Canadian Journal of Earth Sciences
Revue canadienne des sciences de la Terre

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Journal:	<i>Canadian Journal of Earth Sciences</i>
Manuscript ID	cjes-2016-0053.R1
Manuscript Type:	Article
Date Submitted by the Author:	08-Jul-2016
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Keyword:	Hesperornithiform, Paleoecology, High Latitude, Trophic Ecology

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A new hesperornithiform (Aves) specimen from the Late Cretaceous Canadian High Arctic with comments on high latitude hesperornithiform diet

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Abstract

Here we describe a new hesperornithiform specimen from the Upper Cretaceous Kanguk Formation of Devon Island, Nunavut, Canada. This specimen (NUVF 286) is referred to cf. *Hesperornis* sp. based on size and shape of femora and teeth preserved with other skeletal elements. Previous osteohistologic analyses indicate a sub-adult ontogenetic stage at the time of death. This new cf. *Hesperornis* specimen includes the first teeth associated with a high-latitude hesperornithiform, allowing for comments on the trophic behavior of these birds. Paleoeological reconstructions based on current knowledge of polar assemblages and comparisons to modern birds suggest that high-latitude hesperornithiform birds may have had more varied diets than previously assumed.

Key Words: Hesperornithiform, Paleoeology, High Latitude, Trophic Ecology

Introduction

Hesperornithiform bird fossils have been recovered from Late Cretaceous Western Interior Seaway (WIS) deposits stretching from Arkansas to Ellesmere Island (Fig. 1), and are well-documented members of northern hemisphere Late Cretaceous high latitude ecosystems (Russell 1967, Bryant 1983, Hills et al. 1999, Hou 1999, Wilson et al. 2011). To date, two large-bodied taxa have been described from North American Arctic sediments: *Hesperornis* and *Canadaga*. *Hesperornis* has been described from the Northwest Territories (Russell 1967), the North Slope of Alaska (Bryant 1983), and Ellesmere Island (Hills et al. 1999); *Canadaga* has been described from Bylot Island (Hou 1999) and Devon Island (Wilson et al. 2011). Here, we describe a new occurrence of cf. *Hesperornis* from the Campanian Kanguk Formation of Devon Island, Nunavut, Canadian High Arctic. This is the second hesperornithiform specimen and second taxon described from Devon Island.

As pursuit-diving seabirds, hesperornithiforms ostensibly filled an important niche in both mid and high latitude Late Cretaceous marine ecosystems. In the Arctic, adult and juvenile specimens are relatively abundant given the overall limited fossil record from such remote environments. Additionally, hesperornithiforms are one of the few vertebrates that increase in relative abundance with latitude (Nicholls and Russell 1990), highlighting their pervasiveness in these high latitude ecosystems. Although the equator-to-pole temperature gradient was lower during the Late Cretaceous (Amiot et al. 2004), mean annual sea surface temperatures, seasonal photoperiod differences, and other expressions of seasonality likely led to differences in ecosystem structure between mid and high latitudes. Despite this, the trophic roles of hesperornithiforms in different environments along the Seaway have not been explored in detail, especially with regard to the faunal record from polar fossil localities.

Locality and Geologic Setting

A new hesperornithiform specimen (NUVF 286) was collected in 2003 from Late Cretaceous Kanguk Formation sediments of Eidsbotn graben on Devon Island, Nunavut in the Canadian High Arctic. The bones were encased in mostly uncemented fine glauconitic sand. Interpretation of a nearshore environment for the depositional environment of NUVF 286 is supported by the regressive stratigraphic sequence on Devon Island, presence of woody debris (Chin et al. 2008), and characteristic diatom assemblages (Witkowski et al. 2011).

Collections from Eidsbotn graben on Devon Island have revealed a variety of microfossils, invertebrate and vertebrate macrofossils, and coprolites (Fig. 2) (Chin et al. 2008), providing a glimpse of the Late Cretaceous Arctic marine paleoecosystem. Although there appears to be a bias against preservation of calcareous remains in these Arctic sediments, siliceous, phosphatic, and organic fossil remains were recovered (Chin et al. 2008). Microfossil remains are dominated by diatoms (Chin et al. 2008, Witkowski et al. 2011); silicoflagellates (McCartney et al. 2011), radiolarians, and dinoflagellates (Chin et al. 2008) are also present. Macrofossils recovered include hexactinellid sponges (Rigby et al. 2007), lingulid brachiopods, bivalves, decapod crustaceans, cephalopods, cartilaginous fishes (including at least two genera of lamniform sharks and a ratfish), large bony fishes (a sturgeon, ichthyodectids and pachyrhizodontids), smaller bony fish (such as *Enchodus* Agassiz, 1835), polycotylid and elasmosaurid plesiosaurs, and hesperornithiform birds (see also Chin et al. 2008). Other smaller bony fish remains were recovered from shale deposits 100-200m below the fossil-bearing greensands in which NUVF 286 was found, but none were found in coeval sediments.

Materials and Methods

Most of the NUVF 286 fossil material was collected in a 30 x 20 x 20 cm plaster jacket, but some material was collected as float along with all visible vertebrate and invertebrate fossils. A few associated bones below the specimen could not be collected because they were frozen in permafrost. The specimen was prepared by Charles Magovern (Stone Company). NUVF 286 was compared to material described in the literature and with specimens observed during visits to the Yale Peabody Museum (YPM), University of Kansas Museum of Natural History (KUVP), Sternberg Museum of Natural History (FHSM), and Canadian Museum of Nature (CMN) by the primary author. Around 13 kg of sediments were collected from the general vicinity of the NUVF 286 locality on a previous expedition to Devon Island; these sediments were sieved for recognizable fossil material in the greensands.

A JEOL JSM-6480LV low vacuum scanning electron microscope at the Nanomaterials Characterization Facility at the University of Colorado at Boulder was used to capture images of teeth associated with NUVF 286. A low vacuum SEM was used, so teeth were not coated or otherwise altered for this analysis. Images were compiled using ImageJ software and edited in Adobe Photoshop.

Institutional abbreviations

CMN, Canadian Museum of Nature, Ottawa; **FHSM**, Fort Hays State University, Sternberg Museum of Natural History, Hays, Kansas; **KUVP**, University of Kansas, Vertebrate Paleontology, Museum of Natural History, Lawrence, Kansas; **NUVF**, Nunavut Vertebrate Fossil collection (housed at CMN, Ottawa); **PU**, Princeton University (now housed at YPM, New Haven, USA); **YPM**, Yale Peabody Museum, New Haven, Connecticut.

Systematic Paleontology

Aves (Linnaeus 1758)

Hesperornithiformes (Fürbringer 1888)

Hesperornithidae (Marsh 1872b)

Hesperornis (Marsh 1872b)

cf. *Hesperornis* sp.

(Figs. 3-4; Appendix 1)

Referred material

Associated skeleton includes: left and right femora, four teeth, partial left and right ilia, rib fragments, and assorted bone fragments (NUVF 286) (Figs. 3-4; Appendix 1).

Diagnosis

NUVF 286 is referred to the genus cf. *Hesperornis* on the basis of femur morphology as described by Marsh (1880) and Bell and Chiappe (2015a): short, stout femur with a curved shaft that has a C-shaped lateral margin; large, round head with deep pit on articular surface; transversely expanded distal end; large medullary cavity with cortical bone showing osteosclerosis; distinct, rugose ridges on the medial and lateral surfaces for muscle attachments. Other material associated with NUVF 286 is too fragmentary for detailed morphological comparison.

Deposition and Preservation

All elements are assumed to be from one skeleton based on the close spatial association of elements and the relative scarcity of other macrofossils in the greensands. Size correlation (particularly the femora) (Table 1), non-duplication of skeletal elements, similar bone preservation, and the lack of remains from other avian organisms also support the interpretation that the remains belonged to one individual. While the fossil material is highly fragmented, no abrasion is apparent. Some microbial invasion is evident within at least some of the bones, and the right femur shows evidence of invertebrate borings (Fig. 3B).

Fragmentation of the skeletal elements may have occurred due to exposure at the sediment-water interface before burial, and more recent permafrost thawing and frost heaving probably caused further fracturing. Microbial invasion and possible evidence of boring suggest that NUVF 286 was either not immediately buried or was only shallowly buried for some period of time. The low clastic input into the depositional system (as indicated by the glaucony), lack of abrasion or significant weathering, and association of skeletal elements of different sizes, shapes, and densities indicate that the skeleton underwent little to no transport before deposition and burial in the glauconitic sands.

Description

Femora—The femora of NUVF 286 are the most diagnostic bones preserved (Fig. 3). The right femur (Fig. 3A, 3B) is broken into four pieces, with the mid-shaft region, femur head, and inner distal condyle best preserved. Evidence of boring is found on the shaft of the right femur. Although the right femur has portions of periosteal bone missing, pronounced rugosities for

muscle attachments on the medial surface of the femoral shaft are apparent. The left femur is crushed with most of the posterior portion missing (Fig. 3C, 3D). The left femur head was displaced from the rest of the femur and is cemented to an indurated block of sediment containing pelvic fragments. The greater trochanter and distal medial condyle are missing, but the distal lateral condyle is preserved.

Comparisons of the NUVF 286 femora to *Hesperornis regalis* Marsh, 1872 femora described by Marsh (1880), and other YPM, KUVF, and FHSM specimens, reveal NUVF 286 to be morphologically comparable to *H. regalis* specimens from Kansas. Observable femoral synapomorphies shared between NUVF 286 and the genus *Hesperornis*, based on the phylogenetic analysis by Bell and Chiappe (2015a), include: a slightly cranially convex shaft in medial view, and a strong S-shape in the medial margin of the femur shaft. NUVF 286 also has a pocketed patellar sulcus (see Bell and Chiappe 2015b). The size of NUVF 286 and *H. regalis* specimens are equivalent (Table 1), though a previous histologic description of NUVF 286 (Wilson and Chin 2014) indicates that this specimen was a sub-adult approaching skeletal maturity at the time of death. The only apparent difference between *H. regalis* and the new Arctic specimen is that the fibular articular surface of NUVF 286 is more laterally and less posteriorly inflected than other *H. regalis* specimens (Marsh 1880, Bell and Chiappe 2015b, Aotsuka and Sato 2016, personal observation); the ridges on the fibular articular surface also are not as pronounced. However, given the fragmentary nature of the elements, the orientations of some features are difficult to accurately reconstruct. Additionally, since this specimen is a sub-adult, ontogenetic variation cannot be discounted. The NUVF 286 femora are also morphologically similar to specimens informally assigned to *H. chowi* Martin and Lim, 2002, but

this taxon was not supported as distinct from *H. regalis* in the most recent phylogenetic analysis (Bell and Chiappe 2015a) and is now listed as *Hesperornis* sp. on Table 1.

Iliac fragments—The ilia of NUVF 286 are still mostly encased by a cemented glauconitic matrix, which was left intact to support the bones. However the preserved portions of the left and right ilia appear to be articulated. The lateral portion of the left ilium near the acetabula is clearly exposed but is not well preserved (Appendix 1). The head of the left femur was preserved in close association with the left ilium in the region of the acetabulum. No details from these fragments assisted with taxonomic identification.

Teeth—Four teeth were recovered from the plaster jacket along with the cf. *Hesperornis* bones. Because the teeth were detached from jaw elements, we are unable to determine tooth position within the jaw. Tooth crown length ranges from 5.0mm to 6.2mm, which are comparable in size to teeth from YPM 1206 and KUVF 71012. All teeth are labio-lingually compressed and recurved, which is consistent with descriptions of *Hesperornis* teeth by Marsh (1880), and other teeth identified as *Hesperornis* (KUVF 71012) and *Parahesperornis* (KUVF 2287). The two smaller teeth (T_3 and T_4) are more strongly recurved than the two larger teeth (T_1 and T_2 ; Fig. 4). Carinae are present in some teeth (e.g., T_4), but are weak or absent in others. No serrations are evident.

The tip of one tooth (T_1) is broken, but it is unclear whether this reflects post-mortem damage or occurred during prey capture or feeding. No spalling or other macroscopic alteration is evident on the teeth. All teeth show fine wrinkles (crenulations) in the enamel layer, resulting in a rough enamel texture formed by the series of low, irregular ridges that extend longitudinally

from the tooth apex to gum line (Fig. 4). The density of enamel wrinkles varies among the four teeth. Similar ridges have been reported in Kansas *Hesperornis* teeth (Sander 1999).

In general, the size and morphology of the teeth associated with the NUVF 286 specimen are consistent with other *Hesperornis* teeth (Marsh 1880). The NUVF 286 teeth also do not resemble teeth from any other vertebrates recovered from Devon Island. They lack the robust, regular ridges and conical shape of polycotyloid plesiosaur teeth. Some unidentified large fish bones were collected nearby, but the NUVF 286 teeth are much smaller than would be expected of teeth associated with those bones, and do not match the teeth of known fish from the region. Ichthyodectid teeth are typically conical and not recurved, pachyrhizodontid teeth are smooth and conical, and *Enchodus* teeth are either small and smooth, or much larger with regular ridges near the base and a smooth crown. Only *Hesperornis* bones were recovered at this specific locality and there are no duplicate elements (suggesting only one individual is represented). Moreover, sediment sieving in the area demonstrated that vertebrate remains are rare at this locality. We thus infer that the teeth are associated with the other skeletal elements assigned to NUVF 286, and represent cf. *Hesperornis* teeth.

Assorted bone fragments—Additional bone fragments identified as ribs (Appendix 1), vertebrae, and a tibiotarsus are also referred to NUVF 286, but are too fragmentary for accurate measurements or to assist with taxonomic identification. A partial internal mold of one tibiotarsus was also preserved.

Discussion

As noted above, two hesperornithiform genera have been identified from the North American Arctic (Fig. 1): *Canadaga* and *Hesperornis*. The new specimen described in this study thus falls within the established biogeographic range for hesperornithiform birds, and specifically the genus *Hesperornis*. The only *Hesperornis* taxon identified to species from the Arctic is *H. regalis* (Russell 1967), with others identified to genus only (Bryant 1983, Hills et al. 1999). Recent description of a *H. cf. rossicus* Nesson and Yarkov 1993 specimen from Manitoba suggests a holarctic distribution for the species (Aotsuka and Sato 2016). Undescribed specimens attributed to hesperornithiforms have also been collected from Eglinton Island and Horton River (Northwest Territories), and are housed at the CMN.

Despite the crushed and fragmentary preservation of the femora, several key characters are preserved and support taxonomic identification to the genus *Hesperornis*. Comparisons with other hesperornithiform femora show that this new Arctic specimen is comparable in size to *H. regalis* specimens from Kansas and Manitoba (Table 1)—even though histology patterns indicate that NUVF 286 was a sub-adult individual approaching skeletal maturity (Wilson and Chin 2014). The femora of NUVF 286 are larger than a large hesperornithiform specimen from Anderson River, Northwest Territories (CMN 10441) assigned to *H. regalis* by Russell (1967), but the ontogenetic stage of CMN 10441 is unknown. Martin and Lim (2002) suggest that the Anderson River specimens may be assigned to *H. chowi* based on large size. However, no *H. chowi* femora have been formally described in the literature, and *H. chowi* is not supported in the most recent hesperornithiform phylogenetic analysis, as it does not code differently than *H. regalis* (Bell and Chiappe 2015a). The NUVF 286 femora are also more robust than those of the elongate *Baptornis advenus* (Martin and Tate, 1976) and *Paraesperornis alexi* (Martin 1984), and the trochanter ridge of NUVF 286 is laterally expanded away from the shaft (a

Hesperornithidae character) (Bell and Chiappe 2015a). The pocketed patellar sulcus is observable in NUVF 286, distinguishing it from *Baptornis* and the new genus *Fumicollis* (Bell and Chiappe 2015b).

In a previous study, Wilson et al. (2011) described a *Canadaga arctica* specimen (NUVF 284) from Devon Island, and noted that the large *Hesperornis* specimen from the Northwest Territories (CMN 10441) might be assigned to *C. arctica* based on size and proximity to the type locality. Though Hou (1999) referred two fragmentary femora to *C. arctica*, the only thoroughly described and clearly identified *C. arctica* material consists of cervical vertebrae (Hou 1999, Wilson et al. 2011). Until additional material is found, assigning Arctic hesperornithiform appendicular skeletal elements to *C. arctica* is tentative at best, especially when this large hesperornithiform resembles other taxa so closely. Accordingly, based on comparisons with femora held in museum collections and described in the literature—and considering the taxonomic issues discussed above—we assign NUVF 286 to cf. *Hesperornis* sp. We hope that future discoveries of hesperornithiform fossils from the Arctic will shed light on these taxonomic issues, especially regarding the validity of multiple species assigned to *Hesperornis* (sensu Bell and Chiappe 2015a).

Hesperornithiform Feeding Behavior

Hesperornithiforms are assumed to have been piscivorous based on jaw morphology and the presence of teeth (Green 1962, Martin and Tate 1976, Rees and Lindgren 2005, Martin and Naples 2008). Morphological analysis of the mandibles has indicated that lateral movement was possible at the posterior margin of the mandibular bones to enable swallowing of larger prey items (Martin and Naples 2008). While gape (width of jaws at contact with skull) has been

shown to be a controlling factor on prey size (e.g. Hulsman 1981, Erikstad 1990), it cannot be used to determine prey type. The only direct evidence suggesting piscivory is a coprolite/intestinal cast containing fish remains associated with a *B. advenus* skeleton from the Niobrara Chalk of Kansas (Martin and Tate 1976). However, the identification of *B. advenus* as the producer of the coprolite is tenuous, as the association is based solely on proximity to the bird skeleton and the coprolite's lack of a spiral morphology (which is attributable to certain fish taxa).

Despite possible adaptations to piscivory within the clade, there is little evidence that hesperornithiforms were exclusively piscivorous. We propose that these birds exploited more diverse food resources in ancient high latitude ecosystems. Generalized, flexible diets would have offered advantages at high latitudes, regardless of whether hesperornithiforms overwintered in the Arctic or migrated south along the Seaway. Furthermore, as in our present-day interglacial world, Arctic marine ecosystem structure in the greenhouse world of the Campanian appears to have been distinctly different from that of lower latitude ecosystems (Chin et al. 2008). While fossil evidence for the smaller fishes that often characterize seabird diets is abundant in mid latitude Campanian sediments (Nicholls and Russell 1990, Carpenter 2003, 2006, Shimada and Fielitz 2006), studies documenting Late Cretaceous high latitude fossil assemblages (both Arctic and Antarctic) (Kriwet et al. 2006, Martin and Crame 2006, Chin et al. 2008) report a paucity of small- and medium-sized fishes. Chin et al. (2008) reported only one small to medium-sized fish taxon (*Enchodus*) from the greensands of the Campanian Kanguk Formation on Devon Island, even though all observed macrofossils were collected. Around 13 kg of glauconitic sediment collected on a previous expedition in the general vicinity of the NUVF 286 locality was sieved for microvertebrate and invertebrate remains, and only a handful of unidentifiable vertebrate and

invertebrate remains were recovered (Alex Dutchak, personal communication). Similar results of low osteichthyan diversity and abundance, especially teleosts, are reported from Upper Cretaceous sediments of James Ross Basin, Antarctica (Kriwet et al. 2006, Martin and Crame 2006). Kriwet et al. (2006) found fishes at lower levels of the food chain to be lacking in these Antarctic deposits, while larger, top predator fish were significantly more abundant.

Taphonomic bias can offer one explanation for the lack of small- and medium-sized fish in the polar fossil record. Nevertheless, though biostratinomic and diagenetic processes undoubtedly affected fossil preservation in these environments, Martin and Crame (2006) concluded that the low abundance of intermediate and lower trophic level fishes in Late Cretaceous Antarctic deposits represents a genuine absence from the ecosystem rather than a taphonomic bias. Fish bones are fragile, but their teeth are generally more resistant to destructive forces. Given the preservation of diverse fossils recovered from Devon Island (Chin et al. 2008; this study), it seems likely that fish teeth would be more common if small- and mid-sized fish were present in abundances comparable to what has been found at lower latitudes. Seasonal migration of fish populations may also explain the paucity of small to medium-sized fish fossils in the Devon Island assemblage. If some species of fish only seasonally inhabited polar environments, fewer would be preserved, contributing to their poor fossil record.

Despite the Late Cretaceous greenhouse climate (e.g. Barron 1983, Hay et al. 1993, Huber et al. 1995, 2002, Herman and Spicer 1997, Jenkyns et al. 2004, Spicer and Herman 2010, Dennis et al. 2013), organisms at high latitudes were still subject to seasonal changes in photoperiod, temperature, and resource availability. Seasonality likely affected the overall marine trophic structure (Chin et al. 2008) and relative abundance of organisms (Kauffman 1984, Nicholls and Russell 1990), and would have affected hesperornithiform feeding behavior.

Evidence indicates that at least some Campanian Arctic marine food webs in the Devon Island area were relatively short, with fewer trophic levels between primary producers and large predators (Chin et al. 2008). These Campanian Arctic trophic patterns are similar to those in modern high latitude marine ecosystems, which often have shortened food chains where apex marine predators feed directly on smaller organisms at lower trophic levels (Laws 1985, Sanger 1987, Ainley and DeMaster 1990). In modern polar environments, seabirds (which are generally significantly smaller than *Hesperornis* and *Canadaga*) are abundant top predators and feed more often on zooplankton (krill, copepods) and first order carnivores (small fish) than on larger, high-order carnivores (large fish). One benefit of abbreviated food chains is that predators feeding at lower trophic levels are more efficient in utilizing seasonal phytoplankton blooms (Sanger 1987).

Having a more flexible diet would have allowed high latitude hesperornithiforms to adjust to seasonal variations in the availability of different prey species. Diet switching has also been suggested for other toothed Mesozoic (Zhou et al. 2004) and early Cenozoic (Naish 2014) birds. Additionally, the recurved crown, enamel wrinkles, pointed apex, lack of sharp carinae, and absence of serrations in *Hesperornis* teeth (Fig. 4) best align with descriptions of extinct marine reptile teeth that were likely used for piercing or associated with a generalized diet (Massare 1987).

Consequently, hesperornithiform diets probably displayed seasonal fluctuations as these birds switched feeding on different prey organisms. The remains of benthic invertebrates such as lobsters and nektonic invertebrates like squid were found in the Devon Island deposits (Fig. 2), but most soft-bodied invertebrates typically have a poor fossil record. For example, krill have no fossil record, though molecular analysis indicates that the origin of krill dates back to the Early Cretaceous (Jarman 2001). In general, coleoid cephalopod remains are common in sediments

from the Western Interior Seaway, and Elzanowski (1983) suggests that squid may have provided a reliable food source for hesperornithiforms.

In modern systems, soft-bodied invertebrates like krill, copepods, and squid play a large role in seabird diets (e.g., Ashmole and Ashmole 1967, Sanger 1987, Kooyman 2002, Bost et al. 2009). In addition, extant seabirds are known to have variable diets as different prey items migrate in and out of their foraging areas (Shealer 2001, Ainley 2002). In the modern Gulf of Alaska, for example, Common Murres and Marbled Murrelets feed on demersal crustaceans during the winter rather than pelagic fish (Sanger 1987). Sanger speculates that pelagic-benthic coupling (exemplified by seabirds feeding on the benthos) provides a more reliable source of food in highly seasonal environments, in which prey species change and/or become scarce between seasons. Additionally, changes in diet within a species across a geographic range have been documented in some seabirds (e.g., Polito et al. 2002), as well as changes in diet correlated with climatic shifts through time (Emslie et al. 1998, Emslie and McDaniel 2002, Polito et al. 2002).

The discovery of the fossil bird specimen NUVF 286 on Devon Island augments our understanding of the known distribution of *Hesperornis*, and supports the inference that these birds were widespread in the Arctic during the Late Cretaceous. As such, they likely played important roles in ancient polar marine ecosystems through their feeding activities. Reconstructions of the ancient Devon Island food web and comparisons with modern seabird communities offer complementary perspectives on Arctic hesperornithiform diets. The paucity of mid-sized and smaller fossil fish in Arctic sediments does not seem to support the commonly held idea that Arctic hesperornithiforms were primarily piscivorous. This fossil evidence plus studies of extant seabird diets suggest that high latitude hesperornithiform populations had more

varied and seasonally influenced diets than previously hypothesized. Although small- and medium-sized fish may have comprised a portion of their diet, utilization of other organisms—such as crustaceans and cephalopods—may have helped buffer resident or migratory hesperornithiforms from seasonal fluctuations in prey availability.

Acknowledgments

The authors thank J. Kotierk, J. Ross, and D. Stenton of the Nunavut Government Department of Culture, Language, Elders and Youth for access to NUVF 286. R. Geiss of the Nanomaterials Characterization Facility, University of Colorado Boulder assisted with SEM use and photography. J. Bloch, J. Eberle, and J. Storer helped collect fossils and sediments mentioned in this paper. C. Magovern prepared NUVF 286. T. Sato assisted in identifying plesiosaur material and A. Dutchak and D. Patten helped sort bulk sediment. D. Burnham (University of Kansas Museum of Natural History) provided images and measurements of KUVP teeth for comparison. J. Eberle, T. Marchitto, A. Cruz, H. Larsson, and two anonymous reviewers provided helpful feedback on early drafts of this manuscript. NUVF 286 was collected under NSF Polar Programs Award no. 0241002 to K. Chin; a Shell Oil Grant to L. Wilson from the Department of Geological Science at University of Colorado, Boulder provided funding for SEM use. Funds from the late Margaret and Hayes Caldwell help maintain the Chin laboratory.

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Figure captions

Table 1. Femora measurements of NUVF 286 compared to other *Hesperornis* femora. All measurements in millimeters (mm).

Fig. 1. Late Cretaceous North American distribution of specimens attributed to the genus *Hesperornis*. Map ©Colorado Plateau Geosystems 2013, used with permission. **1**, *Hesperornis* sp., Ozan Formation (Davis and Harris 1997); **2**, *Hesperornis regalis*, Niobrara Formation (Marsh 1872a, 1880); **3**, *Hesperornis crassipes*, Niobrara Formation (Marsh 1876); **4**, *Hesperornis* sp., Pierre Shale (Martin and Tate 1976); **5**, *Hesperornis chowi*, Pierre Shale (Martin and Lim 2002); **6**, *Hesperornis bairdi*, Pierre Shale (Martin and Lim 2002); **7**, *Hesperornis regalis*, Niobrara Formation (Martin and Varner 1992); **8**, *Hesperornis altus*, Judith River Formation/Clagget Formation (Marsh 1893, Shufeldt 1915, but see Wilson et al. 2011 for discussion of taxonomy); **9**, *Hesperornis mengeli*, Pierre Shale (Martin and Lim 2002); **10**, *Hesperornis* sp., Pembina Formation (Nicholls and Russell 1990); **11**, *Hesperornis regalis*, *Hesperornis howi*, *Hesperornis macdonaldi*, *Hesperornis mengeli*, *Hesperornis lungairi*, *Hesperornis* cf. *rossicus*, Pembina Formation (Bardack 1968; Aotsuka & Sato 2016); **12**, *Hesperornis* cf. *regalis*, Foremost Formation (Fox 1974); **13**, *Hesperornis* sp., Pierre Shale (Tokaryk 1999); **14**, *Hesperornis regalis*, Smoking Hills Formation (Russell 1967); **15**, *Hesperornis* sp., Ignek Formation (Bryant 1983); **16**, *Hesperornis* sp., Kanguk Formation (this paper); **17**, *Hesperornis* sp., Kanguk Formation (Hills et al. 1999).

Fig. 2. Stacked histograms showing relative number of fossils collected at Eidsbotn and Viks Fiord grabens in the Kanguk Formation on Devon Island. Top (darker) bars indicate numbers of taxa found within coprolites. Note that all body fossils were collected, but only a subset of coprolites were collected.

Fig. 3. Photographs and line drawings of identifiable bones attributed to NUVF 286. Right femur in cranial (A) and caudal (B) views; left femur in cranial (C) and caudal (D) views; ilia (E) embedded in glauconite matrix; rib fragments (F). Abbreviations: b, boring, h, head; lc, lateral condyle; mc, medial condyle; ps, patellar sulcus; tr, trochanter. Note differences in scale bar.

Fig. 4. Scanning electron microscope photomicrographs of the four teeth preserved with NUVF 286. Note the recurved crown, fine crenulations in the enamel, and absence of serrations.

TABLE 1 --Measurements available for NUVF 286 compared to other *Hesperornis* femora. All measurements in millimeters (mm).

	<i>Hesperornis</i> sp.				<i>Hesperornis regalis</i>					
	NUVF 286		PU 18589	PU 17193	YPM 1200*	YPM 1206*	YPM 1207*	YPM 1476*	YPM 1477*	CMN 10441
	Right	Left			Right/Left	Left	Right/Left	Left	Left	Right
Length	94.5	91.8	81.9	88	99/99	96	98.5/101	105	97	>75.8
Antero-posterior diameter of head	21.0	20.0	15.7	15.9	18.5/18.5	-	19/18.5	-	19	-
Transverse diameter of head	18.5	19.5	14.5	12.1	-	18	-	19.5	-	-
Transverse diameter of shaft near middle	22.0	-	23.7	19.9	-	22	-	21	20	24.4
Antero-posterior diameter near middle	18.8	-	15.9	11.3	-	-	18/18	-	-	14.1
Transverse diameter of fibular articulation	-	14.8	15.6	14.9	14/14.5	-	15/16	15.5	15	-
Greatest diameter of fibular articulation	-	21.0	22.2	20.5	-	14	-	-	-	-
Greatest diameter of inner condyle	20.5	-	19	18.6	21/21	21	21/21	20	20	19
Least diameter of inner condyle	17.3	-	12	15	14/14.5	13	13/13	18	12.5	-

*From Marsh (1880)

FHSM 2069

Right

93.87

18.09

16.85

21.57

19.15

-

17.75

-

-

Draft

Late Cretaceous North American distribution of specimens attributed to the genus *Hesperornis*. Map ©Colorado Plateau Geosystems 2013, used with permission. 1, *Hesperornis* sp., Ozan Formation (Davis and Harris 1997); 2, *Hesperornis regalis*, Niobrara Formation (Marsh 1872a, 1880); 3, *Hesperornis crassipes*, Niobrara Formation (Marsh 1876); 4, *Hesperornis* sp., Pierre Shale (Martin and Tate 1976); 5, *Hesperornis chowi*, Pierre Shale (Martin and Lim 2002); 6, *Hesperornis bairdi*, Pierre Shale (Martin and Lim 2002); 7, *Hesperornis regalis*, Niobrara Formation (Martin and Varner 1992); 8, *Hesperornis altus*, Judith River Formation/Clagget Formation (Marsh 1893, Shufeldt 1915, but see Wilson et al. 2011 for discussion of taxonomy); 9, *Hesperornis mengeli*, Pierre Shale (Martin and Lim 2002); 10, *Hesperornis* sp., Pembina Formation (Nicholls and Russell 1990); 11, *Hesperornis regalis*, *Hesperornis chowi*, *Hesperornis macdonaldi*, *Hesperornis mengeli*, *Hesperornis lumgairi*, *Hesperornis* cf. *rossicus*, Pembina Formation (Bardack 1968; Aotsuka & Sato 2016); 12, *Hesperornis* cf. *regalis*, Foremost Formation (Fox 1974); 13, *Hesperornis* sp., Pierre Shale (Tokaryk 1999); 14, *vHesperornis regalis*, Smoking Hills Formation (Russell 1967); 15, *Hesperornis* sp., Ignek Formation (Bryant 1983); 16, *Hesperornis* sp., Kanguk Formation (this paper); 17,

Hesperornis sp., Kanguk Formation (Hills et al. 1999).

105x132mm (300 x 300 DPI)

Draft

Stacked histograms showing relative number of fossils collected at Eidsbotn and Viks Fiord grabens in the Kanguk Formation on Devon Island. Top (darker) bars indicate numbers of taxa found within coprolites. Note that all body fossils were collected, but only a subset of coprolites were collected.

100x111mm (300 x 300 DPI)

Photographs and line drawings of identifiable bones attributed to NUVF 286. Right femur in cranial (A) and caudal (B) views; left femur in cranial (C) and caudal (D) views; ilia (E) embedded in glauconite matrix; rib fragments (F). Abbreviations: b, boring, h, head; lc, lateral condyle; mc, medial condyle; ps, patellar sulcus; tr, trochanter. Note differences in scale bar.

182x236mm (300 x 300 DPI)

Scanning electron microscope photomicrographs of the four teeth preserved with NUVF 286. Note the recurved crown, fine crenulations in the enamel, and absence of serrations.

90x96mm (300 x 300 DPI)