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Vertebrate Paleontology and the Cenozoic History of the North Atlantic Region*

By R. M. West and M. R. Dawson **

Abstract: Fossil vertebrates have been recovered from several lithofacies within the Paleogene Eureka Sound Formation at about 80° north latitude on Ellesmere Island, Canada. Both terrestrial and aquatic vertebrates are present, representing the classes Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves and Mammalia. The fossil vertebrates lend support to paleoclimatic interpretations of the Paleogene Arctic as warm, moist and seasonal. The vertebrates come from two distinct levels in the upper part of the Eureka Sound Formation. The fossiliferous rocks are probably Early to Middle Eocene in age, and the faunas appear to postdate faunal separation from Europe. However, geologic data suggest that actual physical contact between Europe and North America via either Spitsbergen or Iceland was not terminated until at least mid-Tertiary.

Zusammenfassung: Fossile Wirbeltiere wurden aus mehreren Lithofazies-Bereichen innerhalb der paläogenen Eureka Sound-Formation unter etwa 80° nördlicher Breite auf Ellesmere Island, Kanada, geborgen. Vertreten sind sowohl aquatische als auch terrestrische Wirbeltiere aus den Klassen Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves und Mammalia. Die fossilen Wirbeltiere stützen die Vorstellungen eines warmen, feuchten und jahreszeitlich verschiedenen Klimas in der paläogenen Arktis. Die Wirbeltiere kommen aus zwei verschiedenen Lagen im oberen Teil der Eureka Sound-Formation. Die fossilführenden Gesteine sind wahrscheinlich früh- bis mitteleozänen Alters, und die Faunen scheinen jünger als das Datum der Faunen-Trennung von Europa zu sein. Geologische Daten sprechen jedoch dafür, daß der reale Kontakt zwischen Europa und Amerika über Spitzbergen oder über Island nicht vor dem mittleren Tertiär aufhörte.

INTRODUCTION

The vertebrate fossil records of western Europe and western North America show a very high degree of faunal resemblance in the early Eocene (53—49 mya) followed by a

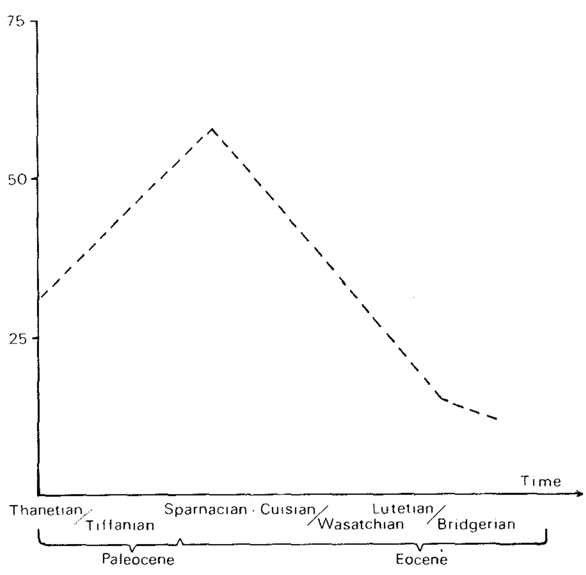

Fig. 1: Degree of mammalian generic similarity between Europe and North America, late Paleocene to late Eocene. Adapted from LEHMANN, 1973.

Abb. 1: Prozentualer Anteil der auch in Nordamerika vorkommenden Gattungen europäischer Säugetier-Faunen vom oberen Paläozän bis oberen Eozän.

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sudden decrease in similarity during the later part of that epoch (49—38 mya) (RUSSELL, 1968; SAVAGE, 1971; McKENNA, 1975) (Fig. 1). Such an abrupt change suggests that in the early Eocene North America and Europe were part of a single zoogeographic realm which was disrupted by middle Eocene time. The current plate tectonics model

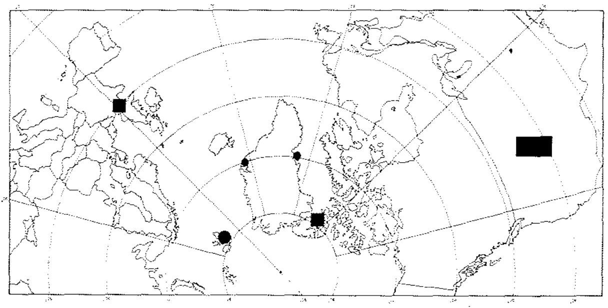

Fig. 2: Distribution of major Eocene fossil vertebrate regions (western United States, Paris—London Basin, and Ellesmere Island indicated by squares) and the major northern Atlantic Paleogene floral regions (Spitsbergen, East Greenland and West Greenland, indicated by the circles).

Abb. 2: Verteilung der bedeutenderen eozänen Vorkommen fossiler Wirbeltiere (westliche Vereinigte Staaten, Paris-Londoner Becken, Ellesmere Island, durch Quadrate bezeichnet) und der bedeutenderen nordatlantischen paläogenen Pflanzen-Vorkommen (Spitzbergen, Ost-Grönland, West-Grönland, durch Kreise bezeichnet).

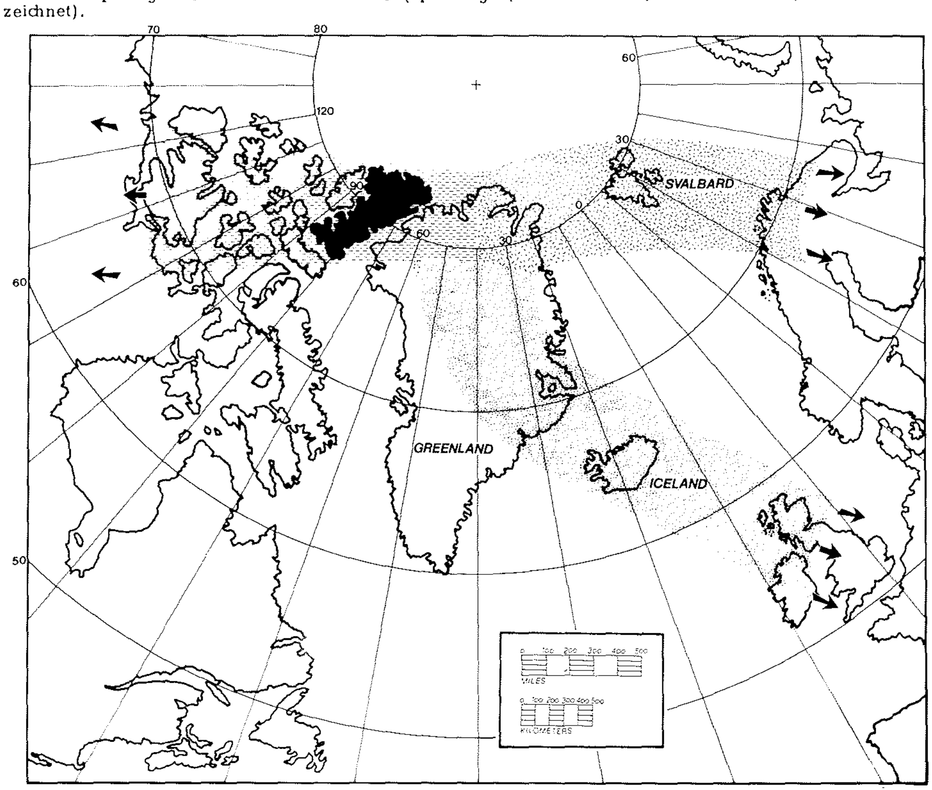

Fig. 3: Potential trans-North Atlantic terrestrial dispersal routes. The northeastern route is termed the DeGeer Route, and the southeastern route is called the Thulean Route.

Abb. 3: Mögliche Trans-Atlantische terrestrische Ausbreitungsbahnen. Die nördliche Bahn wird die de Geer-Route genannt, die südliche die Thule-Route.

of the history of the North Atlantic region (PITMAN & TALWANI, 1972; TALWANI & ELDHOLM, 1977) permits some explanation of this. It suggests that open ocean was being formed in the area between Greenland and Europe by about 58 mya, producing a partial barrier between western European and North American terrestrial faunas. On the other hand, several restricted areas were probably emergent until relatively late in the Tertiary and could have served as conduits for direct faunal exchanges between western Europe and North America.

Until recently, the only significant vertebrate paleontological data available on this matter were derived from the intermontane basins of western North America and the Paris—London Basin area of western Europe (Fig. 2). Our interest in documenting the history of a possible North Atlantic Paleogene terrestrial vertebrate fauna led us to work in the vast intervening area. Our hope was to obtain vertebrate fossil evidence which could contribute to our understanding of the termination of terrestrial biological continuity between Europe and North America.

It is convenient to regard potential Paleogene North Atlantic terrestrial exchange areas as a Y with its base to the west (Fig. 3). The southeast branch of the Y extends from

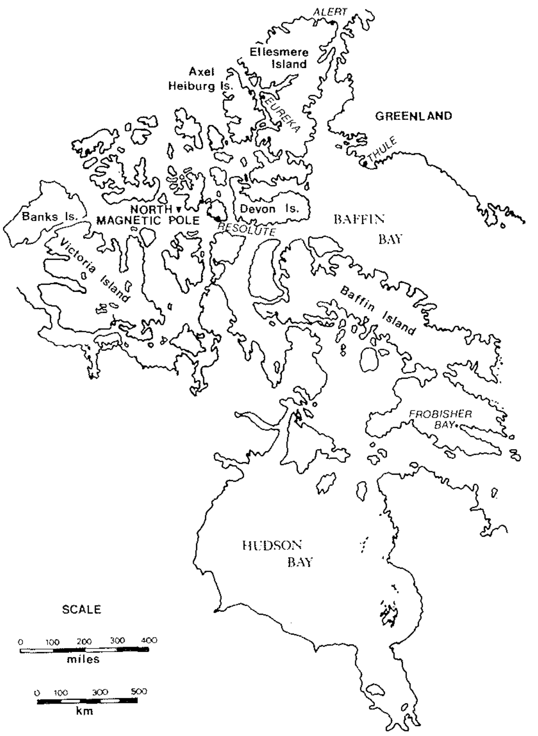

Fig. 4: The Canadian Arctic Islands.
Abb. 4: Die kanadischen arktischen Inseln.

Greenland to the British Isles via the Iceland-Greenland Ridge and the Iceland-Faeroes Ridge; this is referred to as the Thulean route. The northeast branch of the Y extends from Greenland to Scandinavia by way of Spitsbergen and the Barents Shelf; this is called the DeGeer route (McKENNA, 1971). The common western end of the Y extends from Greenland to North America via the northeastern Canadian Arctic. Regardless of which of the eastern possibilities is used, communication from Europe to North America went by way of northeastern Canada. This was the region in which we started our search for geographically intermediate Paleogene faunas.

Late Cretaceous and Paleogene clastic deposition in northern Canada is represented by the Eureka Sound Formation. This unit, which overlaps the limits of the Sverdrup Basin (BALKWILL, 1978), extends from Ellesmere Island on the northeast to Banks Island on the southwest (Fig. 4). Lithologically similar rocks appear in Peary Land, northern Greenland (DAWES, 1976) and along the Saganavirktok River, northern Alaska (DETTERMAN et al., 1975). The formation, which is composed of shales, mudstones, sandstones, local conglomerates and prominent coal seams and coaly deposits, reaches its maximum known thickness, about 3340 meters, south of the eastern end of Bay Fiord, central Ellesmere Island (A. D. MIALL, pers. comm., July 1977). It is locally divisible into a dark shale and sandstone lower unit with modest coals, a light shale and sandstone middle unit, and a variegated shale and sandstone upper unit with prominent coal beds (Fig. 5). The middle unit in the Bay Fiord region is largely marine (WEST et al., 1975), and scattered evidence of marine Eureka Sound has been noted elsewhere (TOZER, 1972; TRETTIN et al., 1972; MIALL, 1976). The lower and upper units represent more marginal to nonmarine paleoenvironments.

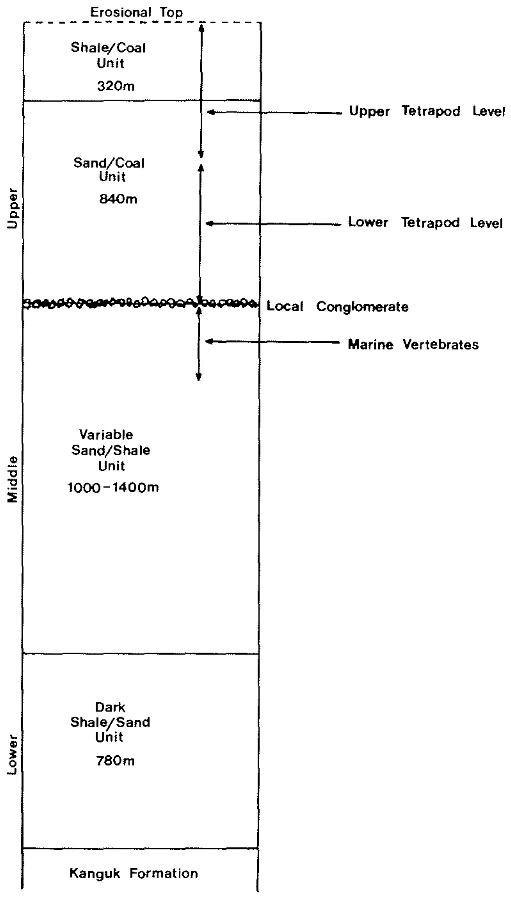

Fig. 5: Diagrammatic stratigraphy of the Eureka Sound Formation, Central Ellesmere Island (based on field work by A. MIALL, 1977).

Abb. 5: Stratigraphische Tabelle der Eureka Sound-Formation im zentralen Ellesmere Island (nach Gelände-Arbeiten von A. MIALL, 1977).

Our field work in the Eureka Sound Formation began in 1973. In 1975 the first tetrapods were found (DAWSON et. al., 1976), and in 1976 and 1977 the record was greatly augmented (WEST & DAWSON, 1977; WEST et al., 1977). The fossil vertebrates from the Eureka Sound Formation now are adequately known for approximate age assignment and some paleogeographic and paleoclimatologic interpretations.

FOSSILS OF THE EUREKA SOUND FORMATION

The Eureka Sound Formation is well exposed on Banks, Ellef Ringnes, Amund Ringnes, Lougheed, Axel Heiberg, Devon and Ellesmere Islands; the most extensive exposures are on Ellesmere and Axel Heiberg Islands (Fig. 6). While plant and invertebrate fossils have been found in most Eureka Sound Formation exposure areas, fossil vertebrates are thus far known only from a small area on west-central Ellesmere Island (Fig. 7). Plant fossils (Fig. 8) are one of the most characteristic features of the Eureka Sound Formation. Fossil wood, silicified, carbonized, and replaced by siderite, occurs in many places. Remains of trees up to 1.5 meters in diameter, and complete with annual rings,

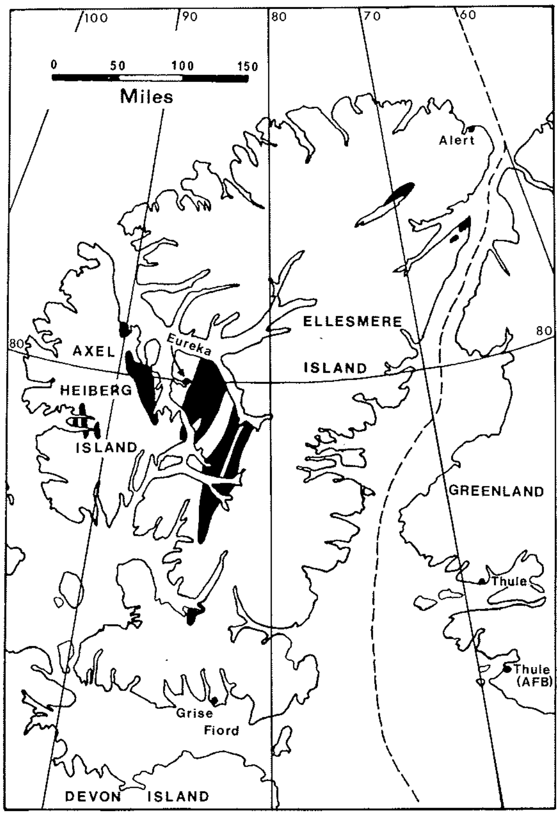

Fig. 6: Exposure of Eureka Sound Formation on Ellesmere and Axel Heiberg Islands.

Abb. 6: Ausstrich der Eureka Sound-Formation auf den Inseln Ellesmere und Axel Heiberg.

are found at several localities. Coal seams and coaly mudstones, often containing identifiable spores and pollen, are also widespread. This pollen gives an age range within the formation from Maastrichtian for pollen from Amund and Ellef Ringnes Islands (FORTIER et al., 1963; HOPKINS, 1973; FELIX & BURBRIDGE, 1973), to Eocene, for pollen from the Lake Hazen region, northern Ellesmere Island (CHRISTIE & ROUSE, 1976). The macrofloras, both leaves and seeds, of the Eureka Sound Formation (listed in FORTIER et al., 1963, and noted by numerous earlier authors) have not been as thoroughly studied as those of the Paleogene of Spitsbergen (SCHWEITZER, 1974) and

Greenland (Koch, 1963), which also give a range in age of Late Cretaceous to Eocene. The Eureka Sound macrofloras have a number of forms in common with the floras of Spitsbergen and Greenland, suggesting a similar age and paleoecology. These various floras all indicate a temperate climate at their localities during the late Cretaceous and Paleogene.

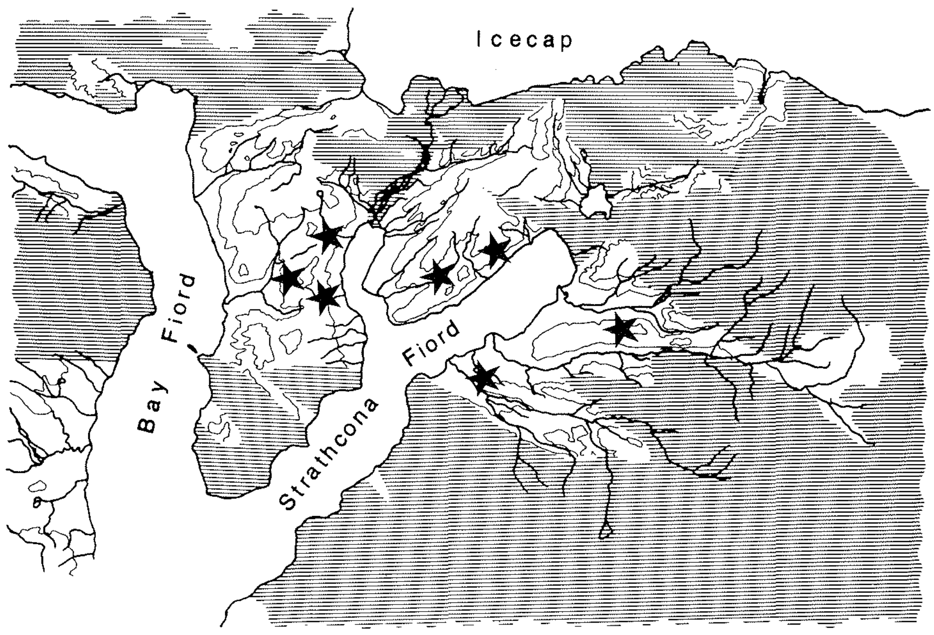

Fig. 7: Strathcona and Bay Fiord area of central Ellesmere Island. Stars indicate major sites of vertebrate fossils.

Abb. 7: Die Gebiete von Strathcona und Bay Fjord im zentralen Ellesmere Island. Sterne geben bedeutendere Fundstellen fossiler Wirbeltiere an.

Prior to our work the main occurrences of invertebrate fossils in the Eureka Sound Formation were a microfossil assemblage from Banks Island (THORSTEINSSON & TOZER, 1962) and pelecypod fragments from the Viks Fiord area, Devon Island (FORTIER et al., 1963), and from the Lake Hazen area, northeastern Ellesmere Island (PETRYK, 1968). In the course of our investigations, marine Foraminifera, scaphopods and pelecypods (WEST et al., 1975) have been found in the middle unit on Ellesmere Island, and freshwater gastropods and pelecypods have been recovered from the lower unit on Devon, Axel Heiberg and Ellesmere Islands and the upper unit on Ellesmere Island. These materials are suitable for oxygen-isotope paleotemperature determinations, but the relationships and age of the specimens are still undetermined.

The only Paleogene vertebrate from within the modern Arctic Circle reported previous to our work is a freshwater amiid fish from ~~Paleogene~~ continental rocks at Heerodden, Spitsbergen (LEHMAN, 1951). Our work has now produced abundant vertebrate remains from a small area (Fig. 7) in the Eureka Sound Formation, in the vicinity of Strathcona Fiord and Bay Fiord, central Ellesmere Island, near the eastern margin of the Sverdrup Basin. All the known vertebrate localities are in the same synclinal valley, the structure of which has preserved the upper beds of the Eureka Sound Formation from removal by erosion. Several fiords and covered areas disrupt continuity of the exposures and the local structure is complex and not yet fully understood. However, the general geological picture is clear, and it is certain that the vertebrate localities are clustered in the upper part of the formation. Fossil plants and invertebrates occur with the vertebrates, permitting relatively complete environmental reconstructions.

Our collecting was done primarily by surface prospecting. Dry and underwater screening of several of the most productive areas produced remains of some smaller animals not found by surface prospecting. Vertebrate fossils are now known to occur in three lithofacies (Fig. 5). Siltstones and fine-grained sandstones of the middle unit of the Eureka Sound Formation have produced otoliths of several genera of marine teleost fish (WEST et al., 1975) and shark teeth of the wide-ranging genus *Odontaspis* (J. H. HUTCHISON, pers. comm., 1977). Gray to brown siltstones and fissile shales low in the upper unit yielded the first Eureka Sound tetrapods (DAWSON et al., 1976); the fauna from this lithofacies consists mostly of aquatic turtles and alligatorines, although mammals and fishes are also present. The most productive vertebrate localities now known are in fine to medium-grained arkosic sandstones cut into light-colored siltstones and interbedded with thick coal seams. These localities have produced fishes, salamanders, a snake, lizards, alligatorines, turtles, birds and mammals. Both of these tetrapod-producing facies are in the upper part of the formation, as indicated in Fig. 5.

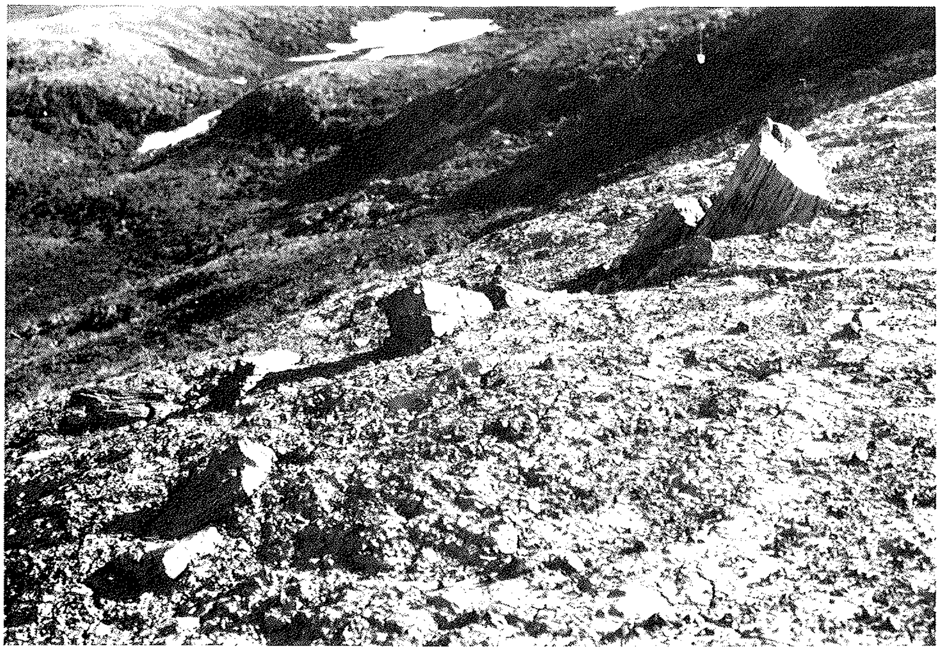

Fig. 8: Fossilized wood exposed by natural erosion, upper Eureka Sound Formation, near Bay Fiord, Ellesmere Island.

Abb. 8: Herausgewittertes fossiles Holz, obere Eureka Sound-Formation, bei Bay Fjord, Ellesmere Island.

Detailed systematic and anatomic studies of the various fossils from the Eureka Sound Formation are still in progress, so comparison with other Paleogene faunas is not complete. However, determinations of the tetrapods to the level of family or genus (Table 1) lead to some well-grounded interpretations of the geographic affinities, age, and environments of the assemblages.

	Occurrence	Geographic Distribution in Paleogene	Temporal Distribution of Most Closely Allied Taxon in Paleogene
Osteichthyes			
Holostei			
Lepisosteidae	Rare, *Lepisosteus*	North America, Europe, Asia	Eocene
Amiidae	Abundant, *Amia*	North America, Europe, Asia	Eocene
Amphibia			
Urodela			
Scapherpetontidae	Rare, *?Scapherpeton*	North America	Paleogene
Batrachosauroididae	Rare, *Piceoerpeton*	North America	Early Eocene
Reptilia			
Chelonia			
Trionychidae	Abundant, *Trionyx*	North America, Europe, Asia	Eocene
Testudinidae	Abundant, cf. *Hadrianus*	North America, Europe, Asia	Early to Middle Eocene
	Abundant, Emydinae, 1 genus	North America, Europe, Asia	Late Paleocene
Carettochelyidae	Rare, *Anosteira*, 1 species	North America, Europe, Asia	Middle Eocene
Cryptodira indet.	1 genus		
Squamata			
Anguidae	Rare, Glyptosauridae, 1 genus	North America, Asia	Eocene
?Varanidae	Rare, 1 genus	North America, Europe	Eocene
Ophidia indet.	Rare, 1 genus		
Crocodilia			
Alligatoridae	Abundant, *Allognathosuchus*	North America, Europe	Early to Middle Eocene
Aves			
Neognathae			
Diatrymatidae	Rare, cf. *Diatryma*	North America, Europe	Early to Middle Eocene
cf. Presbyornithidae	Rare, 1 genus	North America, South America	Middle Eocene
Mammalia			
Multituberculata			
Ectypodidae	Rare, *Neoplagiaulax*	North America, Europe	Late Paleocene
Proteutheria			
Leptictidae	Rare, 1 species	North America, Europe	Early Eocene
Pantolestidae	Rare, *Pantolestes*, 1 species	North America, Europe, Asia	Middle Eocene
Dermoptera			
Plagiomenidae	Abundant, 5± species	North America [1])	Early Early Eocene
Primates			
Paromomyidae	Common, 2 species	North America, Europe, Asia	Early Eocene
Rodentia			
Ischyromyidae	Rare, 3± genera	North America, Europe, Asia	Early to Middle Eocene
Taeniodonta			
Stylinodontidae	Rare, 1 species	North America, Asia	Eocene
Pantodonta			
Coryphodontidae	Abundant, *Coryphodon*, 1 species	North America, Europe, Asia	Early Eocene
Creodonta			
Hyaenodontidae	Rare, *Prolimnocyon*	North America, Europe	Early to Middle Eocene
	Rare, 1 species	North America, Europe, Asia	Early to Middle Eocene
Carnivora			
Miacidae	Rare, *Viverravus*	North America, Europe	Eocene
	Rare, Miacinae	North America, Europe	Eocene
Perissodactyla			
Hyrachyidae	Abundant, *Hyrachyus*, 1 species	North America, Europe, Asia	Late Early to Middle Eocene
Brontotheriidae	Rare, cf. *Manteoceras*	North America, Asia	Middle to Late Eocene
	Moderate, *Lambdotherium*	North America	Late Early Eocene
Equidae	Rare, *Hyracotherium*, 1 species	North America, Europe	Early Eocene

[1]) Dermopterans have been reported from the Eocene of Europe (RUSSELL et al., 1973), but ROSE (1973) and ROSE & SIMONS (1977) consider this an equivocal ordinal assignment.

Tab. 1: Fossil Vertebrates, Eureka Sound Formation: Abundance, Distribution, Age.

Tab. 1: Fossile Wirbeltiere, Eureka Sound-Formation: Häufigkeiten, Verteilung, Alter.

The fossil tetrapods from the upper part of the Eureka Sound Formation represent two discrete faunal levels, each incorporating 300 to 400 meters of sediment (Fig. 5). The lower of these assemblages is by far the most diverse (Table 2) and much the larger numerically. The most striking feature of this assemblage is the abundance and diversity of the dermopterans (flying lemurs) (Fig. 9), which are the most common small mammals known from the Eureka Sound Formation. In contrast, dermopterans are rare in more southerly Paleocene and Eocene localities in North America (ROSE, 1973; ROSE & SIMONS, 1977) and lack the taxonomic diversity shown by the Eureka Sound Formation dermopterans. Preliminary studies suggest the presence of perhaps as many as five species of Arctic dermopterans.

The other most common mammals from the lower faunal zone of the Eureka Sound Formation are the tapiroid *Hyrachyus* and the pantodont *Coryphodon* (Fig. 10), both of which are represented in many more southerly early Eocene localities in North America and western Europe. Pantodonts are also present in the Eocene of eastern Asia, and *Hyrachyus* has been reported from the Chinese Eocene.

	Distribution in Upper Eureka Sound Fm.	
	L	U
Amphibia		
Urodela		
Cryptobranchidae	X	
Reptilia		
Chelonia		
Trionychidae	X	X
Testudinidae	X	X
Carettochelyidae		X
Cryptodira indet.	X	
Squamata		
Anguidae	X	
?Varanidae		X
Ophidia indet.	X	
Crocodilia		
Alligatoridae	X	X
Aves		
Presbyornithidae	X	
Diatrymatidae	X	
Mammalia		
Multituberculata		
Ectypodidae	X	

	Distribution in Upper Eureka Sound Fm.	
	L	U
Proteutheria		
Leptictidae		X
Pantolestidae	X	
Dermoptera		
Plagiomenidae	X	
Primates		
Paromomyidae	X	
Rodentia		
Ischyromyidae	X	X
Taeniodonta		
Stylinodontidae		X
Pantodonta		
Coryphodontidae	X	
Creodonta		
Hyaenodontidae	X	
Carnivora		
Miacidae	X	
Perissodactyla		
Hyrachyidae	X	
Brontotheriidae	X	X
Equidae	X	

Tab. 2: Distribution of fossil tetrapods in upper part of the Eureka Sound Formation.

Tab. 2: Verteilung der fossilen Wirbeltiere im oberen Teil der Eureka Sound-Formation.

The remainder of the fauna from the lower faunal zone includes among the lower tetrapods several specimens of a giant salamander, abundant aquatic and terrestrial turtles, an anguid lizard, a snake, abundant alligators of the genus *Allognathosuchus* (Fig. 10) and several birds, including the large flightless carnivore *Diatryma* and the widespread aquatic *Presbyornis*. The mammals are a multituberculate, a pantolestid proteutherian, two species of paromomyid primates, several genera of ischyromyid rodents, at least two genera of carnivorans, a single specimen referred to the primitive equid *Hyracotherium*, and several teeth most similar to the late Early Eocene North American primitive brontothere *Lambdotherium*.

The upper level is less fossiliferous. Turtles are abundant, and include genera known from the lower level as well as an anosteirine carettochelyid known from the Middle Eocene of the Holarctic. Crocodilians *(Allognathosuchus)* (Fig. 9), and a varanid lizard constitute the remainder of the lower tetrapod assemblage.

Mammals are rare in the upper level, but several are taxa not present in the lower level. They include a leptictid proteutherian, ischyromyid rodents, a taeniodont and an advanced brontothere. Both taeniodonts and advanced brontotheres are known from the Eocene of southern and eastern Asia as well as from North America. The brontothere more closely resembles the Middle Eocene North American genus *Manteoceras* than the smaller Early Eocene *Lambdotherium*.

A conspicuous absence from both assemblages is *Hyopsodus*, a small condylarth that is common in Eocene localities farther south. Other mammals well known in more southerly Eocene faunas but as yet absent from the Eureka Sound Formation include phenacodont condylarths, artiodactyls, many primates, and marsupials.

Fauna	No. of Genera	Probable Age
Eureka Sound Lower	13	53—49.5 mya
Late Wasatchian (N. Am.)	53	
Sparnacian (Eur.)	55	
Eureka Sound Upper	5	49.5—47.5 mya
Bridgerian (N. Am.)	71	
Lutetian (Eur.)	62	
Ganda Kas (Pakistan)	15	53—47.5 mya

Tab. 3: Eocene faunal sizes and radiometric datings.

Tab. 3: Umfang eozäner Faunen und radiometrisches Alter.

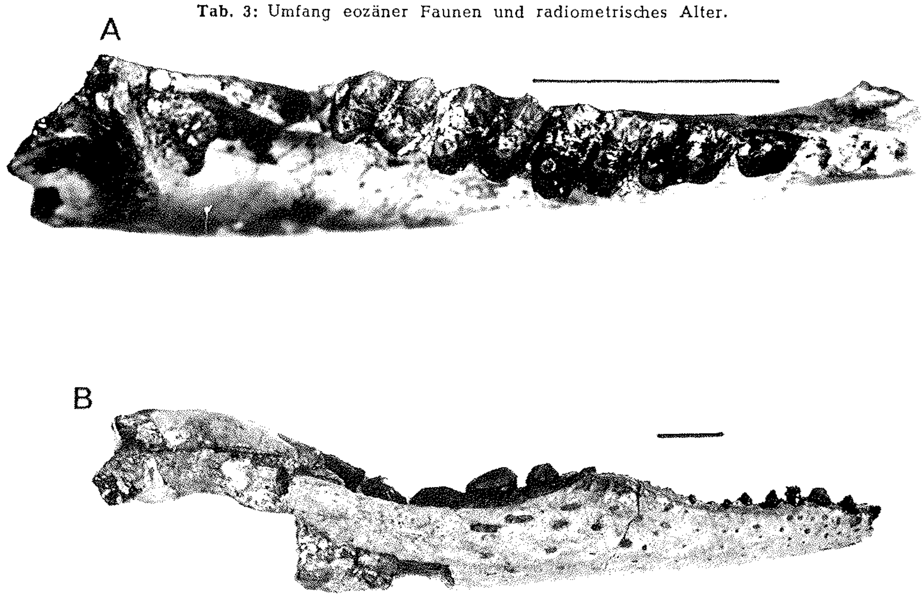

Fig. 9: Eureka Sound Formation vertebrate fossils. The solid bars represent lengths of 1 cm. **A.** cf. *Plagiomene* right mandible, P_3—M_3, National Museum of Canada no. 30859. B. *Allognathosuchus* right mandible, National Museum of Canada uncatalogued.

Abb. 9: Fossile Wirbeltiere aus der Eureka Sound-Formation. Strichlänge = 1 cm. A. cf. *Plagiomene*, rechter Unterkiefer mit P_3 M_3, Kanadisches Nationalmuseum Nr. 30859. B. *Allognathosuchus*, rechter Unterkiefer, Kanadisches Nationalmuseum, nicht katalogisiert.

The low diversity of the Eureka Sound Formation tetrapods may reflect an actual impoverishment, based on collections made during the three seasons' work. In total, about 18 mammalian genera are recognized in the Eureka Sound Formation faunas, 13 from the lower level and five from the upper level. In contrast, the known Sparnacian faunas of western Europe contain about 55 genera, the late Wasatchian of North America about 53 genera, the Bridgerian of North America about 71 genera, and the Lutetian of Europe about 62 genera (Table 3) (RUSSELL, 1968; WEST et al., in press). Comparison with Asian Paleogene faunas is very difficult, as South Asia is inadequately known — the Ganda Kas Eocene of Pakistan contains about 15 genera (GINGERICH, 1977; WEST, unpublished data) — and the Eocene of China and Mongolia is incompletely reported, so a generic count was not attempted for this paper.

A

B

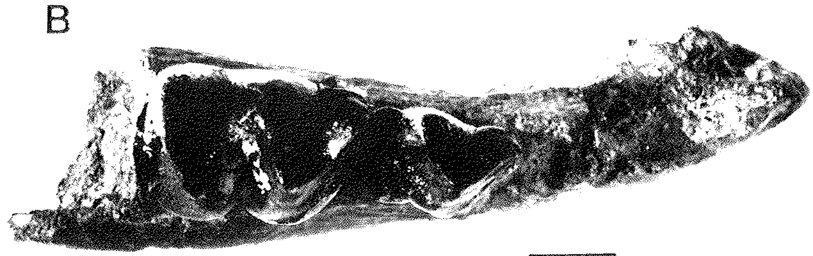

Fig. 10: Eureka Sound Formation vertebrate fossils. The solid bars represent lengths of 1 cm. A. *Hyrachyus* right maxilla, National Museum of Canada no. 30804. B. *Coryphodon* right mandible, dP_3—dP_4, National Museum of Canada no. 30802.

Abb. 10: Fossile Wirbeltiere aus der Eureka Sound-Formation. Strichlänge = 1 cm. A. *Hyrachius*, rechter Unterkiefer, Kanadisches Nationalmuseum Nr. 30804. B. *Coryphodon*, rechter Unterkiefer, dP_3 dP_4, Kanadisches Nationalmuseum Nr. 30802.

The larger assemblage, from the lower productive level, is in detail unlike any other known from North Amèrica or Eurasia. With the exception of *Neoplagiaulax* and *Pantolestes*, all the families and genera are known from the early Eocene (Sparnacian/Cuisian) of western Europe (Table 1). *Neoplagiaulax* is from the Late Paleocene of Europe and North America, while *Pantolestes* is from the middle Eocene of North America. A lower level of similarity can be demonstrated with eastern and southern

Asia. This lower assemblage suggests a late early Eocene age, based on correlations of the North American Wasatchian Land Mammal Age with the European Sparnacian and Cuisian. On the North American radiometric scale this fauna would be dated in the range of 53—49.5 mya (WEST et al., in press).

The small assemblage from the upper beds is not so definitive, as most taxa are known from both Early and Middle Eocene rocks in North America. Again, there are no non-North American endemics in the assemblage. The presence of an anosteirine turtle from low in the upper faunal level, along with a relatively advanced brontothere, is evidence for a significantly later age for this level than for the lower faunal level.

Although the assemblage is small, a Middle Eocene age seems probable, utilizing correlation of the North American Bridgerian with the early part of the European Lutetian. If this is the case, this assemblage would be dated in the range of 49.5—47.5 mya (WEST et al., in press).

DISCUSSION

Climate

The recently recovered fossils from the Eureka Sound Formation add to the evidence already available from diverse geological and paleontological investigations which indicates that areas now within or very close to the Arctic Circle possessed a temperate to warm temperate climate during the Paleogene.

The thick Eureka Sound Formation coal beds were reported by numerous early Arctic explorers, who also made modest collections of fossil wood and leaves. More recently, during Operation Franklin, the Geological Survey of Canada sampled the Eureka Sound Formation paleobotanically (FORTIER et al., 1963), and palynological studies have been conducted in association with petroleum and minerals exploration. Pollen samples have been collected at several of our vertebrate localities, but these are still being processed. Floral lists from the Eureka Sound Formation compare well with those from the more intensively-studied Paleogene of Spitsbergen (MANUM, 1962; SCHWEITZER, 1974), and Greenland (KOCH, 1964). KOCH (1964: 99, 114) regarded the West Greenland Paleogene floras as indicative of temperate to warm temperate humid climates. SCHWEITZER (1974: 3) indicated a close similarity of the Spitsbergen conifers to the modern warm temperate flora of southern Asia. He also pointed out, by analogy, the probable sensitivity of several of the Spitsbergen Paleogene genera to frost, as well as the requirement of modern *Metasequoia*, an abundant Arctic Paleogene taxon, for seasonal rainfall. Thus, the paleobotanical data for the Spitzbergen Paleogene indicate a well-watered, warm temperate area with a January isotherm above 0° C and well-marked seasonality. The incompletely studied Eureka Sound Formation floras also suggest temperate climatic conditions for the Paleogene Canadian Arctic (McGREGOR in CHRISTIE, 1964: 55).

Warm Paleogene conditions in the Canadian Arctic oceans are suggested by oxygen isotope paleotemperatures calculated on scaphopod remains collected from calcareous sandstones below the lower vertebrate level of the Eureka Sound Formation. An average isotherm of 15° C (McKENNA, pers. comm., September, 1978) for the Paleogene ocean water conforms well with the conclusions drawn by CLARK (1974) on early Cenozoic phytoplankton collected in a core taken from ice island T 3 north of Ellesmere Island. This is considerably lower than the Eocene paleotemperatures (20°—30° C) reported from the North Sea by BUCHARDT (1978). Both lines of evidence strongly suggest a warm, ice-free Arctic ocean through the Paleogene.

Some of the fossil vertebrates of the Eureka Sound Formation are further confirmation of the warm Paleogene Arctic. The presence of amphibians, abundant large testudinid tortoises, and alligators testifies to an equable temperate climate (HIBBARD, 1960; BERG, 1964; AUFFENBERG, 1974).

The fossiliferous upper units of the Eureka Sound Formation, including fine-grained sandstones and mudstones interbedded with thick coals, were deposited as part of a deltaic shoreline sequence on the western side of the central Ellesmere Island craton (A. D. MIALL, pers. comm., July, 1977). The common occurrence of aquatic turtles and alligators supports this interpretation. This coastal lowland fauna seems to have lived in a depositional environment more similar to that represented in the western European and South Asian Eocene than to the intermontane basin habitats from which most of the North American Early and Middle Eocene tetrapod assemblages have come. The Paleogene rocks of Spitsbergen lithologically are markedly similar to the productive beds of the Eureka Sound Formation (W. B. HARLAND, pers. comm., Oct. 1978).

Paleogeography

The Eureka Sound Formation tetrapods contribute new data to the problem of paleogeographic relationships between Eurasia and North America. Since the vertebrate fauna from the Early Eocene part of the Eureka Sound Formation has affinities with both North American and western European Early Eocene assemblages, the concept of a North Atlantic faunal continuity is reinforced. It appears that during the Early Eocene this northern faunal exchange area acted as a filter since, 1) both North America and western Europe retained a number of endemic Eocene taxa, and 2) the Eureka Sound Formation fauna is compositionally unique. Also, some groups that are very prominent in the North American Early Eocene (e. g., condylarths) are rare European elements.

The Eureka Sound Formation fossil assemblages also contribute to biochronologic dating of the latest possible time of terrestrial faunal continuity between North America and western Europe across the North Atlantic. The absence of any European endemics and the extension of North American Early Eocene faunal elements northward suggest that this assemblage postdates the faunal disjunction. If this is correct, the severing of the North Atlantic faunal connection was effective by 50 or 51 million years ago.

This faunal date does not correspond well to the current models of the history of the North Atlantic. Based on the presence of anomalies 23 and presumably 24, North Atlantic seafloor in the Greenland-Norwegian Sea region initially came into being sometime prior to 58 million years ago, although there were several areas of longer lasting physical contact between the two continents (e.g., the Spitsbergen-north Greenland, DeGeer, area and the proto-Iceland, Thule, area). TALWANI & ELDHOLM's (1977) reconstruction of the opening of the Norwegian-Greenland Sea indicates that it was not until about 38 million years ago that Spitsbergen became physically separated from Greenland; thus, a land route from North America at least as far east as Spitsbergen was likely until the end of the Eocene or the beginning of the Oligocene. Both submarine topography (HARLAND, 1969) and regional distributions of terrigenous sediments (ELDHOLM & WINDISCH, 1974) indicate that the Barents Shelf was emergent through much, if not all, of the Tertiary; this would then extend the northern land route onto the northern European mainland. However, the early Tertiary North Sea-Baltic basin (ZIEGLER, 1975) may have been a barrier to direct communication with more southerly parts of western Europe.

In a similar fashion physical data from the crest and flanks of the Iceland-Faeroe Ridge show that subaerial weathering of basalts was occurring there until at least mid-

Tertiary times (NILSEN, 1978; NILSEN & KERR, 1978). DSDP site 336 revealed an early Tertiary lateritic paleosoil on the northeastern flank of the Iceland-Faeroe Ridge, some 400 meters below the top of the ridge. This laterite indicates warm, humid conditions during the early Tertiary, a substantiation of biologically-based conclusions mentioned above. It also, however, suggests that the Iceland-Faeroe Ridge did not subside below sea level until perhaps as recently as 20—24 million years ago (NILSEN & KERR, 1978: 176). Thus, the southern exchange route may well have been available well after Early Eocene.

Earlier discussions of the relationships between biological and geological disruptions of the North Atlantic continuity (McKENNA, 1972, 1975; DAWSON et al., 1976; WEST et al., 1977) have presumed that termination of close biological similarity was essentially synchronous with physical geological separation. This now does not seem to be the case. The available vertebrate fossil record does confirm a close connection until approximately early Eocene, but does not pertain to any post-middle Eocene contact. A satisfactory explanation of the abrupt decrease in North American-European faunal similarity prior to the middle Eocene, while one or two terrestrial connections remained viable, is not yet available. However, it can be speculated that the relatively low diversity of the Eureka Sound faunas is a product of a strong climatic filtering effect. Therefore it may tell us more about paleoclimate than about Eocene paleogeography. Two avenues of research may remedy the situation. First, a recent paper by BUCHARDT (1978) documents an abrupt paleotemperature drop in the North Sea in early Oligocene time (37—35 million years ago). An average Oligocene paleotemperature of 5° C or less may have been enough to reduce terrestrial vertebrate occupation of the Arctic and thereby impose an effective climatologic barrier between the two landmasses in spite of the availability of emergent exchange routes. Secondly, during the 1978 field season, the Geological Survey of Canada recovered identifiable mammalian remains from presumed Miocene lacustrine rocks in Haughton Astrobleme on Devon Island at 75° 22'N (FRISCH & THORSTEINSSON, 1978). Preliminary identification of the better specimens shows them to be pikas (Lagomorpha: Ochotonidae) which have a Neogene Holarctic distribution and thus are not paleogeographically useful at this time. Nonetheless, the presence of these specimens indicates the ultimate availability of an Arctic Neogene mammal record which may assist in interpreting North Atlantic relationships over the past 35 million years.

There are also suggestions, based on both lower and middle Eocene Eureka Sound faunal levels, of relationships with Eocene faunas of southern and eastern Asia. Taeniodonts and brontotheres are known from both North America and southern and eastern Asia during the Eocene, but are unknown from western Europe until the Oligocene. Of the lower faunal level taxa, fossil dermopterans are present only in the North American Eocene. The only living representatives are from southeastern Asia. Apart from their occurrence in the Eureka Sound Formation, the fossil record of dermopterans is very poor (ROSE & SIMONS, 1977), but their presence in the North American Eocene and the Recent of southeastern Asia implies some connection between these two areas.

This dual affinity, with western Europe on the one hand and with southern and eastern Asia on the other, imposes the northern part of North America as an exchange area between the two ends of the Eurasian land mass. It obviously served a strong filtering function, as these two regions share very few taxa. However, continued work in late Paleocene—early Eocene rocks of Mongolia is revealing more taxa of North America affinities (DASHZEVEG & McKENNA, 1977), so KURTEN's (1966) model of multiple faunal exchange routes is seen to have increased validity.

The temperate Arctic Paleogene climate indicated by so many disparate lines of evidence raises the question of the Paleogene latitude of these areas. Recent studies (JURDY & VAN DER VOO, 1975) indicate little apparent polar wander since at least the Paleocene. Calculations of Paleogene pole position (SHIVE et al., 1977; BUTLER & TAYLOR, 1978) indicate its placement within a few degrees of the present pole position. Therefore the Eureka Sound Formation was deposited at essentially its present latitude, and under a polar light-dark regime. Obviously the same held true for the Spitsbergen and Greenland floras, and for conditions on the various proposed North American-European Paleogene exchange routes as well.

CONCLUSIONS

The North Atlantic region was occupied, during early and middle Eocene time, by relatively diverse terrestrial vertebrates. These animals lived under temperate climatic conditions, and apparently were not subject to extreme temperatures.

Paleogene vertebrates are found in two stratigraphic zones within the Eureka Sound Formation. The older of these, which is also the larger fauna, is probably early Eocene in age. Its fauna shares numerous elements with western North American Wasatchian assemblages, and several with Sparnacian faunas of western Europe. In contrast, the upper Eureka Sound Formation assemblage has greater affinities with eastern and southern Asia than with western Europe.

These differences suggest termination of biologic continuity across the expanding North Atlantic by about 51 or 50 million years ago, thus permitting increased endemism in both western Europe and North America. Simultaneously, a less efficient exchange began between North America and Asia, utilizing the Beringia area.

Geological data from the North Atlantic region indicate that the Norwegian Sea began to open no less than 58 million years ago. Various lines of evidence show that land areas were present at both the northern (DeGeer) and southern (Thulean) ends of this opening sea until at least the middle Tertiary.

If both geologic and paleontologic data are correctly interpreted, the termination of trans-North Atlantic biologic exchange occurred well before it was geologically necessary. Much additional information on Neogene climate and vertebrates of the North Atlantic region must be gathered before these conflicting models can be resolved.

The recent discovery, by the Geological Survey of Canada, on Devon Island, of a pocket of presumably Miocene mammals, gives hope for extending the North Atlantic region's paleontologic record and possibly answering this question.

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