifically for conifers growing under high relative humidity. Using $\alpha_{\text{Chikaraishi}}$, values of $\delta D_{\text{environmental water}}$ can be reconstructed in the following way:

$$\delta D_{\text{environmental water}}\,[‰] = \frac{[\delta D_{n-\text{alkane}} - (\alpha - 1) \cdot 1000]}{\alpha}.$$

Using the above, calculated $\delta D_{\text{environmental water}}$ ranged from –191‰ to –154‰. These values overlap with the range of $\delta D_{\text{environmental water}}$ estimates made from fossil cellulose $\delta^{18}O$ (–183‰ to –110‰) (Jahren & Sternberg 2003). The above reconstructions of Fossil Forest $\delta D_{\text{environmental water}}$ value are considerably higher than values obtained from the site for modern soil water (average = −200‰), stream water (average = −205‰), and ice pack (average = −208‰). Today, the δD value of precipitation in the Axel Heiberg locale is approximately −220‰ (Bowen & Ravenaugh 2003) or −213 ± 7‰ (Glob. Netw. Isot. Precip. 2001, IAEA/WMO 2006, Global Network of Isotopes in Precipitation. The GNIP Database. Accessible at: **http://isohis.iaea.org**), as measured at Resolute Bay (74.72°N and −94.98°E).

This difference between the stable-isotope values of modern Arctic environmental water and those of middle Eocene environmental water imply a wholly different water cycle within northern high latitudes, relative to today. To illustrate, the Bowen-Wilkinson equation (Bowen & Wilkinson 2002) can be used to calculate the expected oxygen-isotope ratios of precipitation ($\delta^{18}O$) at the latitudes (LAT) and minimum altitudes (ALT) of modern snow and ice fields:

$$\delta^{18}O\,[‰] = (-0.0051 \times \text{LAT}^2) + (0.1805 \times \text{LAT}) + (-0.002 \times \text{ALT}) - 5.247.$$

The δD value of precipitation can then be calculated using the linear relationship given by the global meteoric water line first established by Craig (1961):

$$\delta D\,[‰] = m\,\delta^{18}O + 10,$$

using a slope of $m = 9.5$ (see below) (Jahren & Sternberg 2003).

The relationship between the calculated δD value of precipitation (blue data) and the minimum altitude of present-day snow and ice fields is depicted in **Figure 12**; the red data within represent the reconstructed δD values of environmental water for the Arctic Eocene Fossil Forest based on *n*-alkanes (Jahren et al. 2007). The δD values of Eocene water plot within an area of the graph that shows no overlap with the δD values of modern ice masses within the Northern Hemisphere. On the basis of the general similarity between Eocene and modern tectonic plate configurations, this lack of overlap implies a middle Eocene Arctic lacking in snowfall and certainly lacking sufficient accumulation for an ice pack or a glacier. Taken in conjunction with other stable-isotope data, the δD values of *n*-alkanes within the lignites of the Fossil Forest are consistent with a spatially equable climate system, without extremes of temperature at the poles; these data also preclude the extensive buildup of ice and snow, even through three months of darkness.

Relative Humidity

The exquisite preservation of tree fossil material on Axel Heiberg Island makes possible the implementation of stable-isotope paleoclimatological techniques (reviewed

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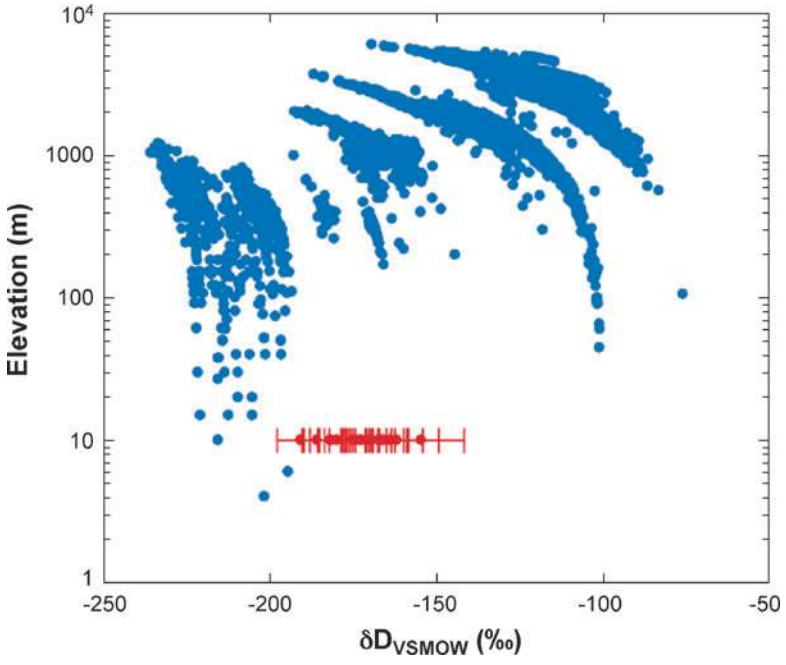

Figure 12

The hydrogen-isotope composition of environmental water as predicted from *n*-alkanes within resin isolated from fossil litter layers (*red data*). These values show no overlap with the hydrogen-isotope composition of ice masses between 0 and 90°N latitude (*blue data*). All values are presented against minimum elevation; *n*-alkane-based predictions are shown with associated standard deviation.

in McCarroll & Loader 2004) usually relegated to Quaternary substrates. For example, workers have obtained $\delta^{18}O$ and δD values from cellulose and cellulose nitrate, respectively, using tree fossils from Axel Heiberg Island. Just as with modern wood, fossil wood was removed of lipids, lignin, and hemicellulose to obtain pure α-cellulose (Sternberg 1989); oxygen in cellulose was converted into CO_2 for $\delta^{18}O$ analysis via reaction with $HgCl_2$ (Sauer & Sternberg 1994). A 200-mg portion of α-cellulose was subjected to standard nitration procedure; water produced by the combustion of cellulose nitrate was recovered as H_2 (Sternberg 1989). This was possible for both bulk fossil wood samples (Jahren & Sternberg 2003), as well as fossil rings, including intraseasonal subsampling (Jahren & Sternberg 2007).

Middle Eocene fossil wood used for analysis was identified as *Metasequoia glyptostroboides* and often represented small subsamples from the large wood samples excavated by Williams et al. (2003b). This identification was based on the gross anatomy and branching pattern in stems, as well as the abundance of *Metasequoia* in Fossil Forest litter layers. Regarding the wood fossil rings that were subsampled to assess intraseasonal variations in paleoenvironment (**Figure 10**), all fossils were identified as of either *Metasequoia* or *Glyptostrobus* genus (G. Visscher, personal communication). This identification was based on the presence or absence of microscopic resin canals in the form of fusiform rays (Jagels et al. 2001, 2003).

Because the ultimate oxygen and hydrogen isotopic composition of cellulose in tree rings is controlled by processes internal and external to the tree, $\delta^{18}O$ and δD values from cellulose and cellulose nitrate, respectively, can be used to interpret environmental water cycling. Processes external to the tree govern the isotopic composition

of environmental water in the ecosystem and contribute to the isotopic labeling of cellulose contained in nonphotosynthetic tissues such as tree trunks and roots, resulting in the heterotrophic component of the plant's isotopic signature. In addition, the plant's internal response to environmental humidity governs the isotopic composition of leaf water and contributes to the isotopic labeling of carbohydrates at the site of photosynthesis, resulting in the autotrophic component of the plant's isotopic signature. The final isotopic value (δ = either δD or δ^{18}O) of tree-ring cellulose can therefore be described by (Roden & Ehleringer 1999)

$$\delta_{\text{cellulose}} = f(\delta_{\text{heterotrophic}}) + (1 - f)(\delta_{\text{autotrophic}}),$$

which separates the heterotrophic and autotrophic contribution of ecosystem processes into fractional (f) contributions to the ultimate cellulose composition.

Previous measurements on three species of trees indicated that 32% of hydrogen and 42% of oxygen atoms in cellulose have undergone exchange with stem water during cellulose synthesis; the remainder retained the isotopic signal acquired during isotopic exchange with leaf water (Roden & Ehleringer 1999, Roden et al. 2000). The net biochemical fractionation between cellulose and water during heterotrophic synthesis of cellulose was observed to be 158‰ for δD and 30‰ for δ^{18}O (Luo & Sternberg 1992; Sternberg et al. 1986, 2006; Yakir & DeNiro 1990). Experiments with *Lemna gibba* have indicated that the total change in isotopic composition due to autotrophic processes between leaf water and carbohydrate intermediates during cellulose synthesis is −171‰ for δD and 27‰ for δ^{18}O (Yakir & DeNiro 1990). These findings lead to the relationship

$$\delta_{\text{cellulose}} = f(\delta_{\text{stem water}} + \varepsilon_{\text{heterotrophic}}) + (1 - f)(\delta_{\text{leaf water}} + \varepsilon_{\text{autotrophic}}),$$

which recasts the heterotrophic contribution as the composition of stem water modified by the net heterotrophic biochemical isotopic fractionation between stem water and carbohydrate intermediates during cellulose synthesis ($\varepsilon_{\text{heterotrophic}}$), and also recasts the autotrophic contribution as the composition of leaf water modified by the net autotrophic biochemical isotopic fractionation between leaf water and carbohydrate intermediates during cellulose synthesis ($\varepsilon_{\text{autotrophic}}$).

The isotopic composition of leaf water undergoing transpiration is described by (as discussed in Yakir & Sternberg 2000)

$$\delta_{\text{leaf water}} = \delta_{\text{stem water}} + E_{\text{eq}} + E_{\text{k}} + (\delta_{\text{vapor}} - \delta_{\text{stem water}} - E_{\text{k}})(e_{\text{a}}/e_{\text{l}}),$$

where δ_{vapor} is the isotopic composition of water vapor in the atmosphere, E_{eq} and E_{k} are the respective equilibrium and kinetic isotopic fractionations between liquid water and the vapor generated during evaporation, and e_{a} and e_{l} represent atmospheric vapor pressure and the vapor pressure inside the leaf, respectively. Environmental water has been shown to enter the plant passively without isotopic fractionation (i.e., $\delta_{\text{stem water}} = \delta_{\text{environmental water}}$) (White 1988). Assuming that atmospheric water vapor is in isotopic equilibrium with environmental water, the isotopic composition of atmospheric water

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vapor can be expressed as

$$\delta_{\text{vapor}} = \delta_{\text{stem water}} - E_{\text{eq.}}$$

In addition, assuming that the temperature of the leaf is nearly equal to that of the atmosphere allows for the vapor pressure ratio e_a/e_l to be approximated by fractional humidity (h):

$$\delta_{\text{leaf water}} = \delta_{\text{stem water}} + (E_{\text{eq}} + E_{\text{k}})(1 - h).$$

One can then write

$$\delta_{\text{cellulose}} = f(\delta_{\text{stem water}} + \varepsilon_{\text{heterotrophic}}) + (1 - f)[\delta_{\text{stem water}} + (E_{\text{eq}} + E_{\text{k}})(1 - h) + \varepsilon_{\text{autotrophic}}].$$

Widespread observation of the linear relationship $\delta D = m\delta^{18}O + b$ in environmental water (Craig 1961) allows one to solve for fractional humidity (h) during the Eocene using the isotopic composition of fossil cellulose. Specification for $\delta^{18}O$ and δD values yields

$$\delta D_{\text{cellulose}} = m\delta^{18}O_{\text{environmental water}} + b + f_H \varepsilon_{\text{heterotrophic-H}} + (1 - f_H)[(E_{\text{eq-H}} + E_{\text{k-H}})(1 - h) + \varepsilon_{\text{autotrophic-H}}]$$

and

$$\delta^{18}O_{\text{cellulose}} = \delta^{18}O_{\text{environmental water}} + (f_O \varepsilon_{\text{heterotrophic-O}}) + (1 - f_O)[(E_{\text{eq-O}} + E_{\text{k-O}})(1 - h) + \varepsilon_{\text{autotrophic-O}}],$$

where m is the slope and b is the y-intercept of the linear relationship between environmental $\delta^{18}O$ and δD values, and the subscripts H and O specify the relevant isotope. Given the known and fixed terms describing the isotopic linear relationship of environmental water, and the biochemical and kinetic fractionations for both isotopes, it is possible to solve the last two equations simultaneously for humidity and $\delta^{18}O_{\text{environmental water}}$ on Axel Heiberg Island during the middle Eocene. Because the solution is highly sensitive to the value of the slope (m) used to characterize the relationship between environmental $\delta^{18}O$ and δD values, and because Jahren & Sternberg (2003) found that fossil cellulose from Axel Heiberg Island exhibited a strikingly high slope ($m = 9.5$), this is the value of m used in calculating Eocene humidity.

Using the above methods, Jahren & Sternberg (2003) calculated an average growing-season-relative humidity of ~67% within the middle Eocene Arctic forests. Assuming MAT $\approx 13.2 \pm 2.0$°C (**Table 5**) implies a climate similar to that experienced within the Pacific Northwest today. Intraseasonal subsampling of growth rings within fossil wood revealed distinct patterns in $\delta^{18}O$ and δD values, which allowed for the calculation of changes in relative humidity during the growing season (Jahren & Sternberg 2007). Intraseasonal subsampling of fossil tree rings from Axel Heiberg Island revealed increases in relative humidity and reflected an end-of-season humidity regime of between 90% and 100% (**Figure 13**). Such massive increases in relative humidity would be expected from an ecosystem that experienced high annual rates

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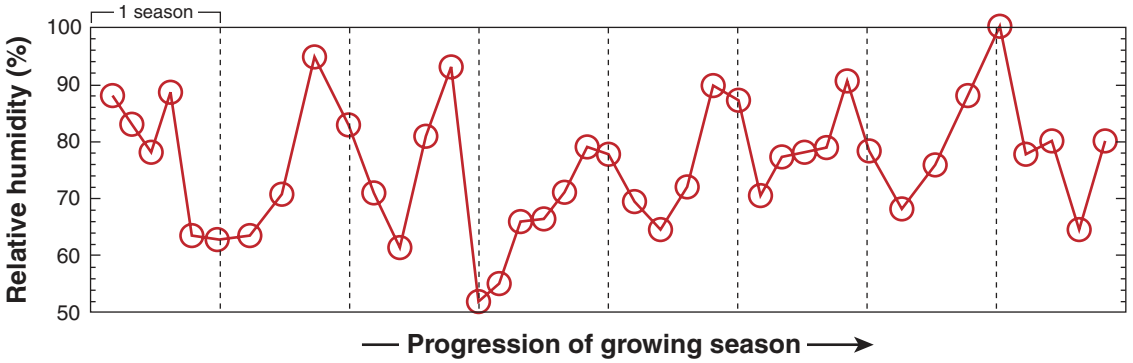

Figure 13

Patterns in changing relative humidity during the growing season, as calculated from the oxygen- and hydrogen-isotope composition of fossil cellulose, sampled within rings of fossilized *Metasequoia*. Intraseasonal variability shows a steady increase in relative humidity to very high levels (approaching 100%) by the end of the growing season.

of evapotranspiration associated with explosive deciduous growth (Mora & Jahren 2003).

Application of the Clausius-Clapeyron equation in conjunction with the ideal gas law allows for the calculation of the actual vapor pressure of water in the atmosphere, as well as its total mass in a given volume. Present-day high-Arctic ecosystems have actual vapor pressure of 4.1 mm Hg during the growing season (4.3 g H_2O per m^3 of atmosphere). Given the relative humidity and temperature estimates discussed here, the Arctic middle Eocene entailed an actual paleo-vapor pressure of ~8.2 ± 0.9 mm Hg on Axel Heiberg Island (8.3 ± 0.9 g H_2O per m^3 of atmosphere). This value is approximately double the atmospheric water content seen in the Arctic today. This increased atmospheric water content would have contributed to a greenhouse effect during the middle Eocene, thus increasing atmospheric mixing and delivering water vapor to higher levels of the Arctic atmosphere. Although such a water-vapor feedback would not have caused middle-Eocene-warm temperatures, it would have helped maintain the warmth, particularly through the dark polar winters.

Carbon Loss through Respiration

Photosynthesis is the basic process by which plants convert CO_2 into carbohydrate, using light energy as an energy source:

$$CO_2 + H_2O + \text{light energy} \rightarrow CH_2O + O_2.$$

Photosynthesis by conifers is always accompanied by the process of photorespiration, which consumes oxygen and releases CO_2 in the presence of light. Photorespiration reduces the efficiency of photosynthesis by wasting the activity of the photoenzyme RuBisCO, resulting in only one molecule of 3-phosphoglycerate and thus reducing

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net carbon fixation during metabolism. Dark respiration is a similar process that occurs during the absence of light, again resulting in carbon leakage from the plant organism. Because of the continuously dark three-month winters implied by the geographical location of the Fossil Forest during the Eocene (**Figure 1** and **Figure 5**), researchers have hypothesized that deciduousness in Arctic *Metasequoia* of the middle Eocene was the primary strategy for eliminating carbon loss due to unabating dark respiration during the winter. However, greenhouse experiments have shown that the quantity of carbon lost annually by shedding a deciduous canopy is significantly greater than that lost by evergreen trees through wintertime respiration and leaf-litter production (Royer & Beerling 2003).

By intraseasonally microsampling tree rings, Helle & Schleser (2004) repeatedly observed a distinct annual pattern in the $\delta^{13}C$ value of modern wood from broadleaf species. These authors interpreted the trends they saw: (*a*) At the beginning of the growing season, a systematic increase in $\delta^{13}C$ value was due to the mobilization of stored carbon with inherently high isotopic value; (*b*) during the growing season, a systematic decrease in $\delta^{13}C$ value was due to the steadily increasing incorporation of recently fixed carbon with inherently low isotopic value; and (*c*) a systematic increase in $\delta^{13}C$ value during the late season was due to respiration, which preferentially removes light carbon from the organism.

Microsampling of Axel Heiberg wood at high resolution (Jahren & Sternberg 2007) revealed the patterns seen in **Figure 14**. On average, the $\delta^{13}C$ values of fossil

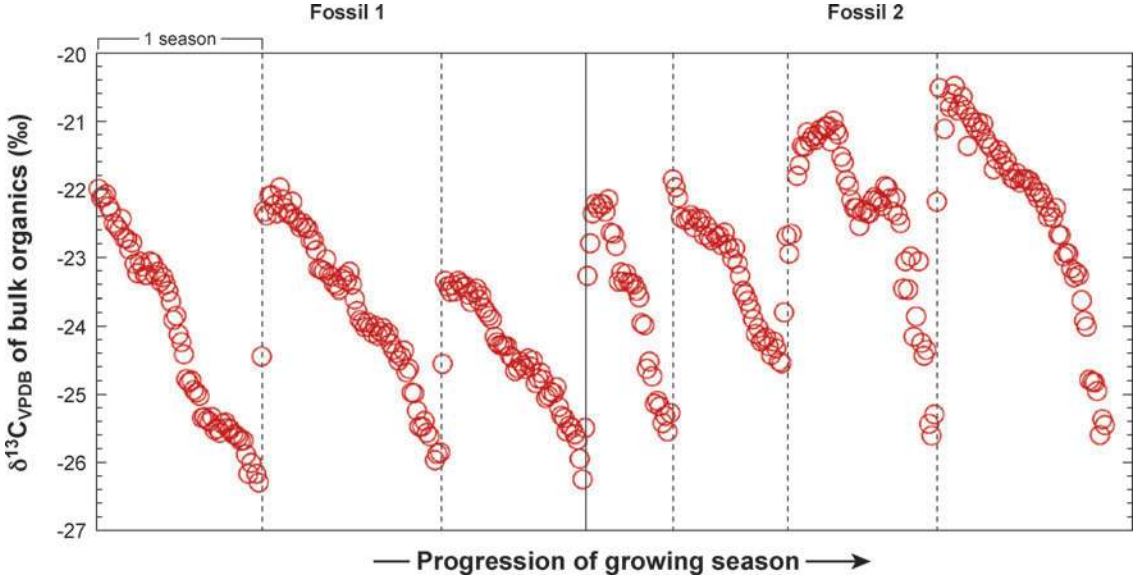

Figure 14

Observed patterns in the carbon-isotope signature of fossil wood, sampled at high resolution. Dashed lines indicate the division between adjacent rings (the late-wood/early-wood boundary); the solid line separates the two fossils analyzed. Each ring was sampled into at least 50 consecutive subsamples.

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rings decreased by approximately 4‰ to 5.5‰ during the course of the growing season; this decreasing trend was apparent for every fossil ring analyzed. This pattern indicates that synthesized wood reflects a switchover from stored carbon to actively photosynthesized carbon during the growing season of these Arctic fossils. These results accentuate the deciduous habit of these trees; conifer trees show a different pattern in $\delta^{13}C$ value as microsampled within tree rings. In particular, Barbour et al. (2002) showed that, within conifers growing at middle-to-high latitudes, lowest $\delta^{13}C$ values occurred when temperatures were highest, relative humidity was lowest, and water stress was most intense. We are confronted with a truly unique ecosystem: that of extensive deciduous conifer forests that persist through polar light-regimes during summer and winter. The short duration of transitional seasons (**Figure 14**) may have led to a rapid shutdown period during the shedding of leaf tissue.

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THE EMERGENT VISION OF THE SITE

The studies discussed here leave us with a unique vision of a middle Eocene ecosystem, thriving above the Arctic Circle. We imagine lush conifer forests, dominated by deciduous *Metasequoia*, complemented by a diverse understory of flowering trees and shrubs. Ferns and fungi inhabited the water-saturated soils, from which significant methanogenesis followed acetate reduction. Temperatures were warm, rarely if ever below freezing, and greater than 12°C as an annual average; we do not believe there was an ice pack in this polar region. Although we do not know the exact CO_2 level, we believe it was not lower than that of today. Relative humidity levels were high, particularly at the end of the growing season, implying a rain forest environment. Finally, the explosive deciduous growth of these conifer forests resulted in a thick organic litter layer that provided shelter for invertebrate and vertebrate animals.

SUMMARY POINTS

1. During the middle Eocene (~45 Ma), extensive forested landmasses located above the Arctic Circle were subject to three months of total darkness and three months of continuous light each year.
2. Paleobotanical excavations of Axel Heiberg Island, in Arctic Canada, have revealed lush deciduous conifer forests of middle Eocene age, dominated by *Metasequoia*.
3. Macrofossil and palynomorph identification revealed the presence of fir, cypress, larch, redwood, spruce, pine, and hemlock trees, with an understory containing maple, alder, birch, hickory, chestnut, beech, ash, holly, walnut, sweetgum, sycamore, oak, willow, and elm trees.
4. Paleosols from the site suggest water-saturated, acidic, and chemically reducing organic soil environments within the Fossil Forest, conducive to methanogenesis via acetate reduction.

5. Diverse methods have indicated that MATs exceeded 12°C within the Fossil Forest, and that heavy frosts did not occur. No consensus exists as to the pCO_2 levels during the time.
6. Stable-isotope analyses of extracted cellulose and *n*-alkanes imply the absence of arctic ice and high relative humidity, often approaching 100% toward the end of the growing season.
7. Intraseasonal carbon-isotope analyses of *Metasequoia* tree rings show a clearly deciduous pattern of carbon storage and photosynthetic carbon assimilation, including efficient senescence prior to the long, dark polar winter.

FUTURE ISSUES

1. An unequivocal estimate of middle Eocene CO_2, confirmed via multiple techniques, is badly needed in order to more fully understand the carbon cycle of the period and related greenhouse conditions.
2. A reliable way of estimating the total amount of geologic time contained within the stratigraphic lignites of the Fossil Forest would allow for high-resolution studies of changing environments, particularly within shifting understory communities.
3. Fieldwork on other middle Eocene sites will help elucidate the general versus specific nature of the Axel Heiberg Fossil Forest.

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