classification purposes. Additional studies could indicate strains with properties that provide useful genetic information. *Methylomonas* sp. 761M, with its responses to the presence of supplemented nutrients, now offers a system for studying the genetics of obligate methane-oxidizers.

Derivatives of broad host-range conjugative and mobilizable plasmids have been constructed and can serve as cloning vectors in methylotrophs. Encoding multiple drug resistances and possessing several cloning sites, these plasmids enable the construction of gene banks that can be maintained in *E. coli* and transferred to methylotrophs. The use of R-prime plasmids for the mobilization of chromosomal markers is an effective way to bypass in vitro recombinant DNA techniques. The application of such in vivo cloning methods to methylotrophs has provided a means for the identification of desired genes. A resident methylotroph plasmid has been implicated in chromosome mobilization, and this could have broader applications for gene transfer.

These developments establish the foundation for advancing the knowledge of methylotroph genetics and for applying this knowledge toward the beneficial use of this interesting group of bacteria.

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RESEARCH ARTICLE

Arctic Terrestrial Biota: Paleomagnetic Evidence of Age Disparity with Mid-Northern Latitudes During the Late Cretaceous and Early Tertiary

Leo J. Hickey, Robert M. West
Mary R. Dawson, Duck K. Choi

During the past century abundant evidence has accumulated of a thriving biota at high Arctic paleolatitudes during the late Mesozoic and early Cenozoic eras. Arctic floras were first described by Heer in his seven-volume *Flora Fossilis Arctica*, published between 1868 and 1883 (*1*). Data on pollen and invertebrates in the Late Cretaceous and early Tertiary are more recent, the result of intensive geological exploration of Spitsbergen (*2*), Greenland (*3, 4*), and the Canadian Arctic Archipelago (*5, 6*). The predominantly terrestrial sequences characterizing the latest Cretaceous and early Tertiary have been dated mainly by comparing them with mid-northern latitude floras, although limited and at times tenuous association with marine or brackish-water beds containing datable invertebrates has been reported for North and West Greenland (*3, 7*), Spitsbergen (*8*), and west-central Ellesmere Island (*6*). The discovery of land vertebrate fossils of early to middle Eocene affinities in the upper part of the Eureka Sound Formation (*9*) at Bay Fiord on Ellesmere Island (locality 4, inset map in Fig. 1) provided an apparently reliable and independent source of relative age dates keyed to the land-mammal sequence of western North America (*10*).

Five areas on Axel Heiberg and Ellesmere islands (inset map in Fig. 1) have now yielded substantial megafloral and palynological collections (*11, 12*) as well as invertebrate (*10, 13*) remains and additional vertebrate material from the Bay

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Fiord area (Fig. 1). The stratigraphic elevation of each of the localities with fossils was determined from measured or reconnaissance sections or from trigonometric extrapolation on aerial photographs.

After detailed sampling in the Bay Fiord area, Vinson (*14*) produced a magnetic anomaly profile through the Eureka Sound Formation, which was later recalibrated and revised (Fig. 2). This revision is based on the magnetic anomaly ages of Lowrie and Alvarez (*15*), recognition of the distinctive "stuttered" magnetic normal interval 24 associated with vertebrates of Eocene affinities, placement of normal zone 25 at the base of the Clarkforkian Provincial Stage in its type area in the Bighorn Basin of Wyoming (*16*), and recognition of long magnetic normal interval 33 near the base of the Eureka Sound sequence. This latter assignment is corroborated by the finding of marine mollusks of late Santonian to early Campanian age in member I of the Eureka Sound Formation on Fosheim Peninsula (locality 2 in Fig. 1) (*6*) and by a diverse assemblage of Campanian dinoflagellates in sediments of member II south of Bay Fiord (locality 4 in Fig. 1) (*17*).

When the stratigraphic ranges of the Arctic vertebrates and plants were plotted with the revised magnetic zonation, striking disparities with the mid-latitude temporal ranges were noted for many

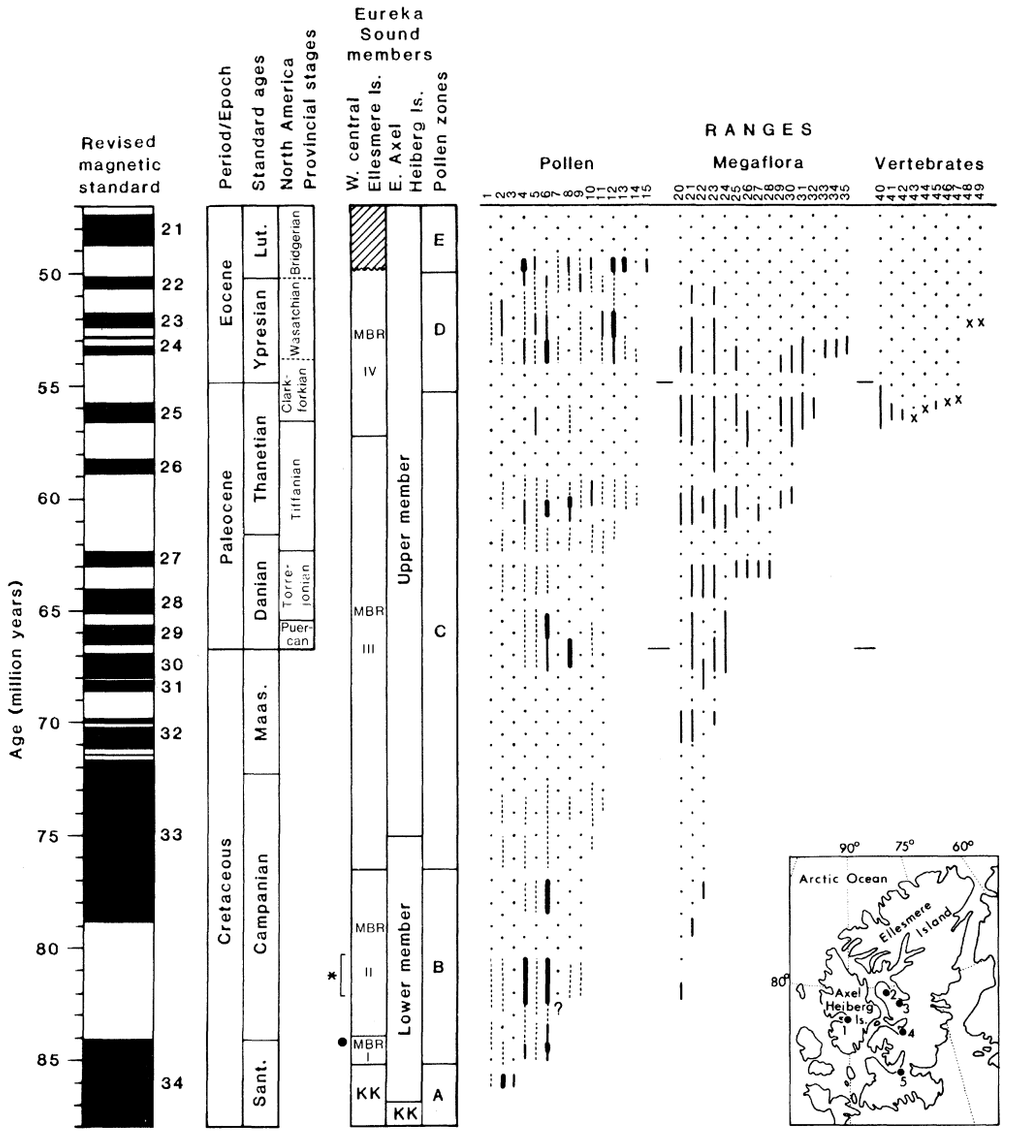

Fig. 1. Magnetostratigraphic, absolute, and relative correlation of units of the Eureka Sound Formation and the ranges of selected plant and vertebrate taxa. Localities of sample sites are shown on the inset map. Chronology of the Revised Magnetic Standard (RMS) and correlation with the standard epochs and ages follow Lowrie and Alvarez (*15*). The RMS was correlated with North American Provincial Stages (*16, 31*) as indicated by the solid lines dividing the provincial ages; the dashed lines indicate our inferred placement of the stage boundaries. Eureka Sound members are designated informally (*6*). The position of a collection of marine mollusks of late Santonian to early Campanian age is shown by the dot to the left of the member column; the asterisk and bracket mark the stratigraphic range of the Campanian dinoflagellate flora (*17*). For pollen ranges, abundance is indicated as follows: dashed line, rare (< 1 percent); thin line, moderate (1 to 5 percent); and thick line, common (> 5 percent). Post-Campanian occurrences of pollen groups 1 and 2 probably represent reworked grains. For megafloral and vertebrate taxa, solid lines indicate occurrence, and x's indicate occurrence at a single locality. Key to taxa: for pollen, 1) "Oculata" groups including *Wodehousia* and *Azonia*, 2) *Expressipollis* and the Triprojectacites group including *Aquilapollenites, Integricorpus, Manicorpus*, and *Triprojectus*, 3) *Tricolpites* n. sp., 4) *Polyvestibulopollenites verus* (Potonie) Thompson and Pflug 1953 (*Alnus* type), 5) "*Betula*" *claripites* Wodehouse 1933 and *Caryapollenites*, 6) *Triporopollenites mullensis* (Simpson) Rouse and Srivastava 1972 and *Paraalnipollenites alterniporus* (Simpson) Srivastava 1975, 7) *Platycaryapollenites* spp., 8) *Ulmipollenites* spp., 9) *Polyatriopollenites stellatus* (Potonie) Pflug 1953, 10) *Pistillipollenites mcgregorii* Rouse 1962, 11) *Triprojectus* sp. cf. *T. echinatus* Mtchedlishvili 1961, 12) Tiliaceae-Bombacaceae, 13) *Ailanthipites berryi* Wodehouse 1933, 14) *Pandaniipites* sp., and 15) *Smilacipites* sp. cf. *S. echinatus* Wodehouse 1933 and a new genus and species of the Triprojectacites group; for megaflora, 20) "*Ampelopsis*" *acerifolia* (Newberry) Chaney, 21) *Metasequoia occidentalis* (Newberry) Chaney, 22) "*Carya*" *antiquorum* Newberry, 23) *Cercidiphyllum* sp. cf. *C. genetrix* (Newberry) Hickey, 24) *Betula stevensonii* Lesquereux, 25) *Glyptostrobus europaeus* (Brongniart) Heer, 26) *Averrhoites affinis* (Newberry) Hickey, 27) *Platanus raynoldsii* Newberry, 28) *Zingiberopsis attenuata* Hickey and Peterson, 29) *Platanus nobilis* Newberry, 30) cf. *Chaetoptelea microphylla* (Newberry) Hickey, 31) *Vinea* sp., 32) *Comptonia cuspidata* Lesquereux, 33) cf. "*Grewiopsis*" *tennesseensis* Berry, 34) "*Pterocarya*" *hispida* Brown, and 35) *Zingiberopsis isonervosa* Hickey; for vertebrates, 40) *Coryphodon* sp., 41) *Hyrachyus* sp., 42) rodents, 43) *Lambdotherium* sp., 44) *Geochelone* sp., 45) phenacolemurid, 46) Emydidae, 47) *Pantolestes* sp., 48) *Manteoceras* sp., and 49) tillodont. Localities on inset map: 1) Strand Fiord, 2) Fosheim Peninsula, 3) South Bay, 4) Bay Fiord, and 5) Stenkul Fiord. Abbreviations: KK, Kanguk Formation; Sant., Santonian; Maas., Maastrichtian; and Lut., Lutetian.

taxa (Fig. 1). Thus, among vertebrates, forms characterizing the Wasatchian (early Eocene) and Bridgerian (middle Eocene) Provincial stages (*18*) at middle northern latitudes occur just above magnetic normal interval 25, or in the late Paleocene, equivalent to the Clarkforkian Provincial Stage (*16*). *Hyrachyus*, known previously from very late Wasatchian and Bridgerian strata, and *Pantolestes*, of apparent Bridgerian age, occur in this Arctic Clarkforkian interval (Fig. 1). Other precocious forms include tortoises and emydid turtles of modern aspect (44 and 46 under vertebrates in Fig. 1) (*13*). In general, these anomalous occurrences are from 2 to 4 million years earlier in the Arctic than at more southern latitudes.

Still more drastic heterochroneity is apparent among plants, especially in the lower- to midportion of the Eureka Sound Formation. *Aquilapollenites, Azonia, Wodehousia* (pollen groups 1 and 2 in Fig. 1), and other members of the typical latest Cretaceous palynoflora of mid-latitude western North America and northeastern Asia disappear, except as reworked material, by the early part of the Campanian Stage. The palynoflora that replaces them (zones B and C) and that persists through the remainder of the Cretaceous in the high Arctic is characteristic of the early and late Paleocene at mid-northern latitudes. The same is true of the associated megaflora. However, the floral sequence returns to synchroneity with that of lower latitudes at the lower boundary of zone D, which coincides approximately with the beginning of the Eocene. Disagreement in apparent ages between pollen and marine assemblages has been recorded previously in the high Arctic but was not recognized as significant (*5, 19, 20*).

Our data provide strong evidence that the terrestrial Arctic biota of the latest Cretaceous and early Tertiary was profoundly out of phase with that of more southerly latitudes until the Eocene Epoch. In the Arctic, forms that characterize Paleocene strata at middle latitudes first occur in early Campanian beds, approximately 18 million years before they appear to the south. Pollen taxa like *Pistillipollenites mcgregorii* (10 in Fig. 1) and numerous megafossils including *Metasequoia occidentalis* and "*Carya*" *antiquorum* (21 and 22 in Fig. 1) probably had their origins in Arctic regions and spread southward during the climatic deterioration of the latest Cretaceous and early Paleocene (*21*). Thus, suggestions of heterochroneity of Late Cretaceous and Tertiary mid- and high-latitude floras (*22*), although recently questioned (*23*), appear to be a reality.

Among vertebrates, a moderately diverse assemblage of perissodactyls appears rather suddenly at mid-latitudes at the beginning of the Eocene. Radinsky has proposed the middle Paleocene phenacodontid condylarths, particularly *Tetraclaenodon,* as plausible ancestors for the primitive perissodactyl *Hyracotherium* (*24*). However, of the two purported late Paleocene occurrences of *Hyracotherium*, the one from Wyoming (*25*) is of dubious provenance (*26, 27*) and that from Baja California (*28*) of somewhat uncertain age (*27*). In addition, the suggestion of a Central American source of perissodactyls (*29*) has only the Baja California occurrence and evidence of climatic warming to support it. On the basis of the magnetic correlation we propose, the primary radiation, if not the origin, of this group may well have taken place not in the subtropics but in the Arctic. Similarly, the dermopteran *Plagiomene* and land tortoises have their first appearance at high latitudes. On the other hand, *Coryphodon* appears synchronously in the Clarkforkian record of both the Arctic and middle latitudes while other forms like the rodents and, among the plants, *Platycarya*, appear approximately synchronously with their earliest occurrences at mid-latitudes. It is important to note, however, that since vertebrate fossils are not found below member IV of the Eureka Sound Formation, these occurrences represent minimum ages for their presence in the Arctic.

Abstract. *Magnetostratigraphic correlation of the Eureka Sound Formation in the Canadian high Arctic reveals profound difference between the time of appearance of fossil land plants and vertebrates in the Arctic and in mid-northern latitudes. Latest Cretaceous plant fossils in the Arctic predate mid-latitude occurrences by as much as 18 million years, while typical Eocene vertebrate fossils appear some 2 to 4 million years early.*

Our magnetic correlations of the terrestrial fossil record of the Arctic during the Late Cretaceous and early Tertiary emphasize that extreme caution must be exercised in extending the temporal connotations of mid-latitude pollen ranges or of the so-called land mammal stages to the Arctic. In addition, evidence for an Arctic origin of a significant portion of the Paleocene and early Eocene flora of mid-latitudes as well as of numerous taxa of terrestrial vertebrates, including members of the perissodactyls, vitiates the view of a warmer Arctic as merely a passive land bridge between North

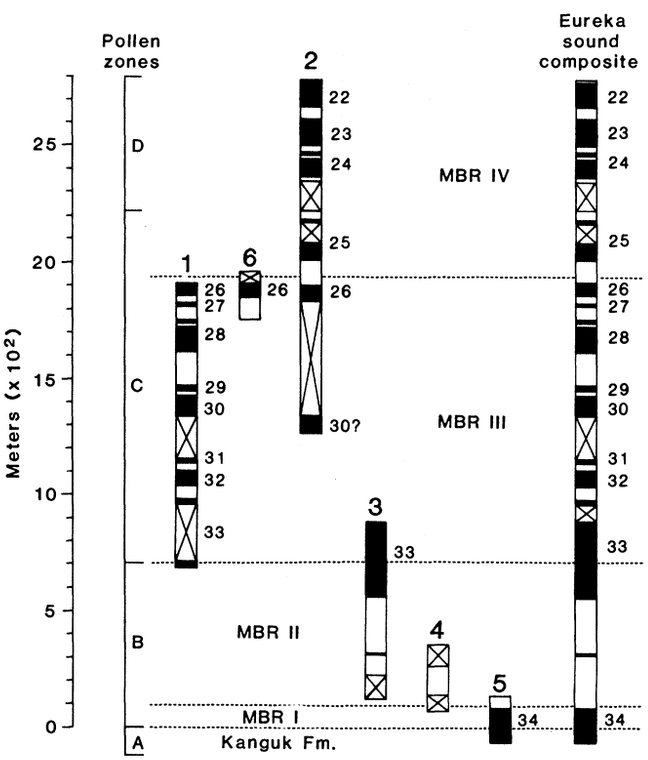

Fig. 2. Composite paleomagnetic sequence for the Eureka Sound Formation assembled from our revision of magnetostratigraphic sections 1 through 6 measured in the vicinity of Bay Fiord (locality 4, Fig. 1) (*14*). The vertical scale shows the stratigraphic elevation from the base of the Eureka Sound Formation. Member (MBR) designations follow West *et al.* (*6*). Magnetic normal intervals are shaded, reversed intervals are white, and covered intervals are indicated by crossed lines. Correlation is to the revised marine standard magnetic sequence (*15*).

America and Eurasia (*10, 26*). For much of earth's history, polar regions had a comparatively mild climate and a biota far richer than that of the current, relatively unusual period of severe refrigeration (*30*). Yet, imprecise correlations and a relatively scanty terrestrial record have allowed the Arctic to be disregarded as an important locus of evolution. However, given the huge land mass of the Arctic, its biota adapted to the unusual combination of a mild climate and a months-long polar day-night cycle, and given our findings on age disparity, it is at least plausible that during much of the Phanerozoic this currently inhospitable region may have served as the birthplace for important biotic innovations and for major groups that later radiated to lower latitudes.

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9. The Eureka Sound Formation is a lignitic, synorogenic molasse in excess of 3000 m thick that consists of cyclically bedded shale, carbonaceous mudstone, sandstone, and lignite with a sequence of marine to lacustrine clay, siltstone, marl, limestone, and sandstone in its middle portion on west central Ellesmere Island. Depositional environments range from delta front, to lower delta plain, to flood plain deposits on the upper delta plain (*6*).
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11. Megafloral remains consisted of 1726 specimens in 53 species from 31 localities. A diverse palynomorph assemblage of over 350 species included 101 species of acritarchs and dinoflagellate cysts, 61 species of bryophytes and ferns, 38 species of gymnosperms, and 94 species of angiosperms collected from 50 localities [D. K. Choi, thesis, Pennsylvania State University, University Park (1983)].
12. The following pollen designations, based on indicator species, were established for the pollen flora: zone A, abundant occurrence of *Expressipollis* and pollen of the Triprojectacites group including *Aquilapollenites* and a new species of *Tricolpites*; zone B, first appearance of *Polyvestibulopollenites verus* and *Paraalnipollenites alterniporus* with rare *Aquilapollenites*; zone C, first appearance of *Pistillipollenites mcgregorii* and *Triprojectus* cf. *echinatus*; zone D, first undoubted occurrence of *Platycarya* with abundant pollen of Tiliaceae-Bombacaceae; and zone E, moderate abundances of *Ailanthipites berryi, Smilacipites* cf. *echinatus*, and a new genus of the Triprojectacites group.
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17. An assemblage of 30 species of dinoflagellates was recovered from locality 7967 south of Bay Fiord (stratigraphic position marked by a bracket on Fig. 1). Among the more important taxa are *Chatangiella* spp., *Isabellidinium acuminatum, Laciniadinium biconiculum, L. firmum, Trithyrodinium suspectum, Ginginodinium ornatum*, and *Saeptodinium eurypylum*, most of which belong to a Campanian boreal assemblage [J. K. Lentin and G. L. Williams, *Am. Assoc. Stratigr. Palynol. Contrib. Ser.* **7**, 27 (1980)].
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20. This disparity between the apparent ages of terrestrial floras and marine faunas appears to extend as well to the earliest Arctic angiosperm floras, middle Cretaceous in age, in Alaska. In the Yukon-Koyukuk Basin, marine sediments dated as Albian to early Cenomanian [R. W. Imlay and J. B. Reeside, *Geol. Soc. Am. Bull.* **65**, 223 (1954); W. W. Patton, Jr., *U.S. Geol. Surv. Prof. Pap. 774-A* (1973), pp. 1–17; R. J. Scott and C. J. Smiley, *U.S. Geol. Surv. Circ. 794* (1979), pp. 89–111] are intercalated with terrestrial sediments bearing a relatively advanced flora of Cenomanian aspect [A. Hollick, *U.S. Geol. Surv. Prof. Pap. 159* (1930); W. A. Bell, *Geol. Surv. Can. Bull. 94* (1963); R. A. Spicer, *Plant Megafossils from the Mid-Cretaceous Yukon-Koyukuk Province, West Central Alaska*, privately published under U.S. Geological Survey contract 14-08-0001-19175 (1981)]. These floras contain a highly diverse assemblage of platanoids and other hamamelid angiosperms—forms with a basic leaf type particularly well adapted to a seasonal climate [T. J. Givnish, thesis, Princeton University (1976)]—as well as gymnosperms, ferns, and magnoliid and rosid angiosperms including *Sapindopsis*, many of which are more typical of the Albian Stage. Because these advanced platanoids and other hamamelids are found in Cenomanian strata at lower latitudes, paleobotanists have questioned the Albian marine dates for this flora. However, the parallels between this situation and the age disparity in the Canadian Arctic suggest that upon reaching high latitudes during the general poleward migration of the flowering plants, the precursors of the more advanced platanoid-hamamelid group underwent rapid diversification in a favorable climatic regime. We propose that the disagreement between the marine and terrestrial dates is the result of the temporal lag between the diversification of the platanoid and hamamelid taxa in the north and their later appearance in lower latitude floras.
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