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A Hadrosaurid (Dinosauria: Ornithischia) from the Late Cretaceous (Campanian) Kanguk Formation of Axel Heiberg Island, Nunavut, Canada, and Its Ecological and Geographical Implications

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ABSTRACT. A hadrosaurid vertebra was recovered during a palynological survey of the Upper Cretaceous Kanguk Formation in the eastern Canadian Arctic. This vertebra represents the farthest north record of any non-avian dinosaur to date. Although highly abraded, the fossil nonetheless represents an interesting biogeographic data point. During the Campanian, when this vertebra was deposited, the eastern Canadian Arctic was likely isolated both from western North America by the Western Interior Seaway and from more southern regions of eastern North America by the Hudson Seaway. This fossil suggests that large-bodied hadrosaurid dinosaurs may have inhabited a large polar insular landmass during the Late Cretaceous, where they would have lived year-round, unable to migrate to more southern regions during winters. It is possible that the resident herbivorous dinosaurs could have fed on non-deciduous conifers, as well as other woody twigs and stems, during the long, dark winter months when most deciduous plant species had lost their leaves.

Key words: Appalachia, Arctic, Campanian, dinosaur, Laramidia, palaeobiogeography

RÉSUMÉ. La vertèbre d'un hadrosauridé a été retrouvée pendant l'étude palynologique de la formation Kanguk remontant au Crétacé supérieur, dans l'est de l'Arctique canadien. Il s'agit de la vertèbre appartenant à un dinosaure non avien qui a été recueillie la plus au nord jusqu'à maintenant. Même si ce fossile est fortement abrasé, il n'en reste pas moins qu'il représente un point de donnée biogéographique intéressant. Pendant le Campanien, lorsque cette vertèbre a été déposée, l'est de l'Arctique canadien était vraisemblablement isolé de l'ouest de l'Amérique du Nord par la mer intérieure occidentale, et des régions plus au sud de l'est de l'Amérique du Nord par le bras de mer Hudson. Ce fossile suggère que de gros dinosaures hadrosauridés auraient pu habiter une grande masse terrestre insulaire polaire pendant le Crétacé tardif, où ils auraient évolué à l'année, étant incapables de migrer vers les régions plus au sud pendant l'hiver. Il est possible que les dinosaures herbivores résidents se soient nourris de conifères non décidus ainsi que d'autres tiges ou brindilles ligneuses pendant les longs mois sombres de l'hiver, lorsque la plupart des espèces végétales décidues avaient perdu leurs feuilles.

Mots clés : Appalachia, Arctique, Campanien, dinosaure, Laramien, paléobiogéographie

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INTRODUCTION

Since the first evidence of polar dinosaurs was discovered in Spitsbergen (Svalbard) in 1960 (de Lapparent, 1960, 1962), Late Cretaceous dinosaurs have been found across much of the Arctic (Rich et al., 2002; Weishampel et al., 2004; Gangloff, 2012). These findings include remains from Russia (Nessov and Golovneva, 1990; Averianov and Sues, 2007; Godefroit et al., 2009), Alaska (Brouwers et al., 1987; Fiorillo and Gangloff, 2000; Gangloff et al., 2005; Fiorillo, 2008; Brown and Druckenmiller, 2011), Yukon (Rouse and Srivastava, 1972; Gangloff et al., 2004; Evans et al., 2012), the Northwest Territories (Russell, 1984), and Nunavut (Russell, 1990; Núñez-Betelu et al., 2005). Additional areas, such as northern Alberta (Currie et al., 2008; Fanti and Miyashita, 2009) and northern British Columbia (Rylaarsdam et al., 2006; Arbour and Graves, 2008), are not considered polar today, but would have been near or north of the Arctic Circle during the Cretaceous.

A hadrosaurid dinosaur vertebra was found on Axel Heiberg Island, Nunavut (Fig. 1), in July 1992 during a stratigraphic and palynological survey of the Kanguk Formation in the northeastern Canadian Arctic (Núñez-Betelu et al., 2005). This same expedition also recovered

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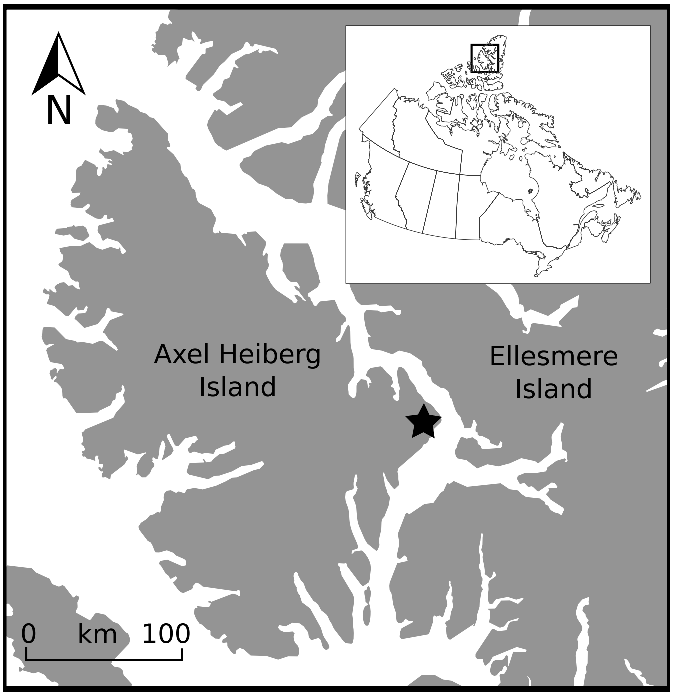

FIG. 1. Location of Axel Heiberg Island, Nunavut, Canada. Star denotes approximate discovery site of the dinosaur fossil at May Point.

additional vertebrate remains of a hesperornithid bird and a large fish (*Xiphactinus* sp.) from nearby Ellesmere Island (Hills et al., 1999), although no non-avian dinosaurs were found on that island. This most northerly occurrence of a non-avian dinosaur has biologic, climatic, and geographic implications for dinosaurs inhabiting this region during the Late Cretaceous.

GEOLOGICAL SETTING

The Sverdrup Basin is a major Carboniferous to Paleogene depocentre within the Canadian Arctic Islands (Embry, 1991; Embry and Beauchamp, 2008), and the Cenomanian/Turonian to Campanian aged Kanguk Formation outcrops extensively within the basin (Núñez-Betelu et al., 1994). In general, the lower Kanguk Formation is composed of dark, organic-rich mudstones that represent a low-oxygen and low-energy environment (Núñez-Betelu et al., 1994). The upper Kanguk Formation strata are composed of claystones, siltstones, and very fine-grained sandstones (Núñez-Betelu et al., 1994). These upper beds record a shallow shelf and nearshore facies and contain an abundant marine and terrestrial microfossil record, as well as inoceramids, ammonites, and indeterminate marine vertebrates (Núñez-Betelu et al., 1994; Hills et al., 1999).

The Kanguk Formation gradationally overlies the Hassel Formation and is gradationally overlain by the Eureka Sound Group on Ellesmere Island. At Cañon Fiord, Ellesmere Island (79.8758˚ N, 82.2378˚ W), the upper Hassel Formation consists of a series of coarsening upward cycles separated by marine mudstones. The last of these cycles is capped by a rooted paleosol and is directly overlain by mudstones of the Kanguk Formation. A similar situation exists at Strathcona Fiord (78.5472˚ N, 82.9153˚ W), but the coarsening upward sequence is less well defined and is replaced by interbedded sandstones, which thin upwards and have interbeds of mudstone that thicken upwards. The coarsening upward sequences gradational to the Eureka Sound Group are coarsest in the east and are thinner and finer-grained to the west. This pattern indicates that the source of the Kanguk Formation lay to the east of May Point along the axis of Ellesmere Island, and thus the dinosaur vertebra was sourced west of the axis of Ellesmere Island.

Hills et al. (1994) described *Scaphites depressus* Reeside from the Kanguk Formation at the head of Glacier Fiord on southwestern Axel Heiberg Island, providing clear evidence of a connection with the Western Interior Seaway. Palynological evidence indicates that the Kanguk Formation at Glacier Fiord is contiguous with the formation at May Point, although the sediments at May Point were deposited farther offshore. Since uplift on Axel Heiberg Island postdates the Kanguk Formation, present-day Axel Heiberg Island was not yet above sea level when the dinosaur fossil was deposited. Therefore, the vertebra must have originated from a nearby terrestrial area.

LOCAL GEOLOGY

The hadrosaurid vertebra was found within the upper portion of the Kanguk Formation, at May Point on Axel Heiberg Island, Nunavut, Canada (Fig. 2). The local sediments also contained a large marine reptile fossil and abundant dinoflagellate cysts (Núñez-Betelu et al., 2005), indicating that the dinosaur bone was preserved in a marine environment. The dinosaur fossil is abraded, suggesting it was likely worn in a fluvial or shoreline environment before being transported out to sea for burial.

PALYNOLOGY

Samples collected 8 m above the dinosaur-bearing horizon yielded dinoflagellate cysts, acritarchs, spores, and pollen (Appendix 1). In particular, the palynomorphs recovered were well preserved, and the assemblage was dominated by the dinoflagellate *Scrinodinium crystallinum* (Núñez-Betelu et al., 2005). The microfossil assemblage correlates well with Biozone 4 of Núñez-Betelu (1994), suggesting a middle Campanian age (Núñez-Betelu et al., 2005).

PALAEOCLIMATE AND PALAEOGEOGRAPHY

The climate during the Late Cretaceous was much warmer than at present (Frakes, 1979; Barron, 1983; Hallam, 1985), and Arctic regions in particular had much higher temperatures, which produced a smaller equator-to-pole

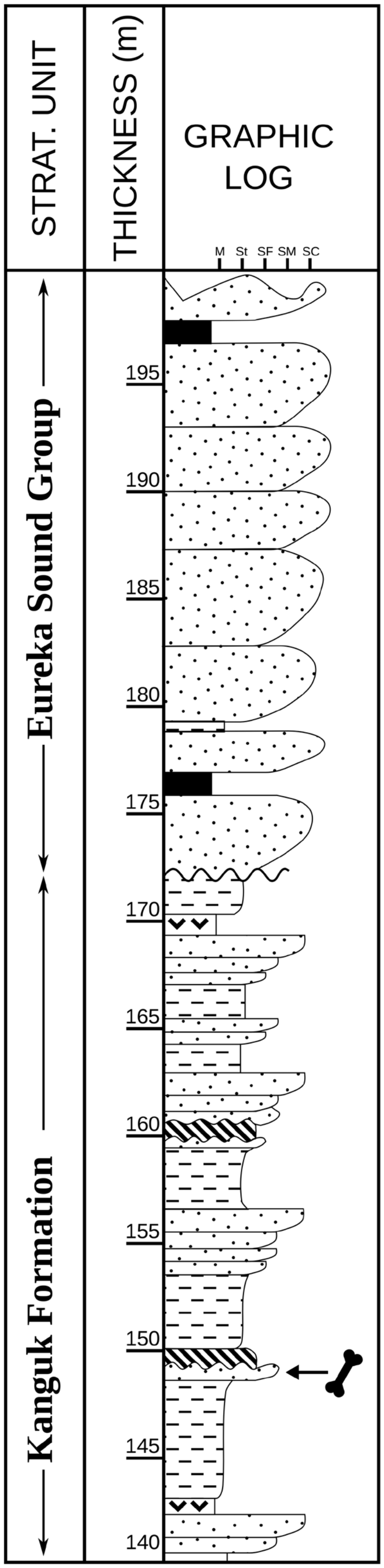

FIG. 2. Stratigraphic section from May Point, Axel Heiberg Island. Stratigraphic position of the vertebra is marked with a bone symbol at the 148 m level. Number scale indicates distance (m) from base of total section. Grain size abbreviations: M = mudstone; St = siltstone; SF = fine sandstone; SM = medium sandstone; SC = coarse sandstone. Patterns of layers are represented by the following: dots for sandstone; dashes for mud and siltstones; down arrows for bentonitic layers; diagonal stripes for paleosols; and black for bituminous mudstones. Modified from Núñez-Betelu (1994).

temperature gradient than exists today (Barron, 1983; Amiot et al., 2004). By the Campanian, global temperatures had declined somewhat from their high in the Turonian (Parrish and Spicer, 1988a; Jenkyns et al., 2004), and Arctic regions during the Campanian may have experienced frosts and some snowfall (Wolfe and Upchurch, 1987; Amiot et al., 2004).

Sea levels during the Late Cretaceous were much higher than at present (Haq et al., 1987), and large portions of North America were flooded by inland seaways (Kauffman and Caldwell, 1993; Smith et al., 1994; Hay et al., 1999). In particular, the large Western Interior Seaway extended from the Arctic Ocean to the Gulf of Mexico for most of the Late Cretaceous, dividing North America into western and eastern sub-continents, sometimes referred to as Laramidia and Appalachia, respectively.

During the Late Cretaceous, North America was at approximately the same latitude as it is today, although it was rotated clockwise relative to its present orientation (Smith et al., 1994; Scotese, 2002). This rotation meant that Alaska, Yukon, northern British Columbia, and Alberta would have been farther north than they are currently, while eastern Nunavut would have been somewhat farther south. The rotation of the continent would have placed several dinosaur-bearing localities in northern British Columbia and Alberta near or north of the Arctic Circle; however, Axel Heiberg Island would have been farther south (at approximately 75˚ N) than it is at present (Scotese, 2002). Therefore, although the dinosaur from Axel Heiberg may be the most northerly occurrence known, its position during the Late Cretaceous would likely have been farther south than contemporaneous dinosaur-bearing localities from the North Slope of Alaska.

SYSTEMATIC PALAEONTOLOGY

Dinosauria Owen, 1842
Ornithischia Seeley, 1887
Ornithopoda Marsh, 1881
Hadrosauridae Cope, 1870
Hadrosauridae indet.
Figure 3

Material: Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada (TMP) 1997.004.0002, partial posterior dorsal vertebra.

Stratigraphy and Locality: Kanguk Formation, eastern Axel Heiberg Island, Nunavut, Canada (79.3275˚ N 84.5408˚ W).

Description: The single recovered element is a centrum of a posterior dorsal vertebra. The neural arch was firmly fused to the centrum; however, only the bases of the pedicels are preserved. Considerable wear and abrasion are evident, and most of the margins of the intervertebral articulations have been damaged. Several large nutrient foramina invade the sides of the centrum near midlength. The centrum is 65 mm long, as measured along

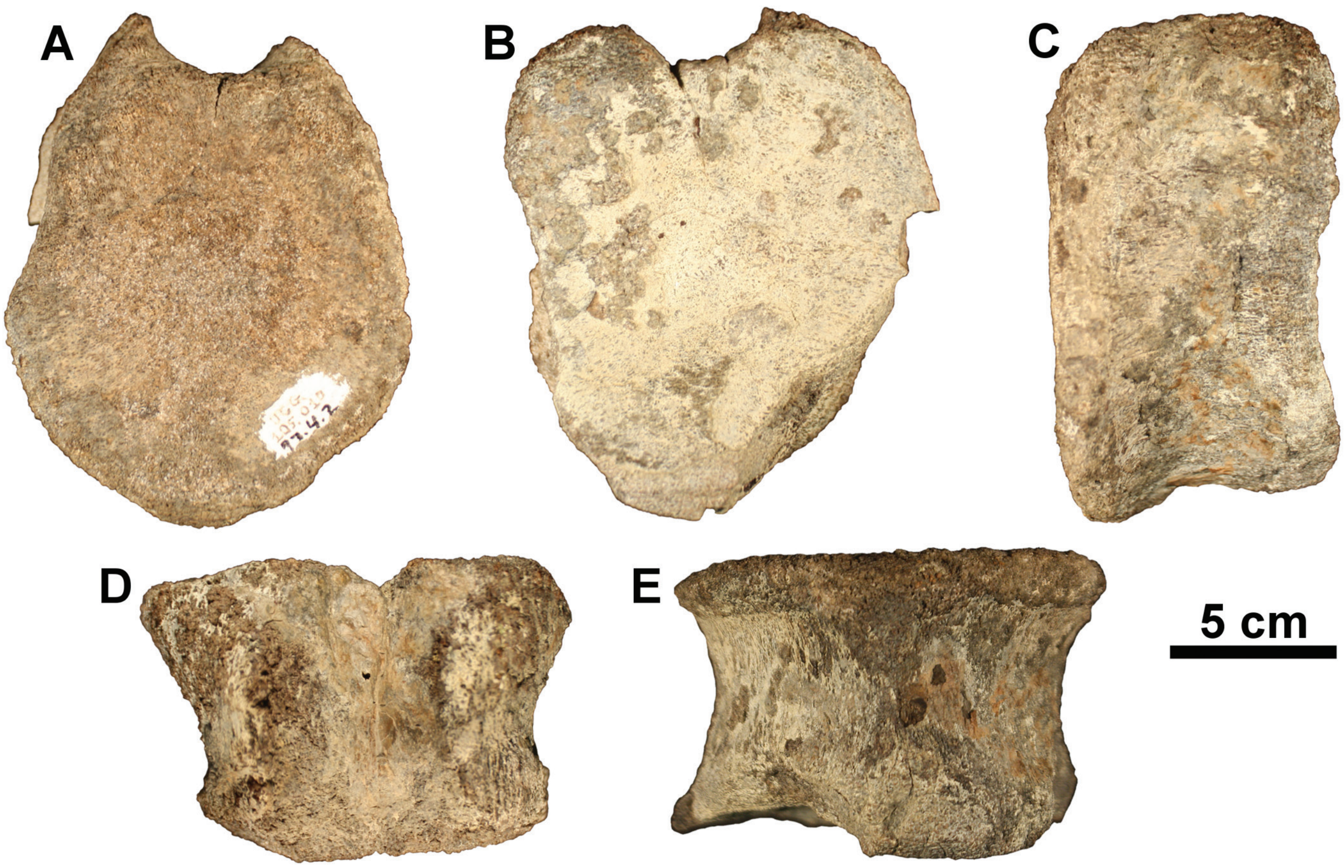

FIG. 3. Hadrosaurid vertebra (TMP 1997.004.0002) in five views: (A) anterior, (B) posterior, (C) left lateral, (D) dorsal, and (E) ventral.

the floor of the neural canal, and 115 mm high between the neural canal and the ventral margin of the anterior intervertebral articulation. The anterior articular surface is 98.5 mm wide, although the edges have been damaged, meaning it was likely larger in life. The centrum is slightly constricted at mid-length, where it has a width of 83 mm. The size of the centrum is comparable to that of the seventeenth dorsal centrum of TMP 1982.038.0001, an adult specimen of *Lambeosaurus lambei*, an individual measuring approximately 8 m in length.

DISCUSSION

There has been some question as to whether dinosaurs were living at high latitudes year-round (Parrish et al., 1987; Paul, 1988; Fiorillo and Gangloff, 2000, 2001; Bell and Snively, 2008; Chinsamy et al., 2012) or were seasonal migrants to polar regions (Hotton, 1980; Parrish et al., 1987; Russell, 1990). Recently, a growing body of evidence, with support coming from histological (Chinsamy et al., 2012), isotopic (Fricke et al., 2009), ecological (Fiorillo and Gangloff, 2001), and biogeographic (Molnar and Wiffen, 1994, 2007; Bell and Snively, 2008) sources, has suggested that dinosaurs did not migrate.

Although only a single hadrosaurid vertebra was found on Axel Heiberg Island, it may nonetheless represent additional support for year-round residence of dinosaurs at high latitudes. For part of the Late Cretaceous, the eastern Canadian Arctic may have been isolated from the rest of North America by the inland Western Interior and Hudson Seaways (Fig. 4; Williams and Stelck, 1975; Kauffman, 1984; Ziegler and Rowley, 1998; Hay et al., 1999). These inland seas would have acted as geographic barriers for any terrestrial animal, limiting movement of animals between the northern and southern portions of Appalachia. Additionally, plate position reconstructions place most of this isolated landmass north of 60˚ N (Hay et al., 1999). If this hadrosaurid from Axel Heiberg were living on a high-latitude insular landmass, it would have been unable to migrate south during the winter. Similar conditions existed for Late Cretaceous dinosaurs from New Zealand (Molnar and Wiffen, 1994, 2007) and the Chatham Islands (Stilwell et al., 2006), as these areas were also high-latitude islands with no land connections to lower-latitude regions (Bell and Snively, 2008).

As only a single indeterminate fossil was found, no phylogenetic comparisons between this hadrosaur and contemporaneous forms in Europe and southern Appalachia can be made. However, palaeogeographic reconstructions suggest that the most probable, and simplest, explanation for the origin of the dinosaurs in the eastern Canadian Arctic is that they were populations that became isolated from others in more southerly regions by the rising sea levels and

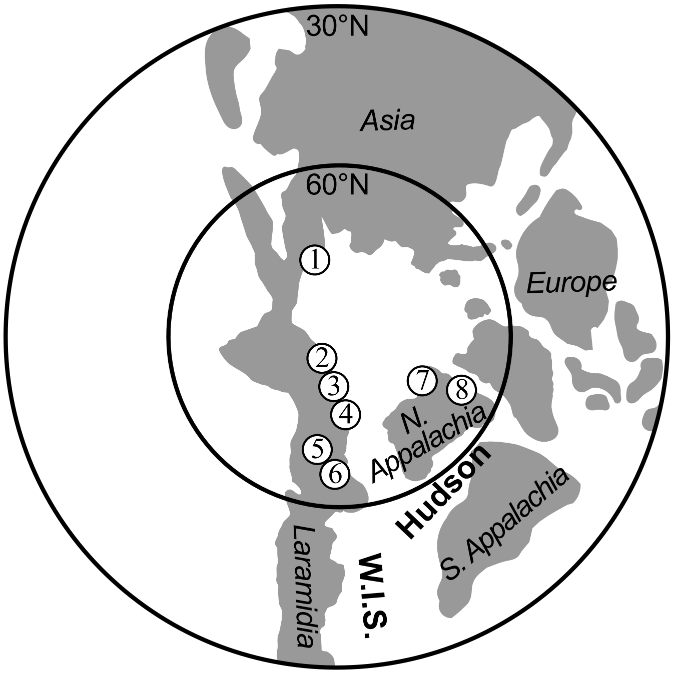

FIG. 4. Palaeogeographic reconstruction for the mid Campanian (approximately 80 million years ago) in north polar stereographic projection, showing locations of inland seas and names of regions within North America. Grey regions represent emergent areas. W.I.S. = Western Interior Seaway; Hudson = Hudson Seaway; N. Appalachia = Northern Appalachia; S. Appalachia = Southern Appalachia. Numbers represent Late Cretaceous polar dinosaur localities: (1) Kakanaut, Russia (Godefroit et al., 2009); (2) North Slope, Alaska (Brouwers et al., 1987); (3) Northern Yukon (Evans et al., 2012); (4) Northwest Territories (Russell, 1984); (5) Sustut Basin, British Columbia (Arbour and Graves, 2008); (6) Grande Prairie, Alberta (Fanti and Miyashita, 2009); (7) Axel Heiberg Island (this paper); (8) Bylot Island (Russell, 1990). Map is re-projected and modified from Smith et al. (1994), with additional data from Hills et al. (1994).

flooding of the Hudson Seaway. Although a biotic interchange between North America and Europe during the Paleogene has been reasonably established (e.g., McKenna, 1983; Sanmartin et al., 2001; Archibald et al., 2011), it is much more difficult to speculate about faunal interchanges of terrestrial organisms between Europe and eastern North America during the Late Cretaceous because of the relative lack of fossil material. Some studies of dinosaur biogeography have found possible support for connections between Europe and North America (Upchurch and Hunn, 2002; Ezcurra and Agnolín, 2012). However, these studies used primarily Laramidian taxa, given the paucity of well-preserved Appalachian forms; therefore, the results may not apply to the eastern portion of North America, as the faunas of the two regions appear to be different from one another (Schwimmer, 1997).

If the hadrosaurids were overwintering on this Arctic insular landmass, they would have had to subsist on local food sources. Other Late Cretaceous Arctic localities have yielded leaf macrofossils from a diverse array of plants, typically dominated by deciduous conifers such as *Parataxodium* and *Metasequoia*, although horsetails, ferns, and a variety of angiosperms were also present (Spicer and Parrish, 1990; Falcon-Lang et al., 2004; Gangloff, 2012), suggesting that there would have been ample, if somewhat seasonal, vegetation to support herds of large dinosaurs. Palynological evidence from the May Point area (Núñez-Betelu, 1994) indicates the presence of abundant and diverse conifers, including both the small, thin-walled non-saccate pollen from species such as *Parataxodium* and *Metasequoia* and bisaccate pollen, produced by species such as *Pinus*, *Picea*, and *Abies*. Significantly, the bisaccate pollen present are diverse in size, shape, ornamentation, and sacci attachment, indicating the presence of more than one genus of non-deciduous conifers in the area. Although surveys of leaf macrofossils from Alaska have found only deciduous conifer species present (Parrish and Spicer, 1988b), the pollen record from May Point and nearby sites in the eastern Canadian Arctic clearly supports the presence of non-deciduous conifers in the area. Gangloff and Fiorillo (2010) have discussed the possibility that hadrosaurs in Alaska may have used alternative food sources, in particular horsetails, during the winter months. A number of horsetail species are known to possess tuberous rhizomes (McIver and Basinger, 1989), and dinosaurs may have consumed these fleshy underground stems (Gangloff and Fiorillo, 2010). There are, however, no anatomical features in hadrosaur skeletons to suggest that they were adapted to digging up rhizomes and stems. It is more likely that they fed on the above-ground plant biomass, including both non-deciduous conifers and woody portions of deciduous plants.

In modern North American ecosystems, both birds and mammals consume conifer leaves during the winter months. The winter food of white-tailed deer (*Odocoileus virginianus*) in eastern Canada is almost exclusively white cedar (*Thuja occidentalis*), but also includes balsam fir (*Abies balsamea*) and eastern hemlock (*Tsuga canadensis*) (Banfield, 1974). In Alberta, white-tailed deer browse on horizontal juniper (*Juniperous horizontalis*) and white spruce (*Picea albertiana*) (Len V. Hills, pers. obs.). Mule deer (*Odocoileus hemionus*) browse on western red cedar (*Thuja plicata*), Douglas fir (*Pseudotsuga menziesii*), and Rocky mountain juniper (*Juniperous scopulorum*) (Banfield, 1974). Both deer species consume decomposing leaves of trembling aspen (*Populus tremuloides*) in winter. Although trembling aspen was not part of the flora during the Campanian, other broad-leaved plants were present and could also have provided a winter source of food.

Spruce Grouse (*Dendragapus canadensis*) and Blue Grouse (*D. obscurus*), descendants of dinosaurs, rely heavily on conifers in their winter diet. According to Pendergast (1969), spruce grouse are in peak winter condition when they use virtually 100% conifer needles for their food. Blue grouse winter in coniferous forests (Campbell et al., 1990), where they feed and roost in non-deciduous conifers. They feed on the unshed needles, as well as buds and seeds, of fir and hemlock (Godfrey, 1966; Stokes and Stokes, 1996), and presumably they also consume portions of Englemann spruce (*Picea englemannii*) and interior Douglas fir in the winter as they reside in these stand types. Although caribou are sometimes invoked as modern analogues of Arctic hadrosaurids (e.g., Parrish et al., 1987), a closer analogue, at least with regard to food sources, may be one of the deer or grouse discussed above.

In addition to conifer needles and seeds, hadrosaurids living in this area may have consumed a larger proportion of woody plant organs during the winter. Previous studies (Béland and Russell, 1978; Chin, 2007) have suggested that hadrosaurids may even have fed preferentially on woody plant materials as a matter of course. It seems doubtful that the lack of green, leafy foliage available during winter would have prevented hadrosaurids from living at high latitudes year-round.

CONCLUSIONS

The most northerly record of a non-avian dinosaur was found on Axel Heiberg Island, Nunavut, Canada, within the marine Kanguk Formation. The fossil indicates that large hadrosaurids inhabited this region of northeastern North America in the Campanian, judging by palynological dates. The eastern Arctic of North America is hypothesized to have been an isolated landmass during the Campanian, and it would have been almost entirely north of 60˚ N, separated by epeiric seaways from other areas within North America as well as from Europe. These seaways would have inhibited migration of terrestrial animals, and this hadrosaurid likely lived year-round in the Arctic. Although the high seasonality in photoperiod would have greatly limited plant productivity during the winter months, hadrosaurids in this area, like modern boreal forest herbivores, may have subsisted on coniferous foliage, as well as woody plant organs such as twigs and branches.

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APPENDIX 1

Marine and terrestrial palynomorphs found in a sample collected 8 m above the hadrosaurid vertebra. Data taken from Núñez-Betelu et al. (2005).

Dinoflagellate cysts
- *Chatangiella granulifera* (Manum 1963) Lentin and Williams 1976
- *Chatangiella spectabilis* (Alberti 1959) Lentin and Williams 1976
- *Chlamydophorella discreta* Clarke and Verdier 1967
- *Elytrocysta druggii* Stover and Evitt 1978
- *Laciniadinium arcticum* (Manum and Cookson 1964) Lentin and Williams 1980
- *Scriniodinium crystallinum* (Deflandre 1938) Klement 1960 (40 specimens)
- *Spiniferites ramosus ramosus* (Ehrenberg 1838) Mantell 1854
- *Subtilisphaera pontis-mariae* (Deflandre 1936b) Lentin and Williams 1976

Acritarchs
- *Palambages morulosa* Wetzel, 1961

Prasinophytes
- *Tasmanites suevicus* (Eisenack 1957) Wall 1965

Spores
- *Schizosporis rugulatus* Cookson and Dettmann 1959

Pollen
- *Expressipollis ocliferius* Khlonova 1961
- *Taxodiaceaepollenites hiatus* Kremp 1949 ex Potonie 1958