

A New Arctic Hadrosaurid from the Prince Creek Formation (Lower Maastrichtian) of Northern Alaska

Authors: Mori, Hirotugu, Druckenmiller, Patrick S., and Erickson, Gregory M.

Source: *Acta Palaeontologica Polonica*, 61(1) : 15-32

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.00152.2015>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

A new Arctic hadrosaurid from the Prince Creek Formation (lower Maastrichtian) of northern Alaska

HIROTSUGU MORI, PATRICK S. DRUCKENMILLER, and GREGORY M. ERICKSON



Mori, H., Druckenmiller, P.S., and Erickson, G.M. 2016. A new Arctic hadrosaurid from the Prince Creek Formation (lower Maastrichtian) of northern Alaska. *Acta Palaeontologica Polonica* 61 (1): 15–32.

The Liscomb bonebed in the Price Creek Formation of northern Alaska has produced thousands of individual bones of a saurolophine hadrosaurid similar to *Edmontosaurus*; however, the specific identity of this taxon has been unclear, in part because the vast majority of the remains represent immature individuals. In this study, we address the taxonomic status of the Alaskan material through a comparative and quantitative morphological analysis of juvenile as well several near adult-sized specimens with particular reference to the two known species of *Edmontosaurus*, as well as a cladistic analysis using two different matrices for Hadrosauroidae. In the comparative morphological analysis, we introduce a quantitative method using bivariate plots to address ontogenetic variation. Our comparative anatomical analysis reveals that the Alaskan saurolophine possesses a unique suite of characters that distinguishes it from *Edmontosaurus*, including a premaxillary circumnarial ridge that projects posterolaterally without a premaxillary vestibular promontory, a shallow groove lateral to the posterodorsal premaxillary foramen, a relatively narrow jugal process of the postorbital lacking a postorbital pocket, a relatively tall maxilla, a relatively gracile jugal, a more strongly angled posterior margin of the anterior process of the jugal, wide lateral exposure of the quadratojugal, and a short symphyseal process of the dentary. The cladistic analyses consistently recover the Alaskan saurolophine as the sister taxon to *Edmontosaurus annectens* + *Edmontosaurus regalis*. This phylogenetic assessment is robust even when accounting for ontogenetically variable characters. Based on these results, we erect a new taxon, *Ugrunaaluk kuukpikensis* gen. et sp. nov. that contributes to growing evidence for a distinct, early Maastrichtian Arctic dinosaur community that existed at the northernmost extent of Laramidia during the Late Cretaceous.

Key words: Dinosauria, Hadrosauridae, Saurolophinae, Edmontosaurini, ontogeny, Cretaceous, Prince Creek Formation, Arctic, Alaska.

Hirotsugu Mori [hmori@alaska.edu], Department of Geosciences, University of Alaska Fairbanks, 900 Yukon Drive, Fairbanks, AK 99775-5780, USA; University of Alaska Museum, 907 Yukon Drive, Fairbanks, AK 99775, USA; and Saikai City Board of Education; Setoitanoura Go, Oseto Cho, Saikai City, Nagasaki Prefecture, 857-2301, Japan.
Patrick S. Druckenmiller [psdruckenmiller@alaska.edu], University of Alaska Museum, 907 Yukon Drive, Fairbanks, AK 99775, USA; and Department of Geosciences, University of Alaska Fairbanks, 900 Yukon Drive, Fairbanks, AK 99775-5780, USA.

Gregory M. Erickson [gerickson@bio.fsu.edu], Department of Biological Science, Florida State University, 319 Stadium Drive, Tallahassee, FL 32306-4295, USA.

Received 10 January 2015, accepted 7 August 2015, available online 22 September 2015.

Copyright © 2016 H. Mori et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License (for details please see <http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

The Prince Creek Formation (PCF) of northern Alaska preserves one of the most diverse and prolific assemblages of polar dinosaurs known anywhere in the world. To date, evidence for at least 13 different dinosaurian taxa are known from early Maastrichtian horizons of the unit, including five ornithischians, seven non-avian theropods, and an avialan theropod (Gangloff 1994; Druckenmiller et al. 2013). However, only three of these taxa have been identified tax-

onomically to the species level (Sullivan 2006; Fiorillo and Tykoski 2012, 2014). The remainder have only been tentatively identified at generic or suprageneric levels (Fiorillo et al. 2009; Brown and Druckenmiller 2011; Druckenmiller et al. 2013; Watanabe et al. 2013). Because all three named dinosaurian species are endemic to the Laramidian Arctic, Erickson and Druckenmiller (2011) hypothesized that the Prince Creek Formation supported a distinctive early Maastrichtian dinosaur polar fauna known as the Paanaqtat Province. Understanding the overall faunal composition of the PCF is critical in order to test this hypothesis and assess

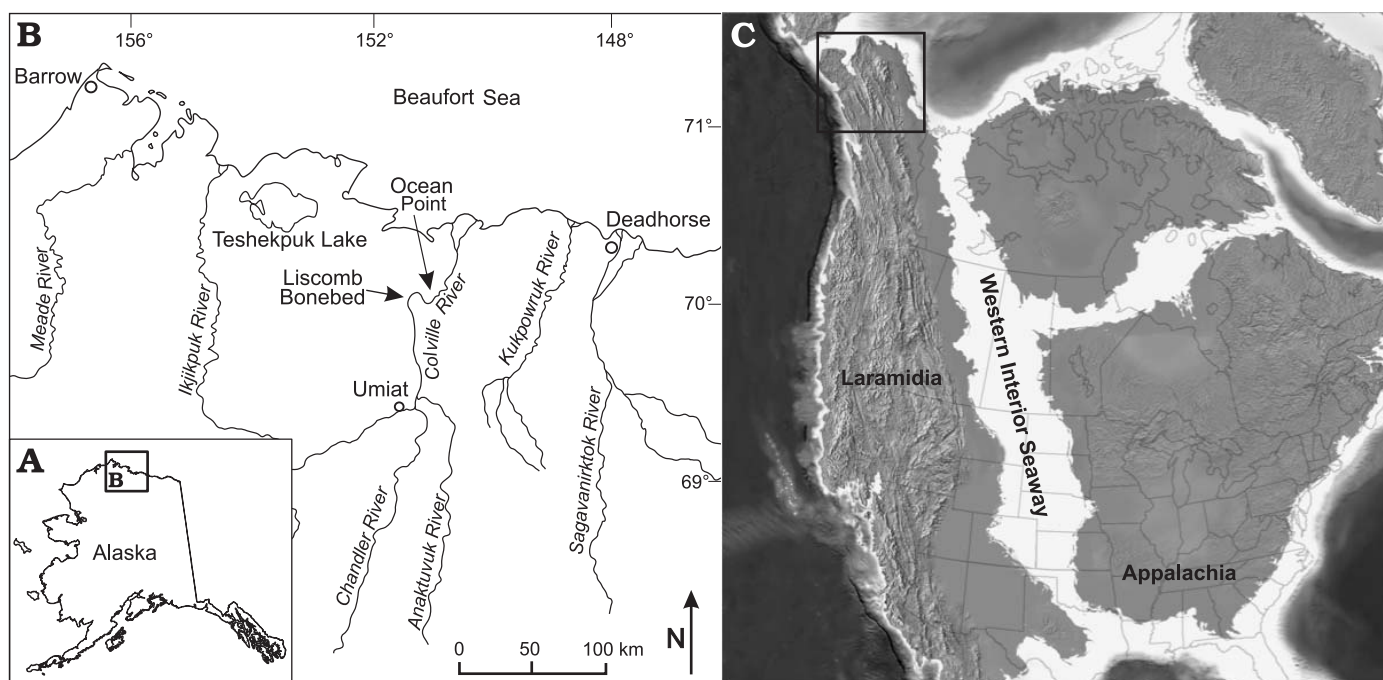


Fig. 1. Study area in northern Alaska, USA (A) and location of the Liscomb bonebed (B). C. Paleogeographic reconstruction of North America at 70 Ma (Blakey, 2009); the box indicates the approximate position of Alaska at that time.

larger questions relating to Laramidian biogeography and dinosaur paleobiology.

Since the 1990s, an abundance of hadrosaurid remains have been recovered from the Prince Creek Formation (Fig. 1). The material is primarily derived from a single well-known horizon known as the Liscomb bonebed (LBB), from which thousands of disarticulated cranial and postcranial dinosaur remains have been excavated (Brouwers et al. 1987; Davies 1987; Nelms 1989; Clemens and Nelms 1993; Gangloff 1994, 1998; Fiorillo and Gangloff 2001; Fiorillo et al. 2007, 2010; Fiorillo 2008a; Flaig 2010; Gangloff and Fiorillo 2010; Erickson and Druckenmiller 2011; Watanabe et al. 2013). The Liscomb remains were first identified as a lambeosaurine hadrosaurid (Brouwers et al. 1987). However, subsequent researchers have reassigned the remains to Saurolophinae (Hadrosauria) and tentatively referred them to the Campanian to Maastrichtian genus *Edmontosaurus* Lambe, 1917, or more specifically to *E. regalis* (Xing et al. 2014). However, a comprehensive anatomical survey of this material has not been conducted and the taxonomic referral formally demonstrated. In part, this stems from the fact the majority of the LBB remains represent individuals approximately one-third adult length and it is difficult to identify the taxonomic status of hadrosaurids from juvenile remains because most are differentiated by adult features (Prieto-Márquez 2008, 2010a; Campione and Evans 2011; Campione et al. 2012).

Here, we provide a description of the hadrosaurid material from the Prince Creek Formation. Based on comparisons with other saurolophines, particularly *Edmontosaurus*, we recognize a new species that can be diagnosed on ontogenetically invariable characters. The recognition of a new

taxon from the LBB contributes to a broader understanding of saurolophine diversity, the taxonomic composition of the PCF and provides important new evidence for testing hypotheses of dinosaur provinciality in Laramidia.

Institutional abbreviations.—AENM, Amur Natural History Museum, Blagoveshensk, Russia; AMNH, American Museum of Natural History, New York City, USA; BHI, Black Hills Institute of Geological Research, Hill City, USA; BMNH, The Natural History Museum, London, UK; CM, Carnegie Museum of Natural History, Pittsburgh, USA; CMN, Canadian Museum of Nature, Ottawa, Canada (formerly NMC, National Museums of Canada); DMNH, Denver Museum of Nature and Science, Denver, USA; FMNH, The Field Museum, Chicago, USA; GMV, National Geological Museum of China, Beijing, China; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; RAM, Raymond M. Alf Museum of Paleontology, Claremont, USA; ROM, Royal Ontario Museum, Toronto, Canada; SM, Senckenberg Museum, Frankfurt, Germany; TMNH, Toyohashi Museum of Natural History, Toyohashi, Aichi, Japan; UMMP, University of Michigan Museum of Paleontology, Ann Arbor, USA; UAMES, University of Alaska Museum, Fairbanks, USA; USNM, Smithsonian National Museum of Natural History, Washington DC, USA; YPM, Yale Peabody Museum of Natural History, New Haven, USA.

Other abbreviations.—LBB, Liscomb bonebed; PCF, Prince Creek Formation.

Nomenclatural acts.—The electronic edition of this article conforms to the requirements of the amended International

Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix “<http://zoobank.org/>”. The LSID for this publication is: urn:lsid:zoobank.org:pub:84BD5626-4F09-4246-9D86-E831E9465D69.

The electronic edition of this work was published in a journal with an eISSN 1732-2421, and has been archived and is available from the following digital repository: <http://www.app.pan.pl/article/item/app001522015.html>

Geological setting and taxonomic composition

The Prince Creek Formation (formerly referred to as the Kogosukuruk Tongue of the PCF; Gryc et al. 1951) is composed of non-marine sandstone, conglomerate, coal, and mudstone layers representing interbedded fluvial (meandering channels and floodplains) and marginal marine sediments that were deposited on a low gradient coastal plain (Mull et al. 2003; Flaig et al. 2011). Palynological (Frederiksen et al. 1988, 2002; Frederiksen 1991) and biostratigraphic data (Brouwers and Deckker 1993) suggest the entire PCF ranges from the Upper Cretaceous to Eocene in age. The numerical age of the dinosaur-bearing section of the formation, where it is exposed along the lower Colville River and including the LBB, has been dated at 71–68 Ma using $^{40}\text{Ar}/^{39}\text{Ar}$ methods (McKee et al. 1989; Besse and Courtillot 1991). The age of LBB is further constrained by an $^{40}\text{Ar}/^{39}\text{Ar}$ age of 69.2 ± 0.5 Ma from a stratigraphically underlying tuff at a locality known as Sling Point (approximately 1 km from the LBB) and from palynological analyses (Flores et al. 2007) consistent with an early Maastrichtian age (Flaig 2010). This age estimate is within the known stratigraphic range of *Edmontosaurus*, notably falling between the last appearance date of *E. regalis* Lambe, 1917 (late Campanian; Campione and Evans 2011; Eberth et al. 2013) and the first appearance of *E. annectens* Marsh, 1892 (late Maastrichtian; Campione and Evans 2011).

The Late Cretaceous paleolatitude of northern Alaska is estimated to range between 67–82° N (Witte et al. 1987; Besse and Courtillot 1991; Lawver et al. 2002), thus the LBB was well within the paleo-Arctic (above approximately 66° N). Although considerably milder than today, paleobotanical evidence indicates a mean annual temperature for the Maastrichtian of northern Alaska at around 5–6°C, with a cold month mean warmer than $2.0 \pm 3.9^\circ\text{C}$ (Parrish and Spicer 1988; Spicer and Parrish 1990; Spicer et al. 1992; Spicer and Herman 2010). From pedogenic and paleobotan-

ical evidence Flaig et al. (2013) concluded that the Arctic coastal plain had polar woodlands with an angiosperm understory, and that it experienced both strong dry and wet seasons. In addition to hadrosaurid remains, the PCF preserves a modestly diverse assemblage of ornithischian and saurischian dinosaurs and mammals (Brouwers et al. 1987; Nelms 1989; Clemens and Nelms 1993; Gangloff 1994; Gangloff et al. 2005; Fiorillo 2008a; Fiorillo et al. 2009; Gangloff and Fiorillo 2010; Brown and Druckenmiller 2011; Fiorillo and Tykoski 2012, 2014; Watanabe et al. 2013). However, to date, no unequivocally ectothermic terrestrial vertebrates have been recovered from the formation. This faunal distribution led Clemens and Nelms (1993) to suggest that the climate was too cold for most terrestrial and amphibious ectotherms, including crocodylians, champsosaurs, choristodires, squamates, and turtles that were more common contemporaneously at lower latitudes.

Taphonomically the dinosaur remains from the LBB are dominated by juvenile specimens of hadrosaurids that have been previously assigned to *Edmontosaurus* (Gangloff and Fiorillo 2010). Other rare elements represented in the bonebed included isolated hadrosaurid material and shed thescelosaurid, tyrannosaurid, and troodontid teeth. The hadrosaurid remains are almost entirely disarticulated, show little evidence of weathering, predation, or trampling, and are typically uncrushed and unpermineralized (Fiorillo et al. 2010; Gangloff and Fiorillo 2010). The LBB occurs in a trunk channel on a distributary channel splay complex and flood plain (Fiorillo et al. 2010; Flaig 2010). The bonebed is posited to reflect a mass mortality event associated with overbank flood deposits (Gangloff and Fiorillo 2010), which could have resulted from rapid snowmelt from the then-rising Brooks Range to the south (Fiorillo et al. 2010).

Material and methods

Material.—More than 6000 hadrosaurid bones from the LBB that form the basis for this study have been collected during expeditions led by the University of Alaska Museum and the University of California Museum of Paleontology (this material is now housed at UAMES). The majority of this material consists of individuals from an immature growth stage (size class 1; humeral length = ~22 cm; SOM 1, Supplementary Online Material available at http://app.pan.pl/SOM/app61-Mori_et_al_SOM.pdf), approximately one-third the adult humerus length of *Edmontosaurus* (approximately 60–70 cm). The remaining material represents size class 2 juvenile individuals (SOM 1) (~29 cm humeral length), and size class 3 subadult individuals (SOM 1) (~43 cm humeral length). The three size classes may represent a mass mortality event of a herd or herds containing yearly cohorts (Gangloff and Fiorillo 2010).

393 specimens bearing phylogenetically informative characters, including cranial and postcranial elements were examined in detail during the course of this study (SOM 1).

Because of the abundance of material, most elements are known from multiple specimens making it possible to account for variation in both size and morphology.

The Alaskan material is compared in detail to *Edmontosaurus*, which has two recognized species, *E. regalis* (late Campanian) and *E. annectens* (late Maastrichtian; Campione and Evans 2011) represented by abundant material from the United States of America and Canada (SOM 2). *Edmontosaurus* was chosen as the primary comparator, particularly for the regression analyses (see below), for four reasons. First, the Alaskan taxon at a coarse anatomical level appears to be *Edmontosaurus* and has been referred to as such (Clemens and Nelms 1993; Gangloff 1998; Fiorillo and Gangloff 2001; Prieto-Márquez 2008; Gangloff and Fiorillo 2010; Campione and Evans 2011; Xing et al. 2014). Specifically, the Alaskan material possesses two of the diagnostic characters of the genus, proposed by Xing et al. (2014); (i) the premaxillary margin is strongly folded dorsoventrally, and (ii) the dorsolateral process of the laterosphenoid is truncated. Also, the PCF material has two premaxillary foramina in the prenasal region of the circumnasal fossa as in *Edmontosaurus*, although we disagree with Xing et al. (2014) in regarding this character as unique to *Edmontosaurus*, as such a structure is also seen in *Maiaasaura* (Horner 1983). Further, the PCF taxon bears numerous other general anatomical similarities to these taxa such as a nasal lacking ornamentation, as seen in some genera of Saurolophinae (Brown 1913; Lambe 1914; Sternberg 1953; Maryńska and Osmólska 1981; Horner 1983, 1992; Gates and Sampson 2007; Prieto-Márquez 2010b, 2012; Prieto-Márquez et al. 2014), the tooth form bears closest similarity to *Edmontosaurus* (Prieto-Márquez 2008; Erickson and Druckenmiller 2011), and the frontal is widely exposed laterally. Second, the Alaskan material occurs within the temporal range of the genus *Edmontosaurus*, although it lies stratigraphically intermediate to both species (Fig. 2). Third, it occurs within the same landmass as *Edmontosaurus* (Laramidia), although north of the known geographic ranges for both species (Colorado, USA to Alberta, Canada). Finally, the Prince Creek Formation taxon and *Edmontosaurus* are also clearly distinct from three closely related Asian taxa (Godefroit et al. 2012; Prieto-Márquez 2013, 2014; Xing et al. 2014). Specifically, the PCF taxon and *Edmontosaurus* differ from *Shantungosaurus* Hu, 1972 in that the dorsal surface of the postorbital is nearly straight, in possessing a smaller anterior portion of the scapula, a less developed supriliac crest of the ilium and the absence of well developed boss in the proximal region of the ischiadic peduncle. Both differ from *Kerberosaurus* Bolotsky and Godefroit, 2004 in lacking a pocket on the basisphenoid process of the prootic, a wide groove for ophthalmic nerve on the laterosphenoid, a prominent palatine process on the maxilla, and a markedly depressed dorsal surface of the postorbital. Finally, the PCF taxon and *Edmontosaurus* differ from “*Kundurosaurus*” Godefroit, Bolotsky, and Lauters, 2012 in possessing a ventrally-projecting posterior buttress of the



Fig. 2. Temporal distribution of *Edmontosaurus* species and *Ugrunaaluk kuukpikensis* gen. et sp. nov. from the Prince Creek Formation in the Late Cretaceous.

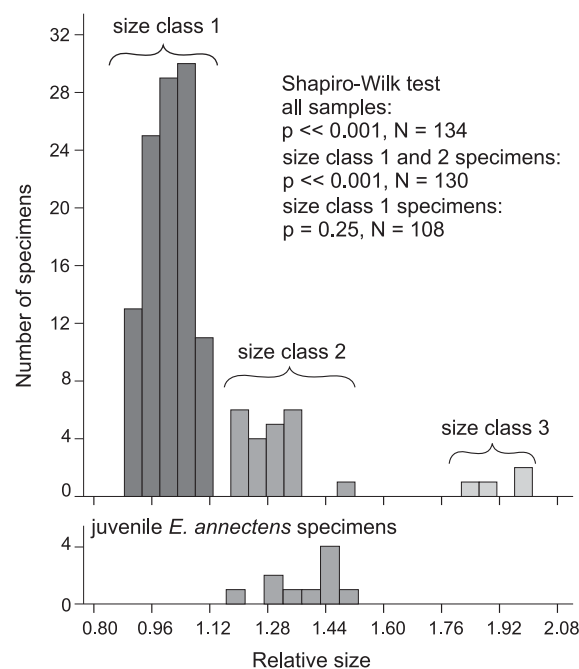


Fig. 3. Histogram of hadrosaurid bones from the Liscomb bonebed (Prince Creek Formation) for which at least 10 specimens are known. Size is standardized by the mean of size classes 1 and 2 for each bone. The relative size is adjusted so that the mean size of the size class 1 specimens becomes 1. The hypothesis of normal distribution for all samples, and samples whose relative sizes range 0.88–1.52, are both rejected ($p < 0.001$). The hypothesis of normal distribution for specimens whose relative size range 0.88–1.12 was not rejected ($p = 0.25$). Relative sizes of juvenile *E. annectens* specimens are also shown at the bottom. Note that due to insufficient numbers of corresponding bone types, size class 3 individuals of *E. annectens* are not shown in the histogram. For raw data, see SOM 3.

scapula, straight anterior process of the nasal, and a ventrally-curved preacetabular process of the ilium, although Xing et al. (2014) consider *Kundurosaurus* to be a junior synonym of *Kerberosaurus*, with which we concur. For these reasons, we assume the PCF taxon is either referable to, or closely related to *Edmontosaurus*.

Size classes in the Liscomb bonebed.—We characterized the size distribution of the individuals in the LBB and a histogram showing size versus specimen counts was prepared depicting size versus the number of specimens (Fig. 3). First,

elements for which at least 10 specimens are known were selected (dentary, frontal, humerus, ulna, radius, tibia, metatarsal II–IV; SOM 3) for size standardization. The length of each bone was divided by the mean length of each element in order to compare the lengths of different bone types. When calculating the mean length, specimens that are more than twice as long as the smallest specimens were removed. Distribution of the sizes were tested for normality using the Shapiro-Wilk test in PAST 3.0 (Harper and Ryan 2001).

The PCF elements can be classified into three ontogenetic stages, all of which are interpreted to represent three different developmental stages (Fig. 3). Approximately 85% of the specimens examined are categorized into size class 1. A three-dimensional composite skull (Fig. 4) was reconstructed from casts of size class 1 individuals and found to measure approximately 33 cm long (measured from the anterior end of the premaxilla to the mid-point of the quadrate). This is 36% of the length of the adult paratype specimen of *E. annectens*, YPM 2182 (91 cm). Size class 2 accounts for about 10% of the examined specimens and the isolated cranial elements are approximately 30% longer than size class 1 specimens, which is equivalent to ~40% of the skull length of YPM 2182. Size class 3 represents less than 5% of the total specimens, and the cranial elements are approximately 80–100% longer than the size class 1 specimens. These correspond to individuals ~60% of the size of YPM 2182.

Fortuitously, *Edmontosaurus* is represented by material spanning a broad ontogenetic range, including specimens of *E. annectens* that overlap in size with the Prince Creek Formation that permit some direct size-standardized anatomical comparisons. Comparative material of *E. annectens* (SOM 3) was also categorized by size class after standardization to mean lengths of the PCF material (Fig. 3). While overlapping material of size class 1 for *E. annectens* and the Alaskan material is not known, there is overlap in size classes 2 and 3 (size class 3 is not included in Fig. 3 because fewer than 10 specimens of a corresponding bone type of the PCF material were available). Among the ontogenetic spectrum of *E. annectens* available for comparison are individuals approximately equivalent to size class 2 (LACM 23504, skull length = estimated 47 cm), size class 3 (e.g., ROM 53530, disarticulated), to subadult (CMN 8509, skull length = 75 cm), and adult (ROM 57100, skull length = 101 cm; MOR 003, skull length = 118 cm) specimens. It should be noted, however, that there is a limited number of PCF specimens that overlap in absolute size with *E. annectens*, thus direct comparisons are not possible for some bones. *E. regalis* specimens are all larger than size class 3 specimens of the PCF taxon and range from subadult (CMN 8399, skull length = 78 cm; BMNH 8937, skull length = 75 cm) to adult (ROM 801, skull length = 107 cm; USNM 12711, skull length = 105 cm).

Regression analysis.—Because the PCF material is generally much smaller than material for *E. annectens* and *E. regalis*, quantitative methods were used to compare many

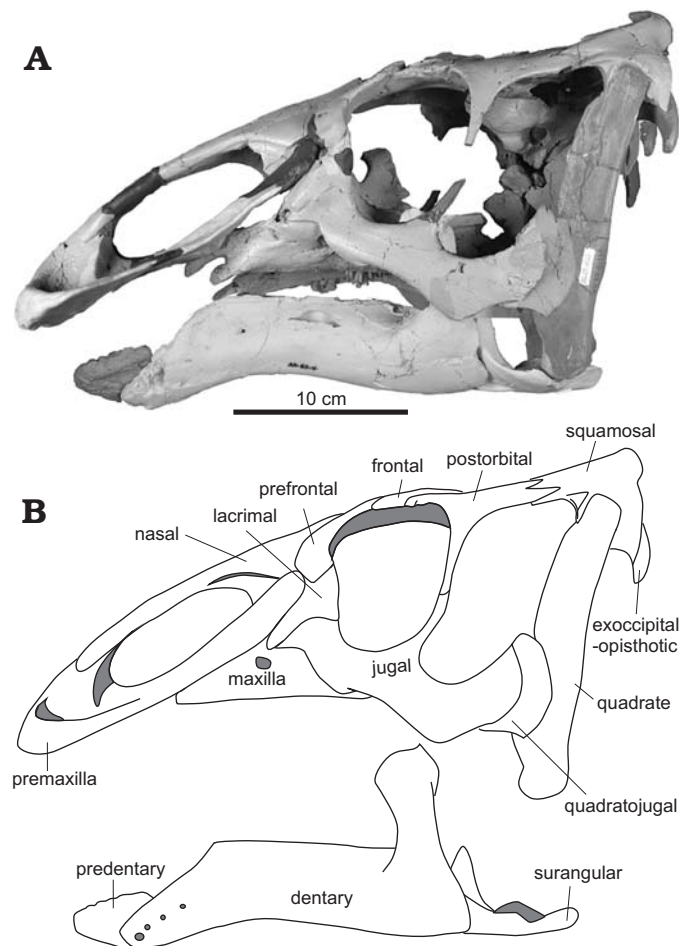


Fig. 4. Cranial reconstruction of *Ugrunaaluk kuukpikensis* gen. et sp. nov. from the early Maastrichtian Prince Creek Formation, Alaska, in left lateral view. Photograph (A) and bone interpretation (B).

elements. Quantitative data on specimens not personally measured were taken from the literature (Lull and Wright 1942; Brett-Surman 1989) or from photographs provided by colleagues. A regression analysis was employed to test if a given feature observed in the PCF material is potentially a juvenile condition of a feature seen in adult *E. annectens* or *E. regalis*. Dodson (1975a–c) demonstrated that among the same species of reptiles, log-transformed lengths of various parts show high correlations against body size. However, because the correlation coefficient is not reliable when the data include outliers (specimens which are much smaller than the others), in this case the PCF specimens themselves (Schuyler 2004), testing whether the relatively small specimens represent juveniles requires a different approach.

In order to address this problem, a new approach was employed in this study. The method is based on the assumption that the growth trend line of *Edmontosaurus*, from juvenile to adult, can be expressed by the following equation:

$$\text{Length} = A \times (\text{body length})^B \quad (1)$$

A and B are constants. This assumption is based on the observations by Dodson (1975c), who reported linear relationships between the skull length and various parts of the

skull in species of lambeosaurines. By logarithmic transformation, the equation above can be transformed as:

$$\text{Log (length)} = B \times \text{Log (body length)} + \text{log (A)} \quad (2)$$

If a log-transformed length of any body part correlates with the log-transformed body length, any sets of log-transformed body lengths would also correlate to each other. Using this assumption, we null-hypothesized that the character condition of the PCF taxon is similar to an extrapolated juvenile of *E. regalis* or *E. annectens*. From this null-hypothesis, growth trend lines of other *Edmontosaurus* species + PCF materials combined were prepared. If these hypothetical growth lines are significantly different ($p < 0.05$) from the growth trend lines of other *Edmontosaurus* specimens alone, or PCF materials alone, we concluded the PCF materials represent a different ontogenetic trajectory for that feature. For the postorbital and quadratojugal, the length of the dentary was used as a proxy for body size. Because nearly all specimens excavated from the LBB are disarticulated, only size class 1 material of the PCF taxon were compared against the mean size of the dentary of size class 1. Because size class 1 specimens represent the majority of the PCF material, other size class 1 material also likely belongs to individuals of the same size. When statistically significant results were discovered, either maximum or minimum limits of the confidence interval of the dentary length (mean length \pm two standard deviations) is adopted as the proxy of the body size, and the regression analysis was conducted again. When a given element length is too short (or long) relative to dentary length, we used the minimum (or maximum) length of the dentary. This alleviates the problem of using disarticulated bones in the regression analysis, and is more conservative. A reduced major axis (RMA) regression line was chosen to calculate the growth trend line, because it minimizes the errors in the both variables (Pearson 1901; Warton et al. 2006; Smith 2009). SMATR ver. 2.0 (Falster et al. 2006) was used to prepare the RMA regression lines, R^2 and P values, and to assess whether two regression lines are statistically different by Wald statistics.

Systematic paleontology

Ornithischia Seeley, 1887

Ornithopoda Marsh, 1881

Hadrosauridae Cope, 1869

Saurolophinae Brown, 1914 sensu Prieto-Márquez, 2010a

Edmontosaurini Brett-Surman, 1989

Genus *Ugrunaaluk* nov.

ZooBank LSID: urn:lsid:zoobank.org:act:8B8256BA-F280-4460-B0F0-31762267586E

Etymology: Transliterated from the Alaskan Iñupiaq noun *ugruṇṇaq*, referring to a grazing animal with a long set of grinding teeth, and the adjective *-aluk*, old. Literally, “ancient grazer”. Intended pronun-

ciation: “oo-GREW-nah-luk”. The name honors the Alaskan Native Iñupiaq culture from the area where the type material was discovered.

Type species: *Ugrunaaluk kuukpikensis* sp. nov., monotypic

Diagnosis.—As for type species, by monotypy.

Ugrunaaluk kuukpikensis sp. nov.

ZooBank LSID: urn:lsid:zoobank.org:act:1CAF186F-11A2-4A9E-A8F9-C3789B97459F

Figs. 4–10.

Etymology: The specific name is derived from the Iñupiaq word *kuuk-pik*, which refers to the Colville River, Alaska, USA along which the type material was found.

Type material: Holotype: UAMES 12995, anterior portion of a size class 1 right premaxilla. Paratypes: All paratypes are of size class 1, unless otherwise specified. UAMES 4271, posterior portion of the right nasal; UAMES 13250, left prefrontal; UAMES 4245, left lacrimal; UAMES 4189, right jugal; UAMES 4272, left quadratojugal; UAMES 4286, right quadrate; UAMES 33308, right postorbital of size class 3; UAMES 4361, right squamosal of size class 2; UAMES 4327, right maxilla; UAMES 15284, left laterosphenoid; UAMES 4357, right prootic; UAMES 4301, basisphenoid; UAMES 4276, basioccipital; UAMES 4309, parietal; UAMES 4291, supraoccipital; UAMES 4095, right exoccipital-opisthotic; UAMES 4240, right ectopterygoid; UAMES 4331, left palatine; UAMES 4215, left pterygoid; UAMES 4437, predentary; UAMES 4946, left dentary of size class 2; UAMES 4457, right surangular; UAMES 6646, dorsal vertebra of size class 3; UAMES 23071, sacrum of size class 3; UAMES 4873, right coracoid; UAMES 12711, right scapula; UAMES 21596, right humerus; UAMES 12525, right ulna; UAMES 6272, left radius; UAMES 6637, left ilium; UAMES 22058, pubis; UAMES 12955, left ischium; UAMES 12515, femur; UAMES 12715, left tibia; UAMES 15553, left fibula; UAMES 21950, astragalus; UAMES 21884, right calcaneum; UAMES 12545, right metatarsal IV of size class 3.

Type locality: Liscomb bonebed, along the Colville River, northern Alaska, USA. The exact location is on file with the Bureau of Land Management Arctic Field Office.

Type horizon: Upper portion of the Prince Creek Formation, lower Maastrichtian (Upper Cretaceous).

Referred specimens.—See SOM 1.

Diagnosis.—Saurolophine hadrosaurid that differs from *Edmontosaurus* in possessing the following unique combination of characters: a circumnarial ridge of the premaxilla that projects posterolaterally without a premaxillary vestibular promontory (*Edmontosaurus* has anteroposteriorly expanded circumnarial ridge with vestibular promontory); groove lateral to the posterodorsal premaxillary foramen is shallow (deep in *Edmontosaurus annectens*); absence of a shallow postorbital fossa (*Edmontosaurus* has a distinct, deep postorbital pocket); dorsoventrally short maxilla (relatively taller in *E. annectens*); relatively gracile jugal (relatively robust in *E. annectens*); the posterior margin of the anterior process of the jugal is strongly angled (less angled in *Edmontosaurus*); wide lateral exposure of the quadratojugal (relatively narrow in *E. regalis*); short symphyseal process of the dentary that is 30% dental battery length (relatively longer in *E. annectens*).

Description.—In this section, only taxonomically informative characters that distinguish *Ugrunaaluk kuukpikensis*

gen. et sp. nov. from *Edmontosaurus annectens* and *E. regalis* are described, along with a description of ontogenetic trajectories for these features. Characters that are ontogenetically variable were excluded. A more comprehensive and detailed description of all skeletal elements of *Ugrunaaluk kuukpikensis* gen. et sp. nov., along with an analysis of ontogenetic variation in the taxon, will be presented elsewhere.

Premaxilla: In size class 1 specimens of *Ugrunaaluk kuukpikensis* gen. et sp. nov., the circumnarial ridge of the premaxilla is narrowly triangular in the parasagittal plane and projects posterolaterally, extending nearly to the lateral margin of the premaxilla. As a result, the circumnarial ridge divides the anterior region of the circumnarial fossa into anterior and posterior premaxillary depressions. In *Edmontosaurus regalis* and *E. annectens*, the circumnarial ridge diverges laterally to form an anteroposteriorly expanded vestibular promontory, giving this structure an inverted fan-shape in dorsolateral view (Fig. 5). The vestibular promontory is not present in any specimens of *U. kuukpikensis* gen. et sp. nov., including a size class 2 specimen (UAMES 4184), which has a poorly preserved circumnarial ridge. In *E. annectens* and *E. regalis*, the vestibular promontory also defines the medial margin of an elongate and well defined lateral premaxillary cavity (accessory fossa of Prieto-Márquez 2011), which is absent in *U. kuukpikensis* gen. et sp. nov. Size class 2 *E. annectens* premaxillae (AMNH 5046, LACM 23504, ROM 53534) also possess the same fan-shaped vestibular promontory as in other adult *E. annectens* specimens, suggesting that this is not an ontogenetically variable feature. Additionally, the Alaskan material bears a shallow groove lateral to the posterodorsal premaxillary foramen. This groove is also seen in other *Edmontosaurus*; however, in *E. annectens*, this groove is more recessed anteriorly and is dorsoventrally much taller, resulting in a conspicuously C-shaped posterior outline of the circumnarial septum, even in size class 2 and adult specimens (e.g., CMN 8509, ROM 53526, LACM 23502, UCMP 128374, AMNH 5046).

Maxilla: Compared to the size class 2 maxilla of *Edmontosaurus annectens* (LACM 23504), the maxilla of *Ugrunaaluk kuukpikensis* gen. et sp. nov. (i.e., UAMES 4219, 4250, 4327) is dorsoventrally short relative to overall length (height to length ratio of 0.41 and 0.32, respectively; Fig. 6). During hadrosaurid ontogeny, the skull becomes relatively elongate anteroposteriorly (Dodson 1975c; Horner et al. 2004; Campione and Evans 2011), implying a similar pattern in maxillary development (Horner and Currie 1994; Prieto-Márquez 2011). Thus, the relatively elongate maxilla of juvenile *U. kuukpikensis* gen. et sp. nov. (size class 2) is not merely an ontogenetic artifact, rather it reflects a true morphological difference when compared to comparably-sized material of *E. annectens* (LACM 23504).

Postorbital: Several postorbitals of size class 1 are known from the LBB. Additionally, an isolated size class 3 postorbital (UAMES 33308) was also collected near the LBB from nearly the same stratigraphic layer. We regard

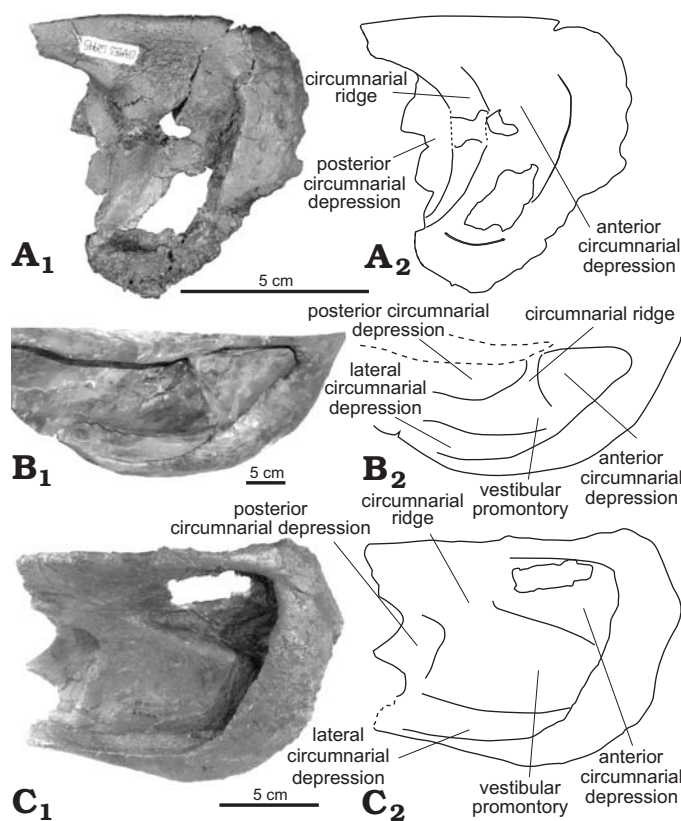


Fig. 5. Premaxilla comparison of a size class 1 *Ugrunaaluk kuukpikensis* gen. et sp. nov. from the early Maastrichtian Prince Creek Formation, Alaska (A, UAMES 12995, anterior portion of right premaxillae in dorsal view, lacking the vestibular promontory and lateral circumnarial cavity); adult *Edmontosaurus regalis* Lambe, 1917 from the late Campanian Edmonton Formation, Alberta, Canada (B, CMN 2289); and size class 3 *Edmontosaurus annectens* Marsh, 1892 from the late Maastrichtian Lance Formation, Wyoming, USA (C, ROM 53526). Photographs (A₁–C₁) and explanatory drawings (A₂–C₂).

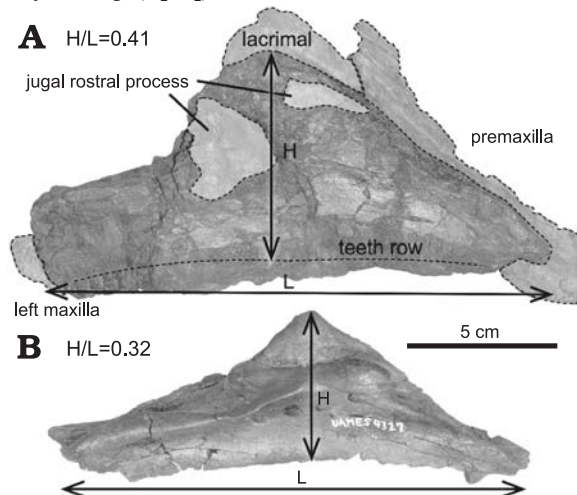


Fig. 6. Maxilla comparison of a size class 2 *Edmontosaurus annectens* Marsh, 1892 from the late Maastrichtian Hell Creek Formation, Montana, USA (A, LACM 23502, right maxilla in lateral view) and a size class 1 *Ugrunaaluk kuukpikensis* gen. et sp. nov. from the early Maastrichtian Prince Creek Formation, Alaska (B, UAMES 4327, right maxilla in lateral view). *U. kuukpikensis* has a relatively low maxilla compared to its length. The height (H) to length (L) ratio is 0.32 whereas that of size class 2 *E. annectens* is 0.41.

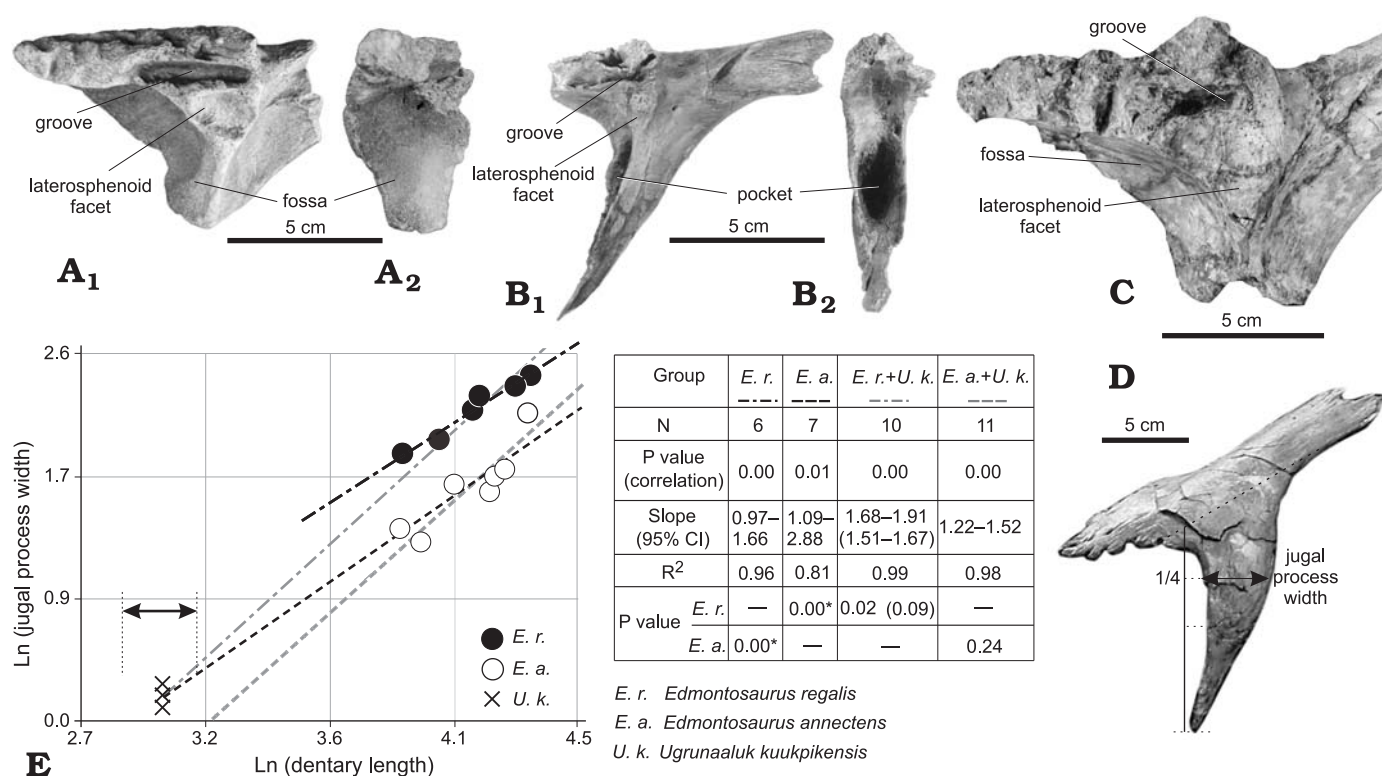


Fig. 7. Postorbital comparison of a size class 3 *Ugrunaaluk kuukpikensis* gen. et sp. nov. (A, UAMES 33308) from the early Maastrichtian Prince Creek Formation, Alaska, right postorbital in medial (A₁) and anterior (A₂) views; size class 2 *Edmontosaurus annectens* Marsh, 1982 (B, ROM 53513, reversed) from the late Maastrichtian Lance Formation, Wyoming, USA, left postorbital in medial (B₁) and anterior (B₂) views; and adult *Kundurosaurus nagorny* (C, AENM 2/921-6) from the Maastrichtian Udurchukan Formation, Kundur, Russia, left postorbital in medial view (from Godefroit et al. 2012: fig. 6). Note that size class 3 of *U. kuukpikensis* does not possess a deep posterior orbital pocket seen in the size class 2 specimens of *E. annectens*, although the articular surface with the frontal is nearly identical. D. Left postorbital of *E. annectens* (CMN 8509) from the late Maastrichtian Lance Formation, Saskatchewan, Canada, showing how the jugal process width is defined. E. Postorbital regression analyses. Biplots of the width of the jugal process measured at one-quarter distance from its dorsal end versus dentary length. *U. kuukpikensis* has a narrower jugal process than *Edmontosaurus regalis*. For *E. regalis* and *U. kuukpikensis* the numbers in the parentheses are those calculated when the minimum dentary length, not average, is adopted as the body size proxy. When the regression lines have statistically indistinguishable slope values but show statistically significant differences in elevation, P values are marked with an asterisk. The 95% confidence interval of *U. kuukpikensis* dentary length is also shown by the bi-directional arrow.

UAMES 33308 as conspecific with *Ugrunaaluk kuukpikensis* gen. et sp. nov. for the following reasons: (i) it is nearly identical in morphology, although larger, than the size class 1 materials from the LBB; (ii) it lacks the dorsal promontorium on the frontal process commonly seen in lambeosaurines (Prieto-Márquez 2008, 2010a) and therefore does not appear to represent an unrecognized hadrosaurid from the formation; and (iii) it is unlikely that two saurolophine taxa co-existed at or near the time the LBB was deposited.

In size class 1 individuals of *Ugrunaaluk*, the jugal process is both anteroposteriorly short and mediolaterally narrow. The regression analysis indicates that *Edmontosaurus regalis* has a wider jugal process than *E. annectens* and that the narrow jugal process of *U. kuukpikensis* gen. et sp. nov. can not be distinguished from an hypothetical juvenile of *E. annectens*. It is narrower than a hypothetical juvenile of *E. regalis*, although this result is not supported when the minimum dentary length is adopted as the proxy for body size (Fig. 7E). The jugal process shows positive allometric growth patterns in *E. annectens*. This is likely true in *U. kuukpikensis* gen. et sp. nov. as well, because the size class

3 specimen of *U. kuukpikensis* gen. et sp. nov. (UAMES 33308; not included in Fig. 7E regression analyses) has a relatively wider jugal process than those of size class 1.

In both postorbital size classes 1 and 3 of *Ugrunaaluk kuukpikensis* gen. et sp. nov., the posterodorsal wall of the orbital rim (the anterior surface of the jugal process) forms a shallow concave fossa, and most significantly, completely lacks a deep posterior postorbital pocket seen in *Edmontosaurus annectens*, including overlapping-sized individuals of size class 2 (Fig. 7A, B). The absence of the postorbital pocket in size classes 1 and 3 of *Ugrunaaluk* and its clear presence in size classes 2 and 3 of *E. annectens* (ROM 53513, ROM 53514) clearly distinguishes the two taxa.

The postorbital morphology also differs from *Kundurosaurus nagorny*, which is morphologically similar to *Edmontosaurus* (Godefroit et al. 2012). The size class 3 postorbital of *Ugrunaaluk kuukpikensis* gen. et sp. nov. (UAMES 33308) has a large concave anterior surface of the jugal process. The anterolateral rim of the jugal process in this specimen is more extensive than in size class 1 *U. kuukpikensis* gen. et sp. nov. (UAMES 4268, 4983, 12965, 18224)

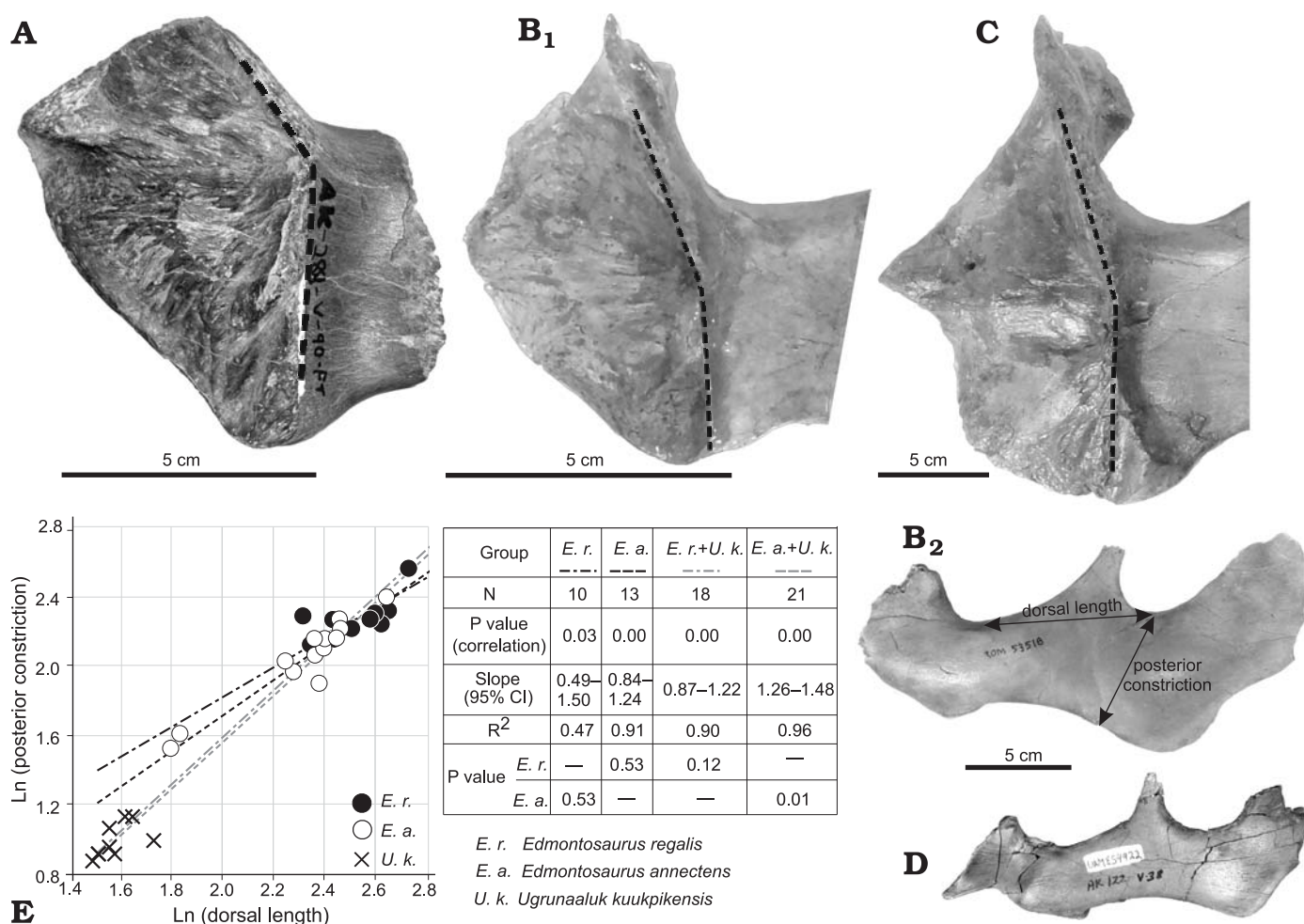


Fig. 8. Jugal comparison of *Ugrunaaluk kuukpikensis* gen. et sp. nov. (A, UAMES 14174, right, size class 3; D, UAMES 4922, left, size class 1) from the Prince Creek Formation, Maastrichtian, Alaska; *Edmontosaurus annectens* Marsh, 1892 (B, ROM 53518, left, size class 2) from the late Maastrichtian Lance Formation, Wyoming, USA, in medial (B₁) and lateral (B₂) views; and adult *Edmontosaurus regalis* Lambe, 1917 (C, CMN 2289, left, reversed) from the late Campanian Edmonton Formation, Alberta, Canada. A, B₁, C. Anterior processes in medial views, the dashed lines delineate the posterior border of the anterior process. In *U. kuukpikensis* this border is angled more strongly than in *Edmontosaurus*. D, B₂. Left jugal in lateral view. Note that *U. kuukpikensis* has a shallower posterior constriction compared to *E. annectens*. B₂ shows how the dorsal length and the posterior constriction are defined. E. Jugal regression analyses. Dorsal length versus posterior constriction of jugal. This suggests the shallower posterior constriction of *U. kuukpikensis* is not attributable to ontogeny.

and in *K. nagorny* (AENM 2/921-6; Godefroit et al. 2012: fig. 6). Unlike *K. nagorny*, the depression on the dorsal surface of the postorbital, dorsal to the jugal process, is not seen in *U. kuukpikensis* gen. et sp. nov. The articular surface of the frontal in *U. kuukpikensis* gen. et sp. nov. is identical to that of size class 2 and 3 of *E. annectens* (ROM 53513, ROM 53514). Dorsal to the laterosphenoid facet on the medial surface of the postorbital is an anteroposteriorly-elongated groove, which ends anteriorly on the dorsal surface of the orbit. The postorbital of *K. nagorny* has a corresponding groove, but is anteroposteriorly shorter, and isolated from the anterior surface of the jugal process (Fig. 7C).

Jugal: Near the level of the anterior spur, the posterior margin of the anterior process angles anteriorly more strongly in *Ugrunaaluk kuukpikensis* gen. et sp. nov. than in both species of *Edmontosaurus* (*E. regalis*, CMN 2289; *E. annectens*, ROM64076, ROM 53518; Fig. 8B). There does

appear to be ontogenetic and possibly some individual variation in this feature, as a similar strong degree of angling is also seen in juvenile specimens *E. annectens* (size class 2, MOR 601-J.1.1; Nicolás E. Campione, personal communication 2015). However, size class 3 specimens of *Ugrunaaluk* (UAMES 14174) differ markedly from similar sized material of *E. annectens* (ROM 53518; Fig. 8B), suggesting each species follows a different ontogenetic trajectory by this stage of development.

Additionally, the jugal of *Ugrunaaluk kuukpikensis* gen. et sp. nov. is more gracile than in *Edmontosaurus*, as measured by the ratio between the posterior constriction depth and the distance between the lower-most points of the infra-temporal fenestra and orbit (jugal dorsal length; Fig. 8B₂). The jugals of size class 1 *Ugrunaaluk kuukpikensis* gen. et sp. nov. (UAMES 4922; Fig. 8D, SOM 4) have a much smaller value for the posterior constriction/dorsal length

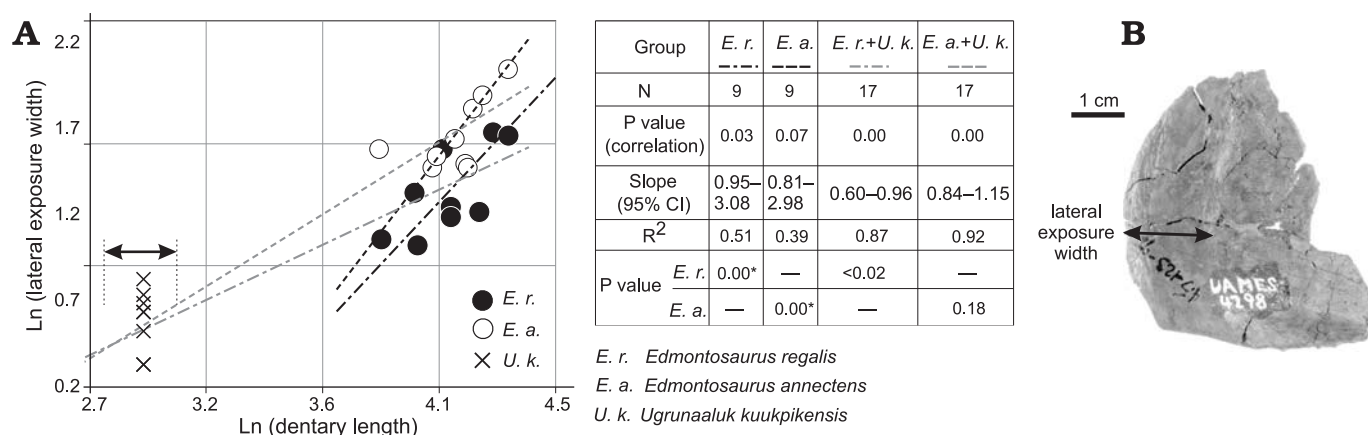


Fig. 9. **A.** Quadratojugal regression analyses. Biplot of the lateral exposure width of the quadratojugal versus dentary length and quadratojugal shown in lateral view of *Ugrunaaluk kuukpikensis* gen. et sp. nov. *Ugrunaaluk kuukpikensis* is similar to *Edmontosaurus annectens* in the lateral exposure width of the quadratojugal, but different from *Edmontosaurus regalis*. The 95% confidence interval of *U. kuukpikensis* dentary length is also shown by the bi-directional arrow. When the regressions show statistically indistinguishable slope values but statistically significant differences in elevation, P values are marked with an asterisk. **B.** Right quadratojugal of *U. kuukpikensis* (UAMES 4298) from the early Maastrichtian Prince Creek Formation, Alaska, showing how the lateral exposure width is defined.

ratio (0.56 ± 0.09 , 2σ) than do size class 2 materials of *E. annectens* (0.76 ± 0.11 , 2σ ; ROM 53518; Fig. 8B; SOM 4). The regression analysis also indicates that *U. kuukpikensis* gen. et sp. nov. does not resemble the juvenile condition of *E. annectens* and that *E. regalis* and *E. annectens* are indistinguishable. However, the regressions (Fig. 8E) also fail to reject the hypothesis that *U. kuukpikensis* gen. et sp. nov. represents a hypothetical juvenile of *E. regalis*. Thus, these data suggest the jugal of *Ugrunaaluk* is relatively gracile with respect to *E. annectens*, but is equivocal with regard to this element in *E. regalis*.

Quadratojugal: The posterior portion of the quadratojugal, where it is not covered by the jugal laterally and thus is slightly elevated, is narrower in *E. regalis* (e.g., CMN 2289, CMN 8744, and ROM 658) than in *E. annectens* (e.g., CMN 8509, ROM 57100, UMMP 20000; Fig. 9). The regression analysis shows that *U. kuukpikensis* gen. et sp. nov. has a wider area of lateral exposure as in *E. annectens*, but is not similar to a hypothetical juvenile of *E. regalis* (Fig. 9).

Dentary: The length of the posterior portion of the symphyseal process (the distance between the posterior-most point of articulation with the prementary and the anterior-most tooth socket) is a character traditionally employed in hadrosaurid cladistic analysis (Prieto-Márquez 2008, 2010a, 2013; Godefroit et al. 2012; Xing et al. 2014). The regression analysis (Fig. 10D) indicates that the length of the posterior part of the symphyseal process changed as *Edmontosaurus* grew, being longer in *E. annectens* than in *E. regalis* (Campione and Evans 2011). The dentary from size class 2 *Ugrunaaluk kuukpikensis* gen. et sp. nov. (UAMES 4946; Fig. 10A) shows a markedly shorter symphyseal process than *E. annectens* of comparable size (e.g., ROM 53530, BHI-6218; Fig. 10B). A similar pattern is reflected in the regression analysis, thereby excluding the possibility that *Ugrunaaluk kuukpikensis* gen. et sp. nov. is similar to juveniles of *E. annectens* in this respect (Fig. 10D), although the

former cannot be distinguished from hypothetical juveniles of *E. regalis* using this feature.

Stratigraphic and geographic range.—Type locality and horizon only.

Cladistic analysis

To test the systematic position of *Ugrunaaluk kuukpikensis* gen. et sp. nov., we conducted a cladistic analysis using the matrices of the two most recent phylogenetic studies of hadrosaurids (Xing et al. 2014; Prieto-Márquez 2013). First we scored the Alaskan taxon into a modified version of the Xing et al. (2014) character matrix, consisting of 60 taxa and 346 equally weighted and unordered characters. Two versions of the data matrix were prepared. In the first, *Ugrunaaluk kuukpikensis* gen. et sp. nov. was scored as-is without consideration of possible ontogenetic changes (17% missing data; SOM 6: Matrix 1). In the second, ontogenetically variable characters were scored as missing (30% missing data; SOM 7: Matrix 2) based on a more comprehensive analysis of the Alaskan material and *Edmontosaurus* (summarized in SOM 5; Mori 2014). We further tested the sister group relationships of *Ugrunaaluk* by scoring it into the matrix of Prieto-Márquez (2013), consisting of 35 taxa and 265 characters. As for the Xing et al. (2014) matrix, *U. kuukpikensis* gen. et sp. nov. was scored both as-is (12% missing data; SOM 8: Matrix 3) and with ontogenetically variable characters missing (17% missing data; SOM 9: Matrix 4). Character data was input using Mesquite 3.0.2 (Maddison and Maddison 2011). For both the Xing et al. (2014) and Prieto-Márquez (2013) matrices, we revised the character concerning the lateral premaxillary cavity (characters 81 and 53, respectively) so that it more accurately describes the morphology of the circumnarial ridge and vestibular promontory (see SOM 5).

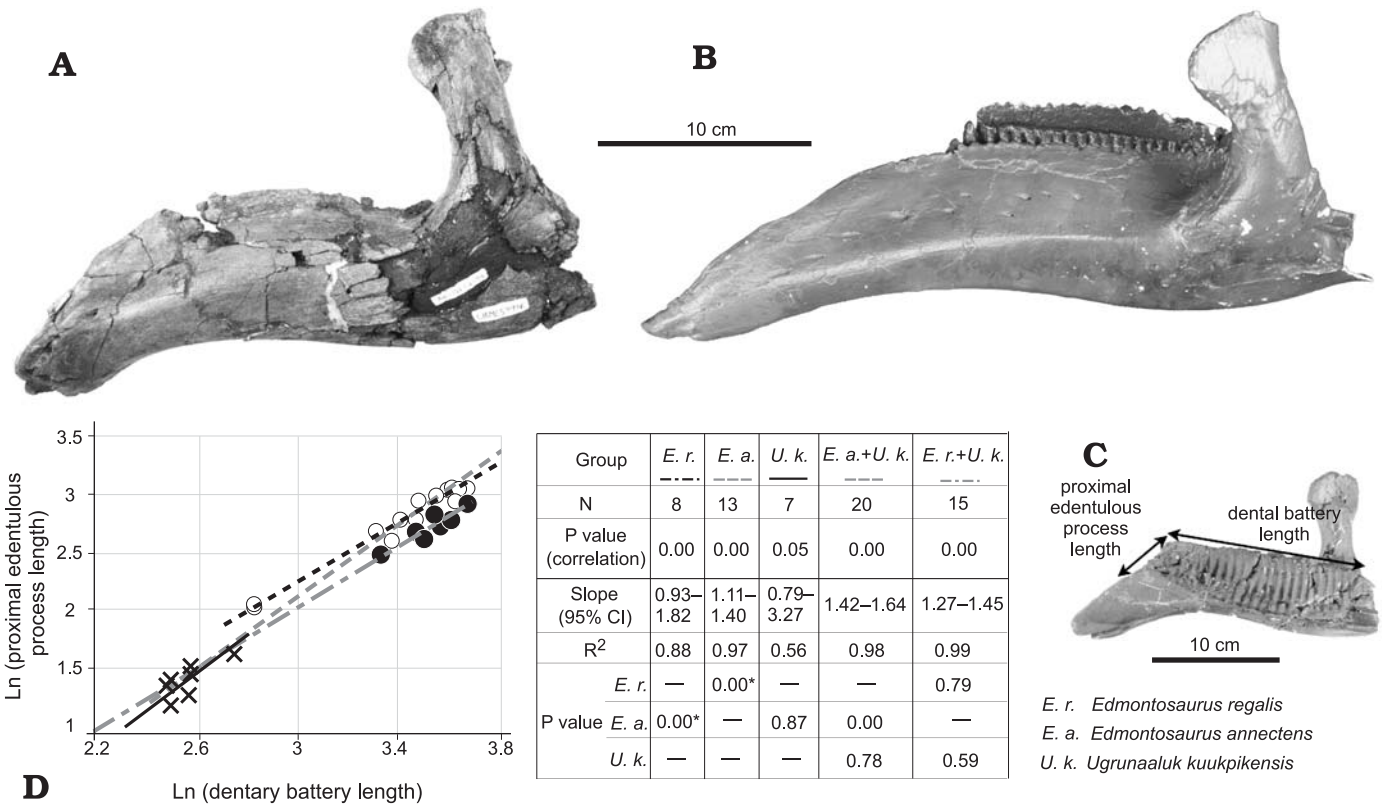


Fig. 10. Dentary comparison of size class 2 *Ugrunaaluk kuukpikensis* gen. et sp. nov. (A, UAMES 4946, left; C, UAMES 12941, right) from the late Maastrichtian Prince Creek Formation, Alaska, dentary in lateral view; and size class 2 *Edmontosaurus annectens* Marsh, 1892 (B, BHI-6218, cast, reversed) from the late Maastrichtian Hell Creek Formation, South Dakota, USA, right dentary in lateral view. Note that *U. kuukpikensis* has a shorter edentulous process than *E. annectens*. C. Right dentary of *U. kuukpikensis* showing how the proximal edentulous process length and dental battery length are defined. D. Dentary regression analyses. Biplot of posterior symphyseal process length versus dental battery length. *U. kuukpikensis* has a shorter symphyseal process than in *E. annectens*. When the regressions show statistically indistinguishable slope values but statistically significant differences in elevation, P values are marked with an asterisk. Because the lines for *E. regalis* and *U. kuukpikensis* are statistically indistinguishable, only one is shown.

The cladistic analysis was conducted using TNT 1.1 (Goloboff et al. 2008). Following Xing et al. (2014) and Prieto-Márquez (2013), *Ouranosaurus nigeriensis* and *Equijubus normani* were designated as outgroups, respectively. The most parsimonious trees were sought using the “New Technology search” option with “Sectional search” and “Tree fusing options”. The minimal length was searched for 100 times, with 100 random seeds and 5 initially added sequences. The maximum number of trees stored in memory is set to 10000. Bremer support values were calculated using a Bremer Support Script made by Goloboff (2008) with the default setting (1000 replicates). Bootstrap values were calculated using the resampling function of TNT, with the standard (sample with replacement) and traditional search options and 100 replicates, and the results were output as absolute frequencies.

The analyses based on Xing et al. (2014) resulted in 288 MPTs (1059 steps) from Matrix 1 in SOM 6 (*Ugrunaaluk kuukpikensis* gen. et sp. nov. scored as-is) and 160 MPTs (1036 steps) from Matrix 2 in SOM 7 (ontogenetic characters of *Ugrunaaluk kuukpikensis* gen. et sp. nov. scored as missing). The strict consensus trees of both analyses (cladograms 1 and 2) are summarized in Fig. 11. In both analyses, *Ugrunaaluk kuukpikensis* gen. et sp. nov. was recovered as

the sister group of *Edmontosaurus annectens* + *E. regalis*, although bootstrap and Bremer support values were relatively low in SOM 6: Matrix 1 compared to SOM 7: Matrix 2 (39/1 and 79/2, respectively). Overall tree topology of both analyses was also largely congruent; however, in cladogram 1 (*Ugrunaaluk kuukpikensis* gen. et sp. nov. scored as-is), *Shantungosaurus*, *Kerberosaurus*, and *Edmontosaurus* + *Ugrunaaluk kuukpikensis* gen. et sp. nov. collapsed to form a polytomy with the clade *Lophorhothon* (*Prosaurolophus* + *Saurolophus*), and the clade including *Secernosaurus*, *Kritosaurus*, and both species of *Gryposaurus* was also unresolved.

In cladogram 1, five synapomorphies unite *Ugrunaaluk kuukpikensis* gen. et sp. nov. + *Edmontosaurus*, including: 27.1, angle between the anteroventral margin of the anterior end and the dorsal margin of the lateral process of the prementary in lateral view is 56–74°; 51.1, presence of a sharp projection on the posterodorsal surface of the coronoid process; 77.1, presence of a premaxillary accessory foramen which shares a common chamber with the premaxillary foramen; 204.1, finger-shaped, anteroposteriorly long and mediolaterally narrow median anterior process of the parietal; 221.1, greatly reduced length of the postorbital process of the laterosphenoid; 234.1, the angle of the ventral

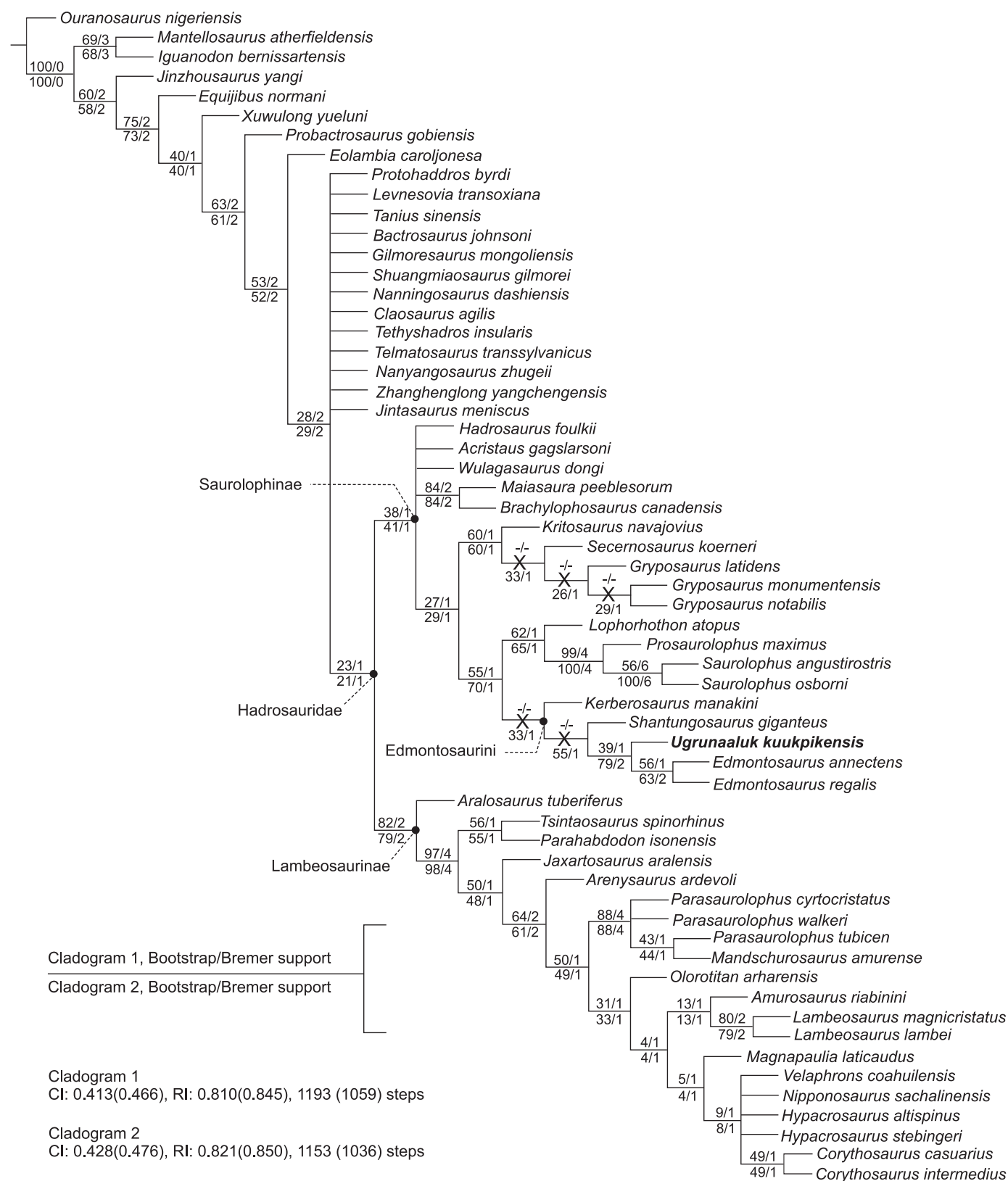


Fig. 11. Results of the cladistic analyses of Matrix 1 (SOM 6) and Matrix 2 (SOM 7) based from Xing et al. (2014), showing the phylogenetic position of *Ugrunaaluk kuukpikensis* gen. et sp. nov. Matrix 1 resulted in 288 most parsimonious trees (MPTs), and Matrix 2 resulted in 160 MPTs. The strict consensus tree based on Matrix 1 (characters scored as-is, cladogram 1) was identical to the strict consensus tree based on Matrix 2 (ontogenetic characters removed, cladogram 3), except that some clades, marked by "X" were collapsed in cladogram 1. Bootstrap, Bremer support values, Consistency and Retention indices of the strict consensus trees are also shown. For the clades collapsed in the cladogram 1, these values are substituted by a dash. Those indices and steps of the parsimonious trees are also shown in the parentheses below the tree.

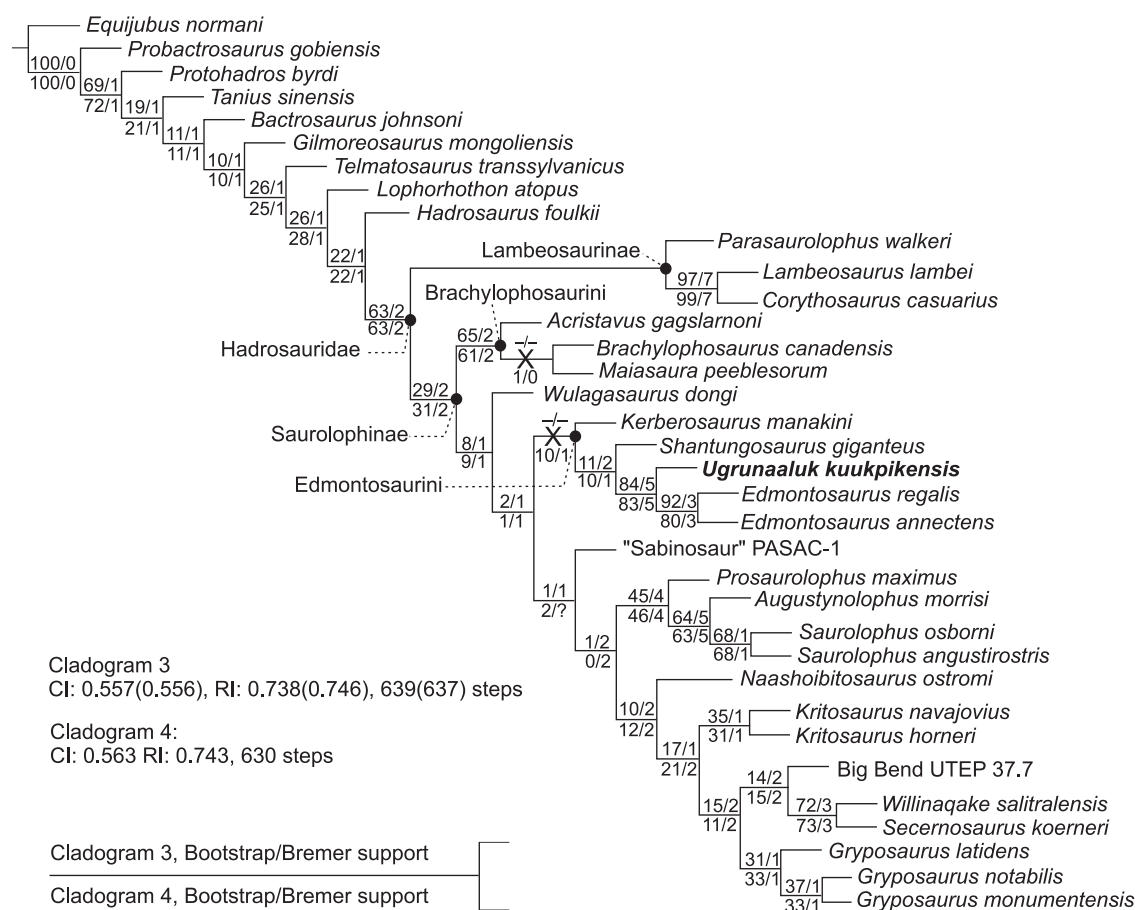


Fig. 12. Results of the cladistic analyses based of Matrix 3 (SOM 8) and Matrix 4 (SOM 9) based from Prieto-Márquez (2013), showing the phylogenetic position of *Ugrunaaluk kuukpikensis* gen. et sp. nov.; Matrix 3 resulted in 2 most parsimonious trees, and Matrix 4 resulted in one fully resolved cladogram. The strict consensus tree based on Matrix 3 (characters scored as-is, cladogram 3) was identical to the most parsimonious tree based on Matrix 4 (ontogenetic character removed, cladogram 4), except that some clades, marked by "X", were collapsed in cladogram 3. Bootstrap, Bremer support values, Consistency and Retention indices of the phylogenetic trees are also shown. For the clades collapsed in the cladogram 3, these values are substituted by a dash. Those indices and steps of the parsimonious trees based from Matrix 3 are also shown in the parentheses below the tree.

deflection of the occipital condyle relative to the horizontal line is less than 155° (Xing et al. 2014). In the better resolved cladogram 2, *Ugrunaaluk* + *Edmontosaurus* is supported by two synapomorphies, 51.1 and 221.1 (explained above). *Edmontosaurus regalis* + *E. annectens* are united by three synapomorphies: 12.1, the marginal denticles of dentary teeth are composed of a single rounded knob; 81.1, presence of additional premaxillary accessory fossae located lateral to the premaxillary accessory narial fossa and anterior to the circumnarial fossa, separated from the premaxillary anterior fossa by a well developed vestibular promontory (modified character); 182.1, presence of bulging jugal process with a deep pocket of the postorbital.

The analyses based on Prieto-Márquez (2013) resulted in 2 MPTs (637 steps) from Matrix 3 in SOM 8 (characters scored as-is) and 1 MPT (630 steps) from Matrix 4 in SOM 9 (ontogenetic characters of *Ugrunaaluk* scored as missing). The strict consensus trees of both analyses (cladogram 3 and 4) are summarized in Fig. 12. Again, *Ugrunaaluk kuukpikensis* gen. et sp. nov. was recovered as the sister group of *Edmontosaurus annectens* + *E. regalis* in both analyses,

although in cladogram 3 (characters scored as-is), the position of *Kerberosaurus* was not resolved. Clade support for *Ugrunaaluk* + *Edmontosaurus* in cladograms 3 and 4 was strong for both bootstrap and Bremer values (84/4 and 85/5, respectively). There was also less resolution in other clades of Saurolophinae (Fig. 12).

In cladograms 3 and 4, five synapomorphies unite *Ugrunaaluk* + *Edmontosaurus*, including: 34.1, presence of a sharp projection on the posterodorsal surface of the coronoid process; 179.1, relative widths of the skull across the postorbitals and squamosals is more than 25%; 196.1, expansion of the scapular blade; 219.1, moderately developed suprailiac crest of the ilium; 242.0, lack of the protuberance on the proximal region of the pubis ischial peduncle. These characters correspond 51.1, 232.1, 258.0, 298.1, and 316.0 respectively in the matrix by Xing et al. (2014). In cladogram 4, *Edmontosaurus regalis* + *E. annectens* are united by two synapomorphies (53.1, presence of premaxillary additional accessory fossa (modified), and 119.2, presence of the postorbital pocket, both of which were also identified as synapomorphies in cladograms 1 and 2.

Discussion

Cladistic analysis.—The results of all the cladistic analyses based on the data matrices of both Xing et al. (2014) and Prieto-Márquez (2013) recover *Ugrunaaluk kuukpikensis* gen. et sp. nov. as the sister taxon to *Edmontosaurus*. In none of the trees, including those in which characters considered ontogenetically variable are scored as missing, is *U. kuukpikensis* gen. et sp. nov. recovered as the sister taxon to either *E. annectens* or *E. regalis*. The major differences between the analyses of the Xing et al. (2014) and Prieto-Márquez (2013) matrices are found in non-hadrosaurid hadrosauroids, which is beyond the focus of this study.

The analyses of the Xing et al. (2014) and Prieto-Márquez (2013) matrices identify 3 and 2 synapomorphies, respectively, that unite *Edmontosaurus regalis* and *E. annectens*, to the exclusion of *Ugrunaaluk kuukpikensis* gen. et sp. nov. To what extent might ontogenetic status influence the validity of these synapomorphies, and in turn the taxonomic status of *Ugrunaaluk kuukpikensis* gen. et sp. nov.? The degree to which ontogeny may influence the number and/or morphology of marginal denticles (Xing et al. 2014: character 12.1) is poorly studied and difficult to assess. However, the analyses of both the Xing et al. (2014) and Prieto-Márquez (2013) matrices identify two other identical synapomorphies relating to morphology of the premaxilla (81.1 and 53.1, respectively) and the postorbital (182.1 and 119.2, respectively) that are not biased by the ontogenetic status of the Alaskan material. With respect to the premaxilla, the circumnarial ridge of *U. kuukpikensis* gen. et sp. nov. is narrow and projects posterolaterally. In marked contrast, the circumnarial ridge in *Edmontosaurus annectens* and *E. regalis* has a vestibular promontory, which is also present in juveniles (size classes 2 and 3) of *E. annectens*. Therefore, this character is not ontogenetically variable in *E. annectens*, and we reasonably assume it is not so in *E. regalis*. Likewise, a postorbital pocket is absent in all size classes of *Ugrunaaluk kuukpikensis* gen. et sp. nov., including a large size class 3 specimen that represents an animal approximately 60% the adult body length of *Edmontosaurus*. In contrast, a deep postorbital pocket is present even in size classes 2 and 3 of *E. annectens* (ROM 53513, ROM 53514). A postorbital pocket is also well devel-

oped in adult *E. regalis*, but status of this feature is unknown in juveniles; however, we assume that if the pocket was well developed in all juvenile size classes of *E. annectens*, then it is likely also present in juvenile *E. regalis*, although ultimately the discovery of juvenile material of this taxon will be required to test this assumption. Therefore, given the results of both cladistic analyses and available evidence, we consider that both the premaxillary and postorbital characters can be used to distinguish *Ugrunaaluk kuukpikensis* gen. et sp. nov. from *Edmontosaurus*.

Taxonomic status of *Ugrunaaluk kuukpikensis*.—Although most previous work on the LBB material referred *Ugrunaaluk kuukpikensis* gen. et sp. nov. to *Edmontosaurus*, the results of our comparative, quantitative and cladistic analyses indicate important morphological differences between the Alaskan taxon and both species of *Edmontosaurus* (Table 1). *Ugrunaaluk kuukpikensis* gen. et sp. nov. differs from *Edmontosaurus* in that the former has a posterolaterally projected circumnarial ridge of the premaxilla, an angled posterior margin of the anterior process of the jugal, and lacks a deep postorbital pocket. The deep pocket on the jugal process of the postorbital has been considered a diagnostic character of *Edmontosaurus* (Campioni et al. 2011). Recently, Xing et al. (2014) noted that *Kerberosaurus* and *Shantungosaurus* possess a shallow postorbital fossa, and that this is a common character seen in Edmontosaurini. The presence of the shallow fossa in *Ugrunaaluk kuukpikensis* gen. et sp. nov. supports its inclusion in Edmontosaurini, but suggests it is plesiomorphic with respect to the deep pocket that is diagnostic for *Edmontosaurus*. While *Ugrunaaluk kuukpikensis* gen. et sp. nov. is similar to *Kerberosaurus* and *Shantungosaurus* in possessing a shallow postorbital fossa, it also differs from both taxa in that the dorsal border of the jugal process is nearly straight, more like the condition seen in many specimens of *Edmontosaurus* (although not all). Additionally, the articular surface on the medial side of the postorbital in *Ugrunaaluk kuukpikensis* gen. et sp. nov. differs from that of *Kerberosaurus*, but is nearly identical to that in *E. annectens* (Fig. 7). In these regards, the postorbital morphology of *Ugrunaaluk kuukpikensis* gen. et sp. nov. appears to be “intermediate” between that of *Kerberosaurus*/*Shantungosaurus* and *Edmontosaurus*.

Table 1. Comparison of *Ugrunaaluk kuukpikensis* and *Edmontosaurus* spp.

Character	<i>Ugrunaaluk kuukpikensis</i>	<i>Edmontosaurus annectens</i>	<i>Edmontosaurus regalis</i>
Premaxilla	circumnarial ridge projects posterolaterally; no vestibular promontory and lateral premaxillary cavity	circumnarial ridge is fan-shaped, anteroposteriorly wide, with a vestibular promontory and lateral premaxillary cavity; deep groove lateral to the posterodorsal premaxillary foramen	circumnarial ridge is fan-shaped, anteroposteriorly wide, with a vestibular promontory and lateral premaxillary cavity
Maxilla (of juvenile)	dorsoventrally short	dorsoventrally tall	no juvenile specimen is known
Jugal process of the postorbital	narrow, with a shallow fossa	narrow, with a pocket	wide, with a pocket
Jugal	gracile, the posterior border of the rostral process angled	robust, the posterior border of the rostral process relatively straight	robust, the posterior border of the rostral process relatively straight.
Lateral exposure of the quadratojugal	wide	wide	narrow

At the species level, *Ugrunaaluk kuukpikensis* gen. et sp. nov. clearly differs from *Edmontosaurus annectens* in that the former possesses a dorsoventrally short and elongate maxilla (Fig. 6), a relatively gracile jugal (Fig. 8), and a short symphyseal process of the dentary (Fig. 10). Likewise, *U. kuukpikensis* gen. et sp. nov. can be differentiated from *E. regalis* in having a narrower jugal process of the postorbital (Fig. 7E) and wider lateral exposure of the quadratojugal (Fig. 9), although the results of our regression analyses (Fig. 7E) are not fully conclusive and overlapping-sized juvenile material with *Ugrunaaluk kuukpikensis* gen. et sp. nov. are not available. However, with respect to premaxillary morphology, the presence of a vestibular promontory is well developed in juvenile *E. annectens* and therefore may also have been present in juvenile *E. regalis*. Similarly, given that adult *E. regalis* has a much wider jugal process than *E. annectens* (Fig. 9), it seems likely that juvenile *E. regalis* had a wider jugal process as well.

Recently, Xing et al. (2014) interpreted the Alaskan material to represent the juvenile form of *E. regalis* because of its anteroposteriorly short premaxilla and oblique and enlarged postorbital articular surface of the jugal. However, premaxillary length displays positive allometry in *Edmontosaurus* (Campione and Evans 2011), thus the short premaxillary length seen in juvenile *Ugrunaaluk kuukpikensis* gen. et sp. nov. specimens likely represent a generalized juvenile state for all Edmontosaurini. Also, based on extensive examination of many specimens of *Ugrunaaluk kuukpikensis* gen. et sp. nov., we do not consider the postorbital articular surface of the jugal to be enlarged in a manner similar to *E. regalis*. In light of other significant differences between the two species listed above, we do not consider the Alaskan material to be a juvenile form of *E. regalis* (Xing et al. 2014).

The results of the cladistic analyses provide additional support that the Alaskan material represents a distinct new hadrosaurid taxon. *Ugrunaaluk kuukpikensis* gen. et sp. nov. was recovered as the sister taxon to *Edmontosaurus regalis* + *E. annectens* in two separate phylogenetic analyses using different matrices (Prieto-Márquez 2013; Xing et al. 2014), even when ontogenetically variable characters were scored as missing (cladograms 2 and 4). None of the analyses recovered *Ugrunaaluk kuukpikensis* gen. et sp. nov. nested within *Edmontosaurus*. Because species-specific characters tend not to appear until later stages of development (Baer 1828; Nelson 1978; Kitching et al. 1998), the phylogenetic position of juvenile specimens may be recovered in a more basal position than is actually true (Tsuihiji et al. 2011; Campione et al. 2012). However, *Ugrunaaluk kuukpikensis* gen. et sp. nov. was consistently recovered as the sister taxon to *Edmontosaurus* even in analyses where ontogenetically variable characters were removed, and in a relatively derived position compared to *Shantungosaurus*, which is based on adult material. Furthermore, Prieto-Márquez (2014) recently described and conducted a cladistic analysis of a size class 2 juvenile of *E. annectens* (LACM 23504), in which its ontogeneti-

cally variable characters were scored as missing. It is notable that LACM 23504 was recovered as the sister taxon to *E. annectens* but not as a sister taxon to *E. annectens* + *E. regalis*. This suggests that scoring ontogenetically variable characters as missing can be successfully employed when assessing relationships among juvenile saurolophines, including *U. kuukpikensis* gen. et sp. nov. Therefore, we interpret that our analysis correctly represents the phylogenetic position of the Alaskan taxon. Our results are also largely congruent with those of Xing et al. (2014) who recover *Kerberosaurus* and *Shantungosaurus* as successive sister taxa to *Ugrunaaluk kuukpikensis* gen. et sp. nov. + *Edmontosaurus* within Edmontosaurini.

In summary, our results indicate *Ugrunaaluk kuukpikensis* gen. et sp. nov. is more closely related to *Edmontosaurus* than any other saurolophine; however, even when ontogenetic effects are taken into consideration, *U. kuukpikensis* gen. et sp. nov. is not referable to either *E. regalis* or *E. annectens*. *Ugrunaaluk kuukpikensis* gen. et sp. nov. can be diagnosed on a unique combination of characters and becomes the first formally recognized hadrosaurid taxon from the Prince Creek Formation.

Paajaqtat fauna.—The recognition of a new saurolophine hadrosaurid, *Ugrunaaluk kuukpikensis* gen. et sp. nov. provides further evidence in support of a distinct, early Maastrichtian polar fauna, provisionally termed the Paajaqtat Province (Erickson and Druckenmiller 2011; Druckenmiller et al. 2013). The Paajaqtat fauna is characterized by polar dinosaurian species that are endemic to the Prince Creek Formation, including the pachycephalosaurid *Alaskacephale gangloffii* (Gangloff et al. 2005; Sullivan 2006), the centrosaurine ceratopsid *Pachyrhinosaurus perotorum* (Fiorillo and Tykoski 2012), and the tyrannosaurid *Nanuqsaurus hoglundi* (Fiorillo and Tykoski 2014). Additional evidence suggests a potentially unique orodromine and thescelosaurine thescelosaurid (Brown and Druckenmiller 2011; Druckenmiller et al. 2013) and a distinct large-toothed species of *Troodon* (Fiorillo 2008b; Druckenmiller et al. 2013) that cannot be referred to any known species from more southerly latitudes. More broadly, *U. kuukpikensis* gen. et sp. nov. also can add new support for the presence of latitudinally arrayed centers of dinosaurian endemism in Laramidia (Gates et al. 2010; Sampson et al. 2010, 2013).

Conclusions

In this study, we; (i) identify and name a new taxon of saurolophine hadrosaurid, *Ugrunaaluk kuukpikensis* gen. et sp. nov. from the Prince Creek Formation of Alaska; (ii) demonstrate that skeletally immature specimens can be reliably used in addressing taxonomic problems within Hadrosauridae based on a detailed understanding of the growth patterns of closely related taxa; and (iii) show that *Ugrunaaluk kuukpikensis*

gen. et sp. nov. does not represent a juvenile form of either recognized species of *Edmontosaurus*. Further morphological description of the new Alaskan taxon and greater clarification of its differences from *Edmontosaurus* will require discovery of adult material from the Prince Creek Formation and/or description of other juvenile specimens from *E. regalis* and *E. annectens*.

The establishment of a new species of hadrosaurid, *Ugrunaaluk kuukpikensis* gen. et sp. nov. further clarifies the faunal composition of the Prince Creek Formation and contributes to a growing body of evidence that the paleo-Arctic hosted a distinct and endemic polar, early Maastrichtian dinosaurian fauna. Ongoing field work in the formation and taxonomic clarifications of existing material will help to further establish the faunal composition of the unit and add critical new data to test hypotheses of dinosaur provinciality in Laramidia during the latest Cretaceous.

Acknowledgements

We kindly acknowledge the help of the Bureau of Land Management and particularly the Arctic Field Office for years of logistical support in the excavation of the Alaskan material. We thank Kevin May, Roland Gangloff, David Norton, Anne Pasch, and Andi Krumhardt (all UAMES); Bill Clemens, Mark Goodwin, and Howard Hutchison (all University of California Museum of Paleontology, Berkeley, USA), and the numerous volunteer field crews who helped collect and prepare material from the Liscomb bonebed. We acknowledge Ron Brower (University of Alaska Fairbanks, Fairbanks, USA) for his kind assistance in helping create the binomial of the new Alaskan species. This work was part of a doctoral dissertation by HM, who thanks his graduate committee members, Sarah Fowell, Kris Hundertmark, and Matthew Wooller (all University of Alaska Fairbanks, Fairbanks, USA) for their support. We thank Albert Prieto-Márquez (University of Bristol, Bristol, UK), David Evans (University of Toronto, Toronto, Canada), Nicolas E Campione (Uppsala University, Uppsala, Sweden), and Pascal Godefroit (Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium) for providing us with photos of *Edmontosaurus*, and Ron Blakey (Northern Arizona University, Flagstaff, USA), Kieran Shepherd, Margaret Beckel (both Canadian Museum of Nature, Gatineau, Canada), Kevin Seymour (University of Toronto, Toronto, Canada), Jack Horner (Montana State University, Bozeman, USA), Alana Gishlick, Carl Mehling (both American Museum of Natural History, New York, USA), Daniel Brinkman (Yale Paleontology Museum, New Haven, USA), Phil Currie (University of Alberta, Edmonton, Canada), and Hiroaki Yoshikawa (Toyohashi Museum of Natural History, Toyohashi, Japan) for their assistance. We thank Daniel Falster (Macquarie University, Sydney, Australia), Davit Warton (University of New South Wales, Sydney, Australia), Ian Wright (Macquarie University, Sydney, Australia), and Pablo A. Goloboff (National Scientific and Technical Research Council, Buenos Aires, Argentina), James S. Farris (American Museum of Natural History, New York, USA), Kevin Nixon (Cornell University, Ithaca, USA), and the Willi Henning Society for providing us with their latest software (SMATR, TNT). We also thank Nicolas E. Campione (Uppsala University, Uppsala, Sweden) and an anonymous reviewer for their helpful comments. We thank Albert Prieto-Márquez (University of Bristol, Bristol, UK) and Xing Hai (Canadian Museum of Nature, Canada) for providing us with their matrices for the cladistic analyses. This work was supported by US National Science Foundation awards

EAR 1226730 (co-PI's PSD and GME), DBI-1057426 (PI PSD) and EAR 0959029 (PI GME), O.W. Geist Fund scholarships (to HM) and a dissertation fellowship from the UAF Graduate School (to HM).

References

- Baer, K.E.V. 1828. *Über Entwicklungsgeschichte der Thiere. Beobachtung und Reflexion, Theil 1*. 734 pp. Gebrüder Bornträger, Königsberg.
- Besse, J. and Courtillot, V. 1991. Revised and synthetic apparent polar wander paths of the African, Eurasian, North American and Indian plates, and true polar wander since 200 Ma. *Journal of Geophysical Research* 96: 4029–4050.
- Blakey, R.C. 2009. *Paleogeography and Geologic Evolution of North America* <http://cpgeosystems.com/nam.html>
- Bolotsky, Y. L. and Godefroit, P. 2004. A new hadrosaurine dinosaur from the Late Cretaceous of Far Eastern Russia. *Journal of Vertebrate Paleontology* 24: 351–365.
- Brett-Surman, M.K. 1989. *A Revision of the Hadrosauridae (Reptilia: Ornithischia) and Their Evolution During the Campanian and Maastrichtian*. 297 pp. Unpublished Ph.D. Thesis, George Washington University, Washington DC.
- Brouwers, E.M. and Deckker, P.D. 1993. Late Maastrichtian and Danian ostracode faunas from Northern Alaska; reconstructions of environment and paleogeography. *Palaaios* 8: 140–154.
- Brouwers, E.M., Clemens, W.A., Spicer, R.A., Ager, T.A., Carter, L.D., and Sliter, W.V. 1987. Dinosaurs on the North Slope, Alaska: High latitude, latest Cretaceous environments. *Science* 237: 1608–1610.
- Brown, B. 1913. The skeleton of *Saurolophus*, a crested duck-billed dinosaur from the Edmonton Cretaceous. *Bulletin of the American Museum of Natural History* 32: 387–393.
- Brown, B. 1914. *Corythosaurus casuarius*, a new crested dinosaur from the Belly River Cretaceous; with provisional classification of the family Trachodontidae. *Bulletin of the American Museum of Natural History* 33: 559–565.
- Brown, C.M. and Druckenmiller, P.S. 2011. Basal ornithomimid (Dinosauria: Ornithischia) teeth from the Prince Creek Formation (early Maastrichtian) of Alaska. *Canadian Journal of Earth Sciences* 48: 1342–1354.
- Campione, N.E. and Evans, D.C. 2011. Cranial growth and variation in edmontosaurs (Dinosauria: Hadrosauridae): Implications for latest Cretaceous megaherbivore diversity in North America. *PLoS ONE* 6: e25186.
- Campione, N.E., Bink, K.S., Feedman, E.A., McGarrity, C.T., and Evans, D.C. 2012. “*Glishades ericksoni*”, an indeterminate juvenile hadrosaurid from the Two Medicine Formation of Montana: implications for hadrosaurid diversity in the latest Cretaceous (Campanian–Maastrichtian) of western North America. *Palaebiodiversity and Palaeoenvironments* 93: 65–75.
- Clemens, W.A. and Nelms, L.G. 1993. Paleoeological implications of Alaskan terrestrial vertebrate fauna in latest Cretaceous time at high paleolatitudes. *Geology* 21: 503–506.
- Cope, E.D. 1869. Synopsis of the extinct Batrachia and Reptilia of North America. *Transactions of the American Philosophical Society* 14: 1–252.
- Davies, K.L. 1987. Duck-bill dinosaurs (Hadrosauridae, Ornithischia) from the North Slope of Alaska. *Journal of Paleontology* 61: 198–200.
- Dodson, P. 1975a. Functional and ecological significance of relative growth in *Alligator*. *Journal of Zoology* 175: 315–355.
- Dodson, P. 1975b. Relative growth in two sympatric species of *Sceloporus*. *American Midland Naturalist* 94: 421–450.
- Dodson, P. 1975c. Taxonomic implications of relative growth in lambeosaurine hadrosaurs. *Systematic Zoology* 24: 37–54.
- Druckenmiller, P.S., Erickson, G.M., Brinkman, D., Brown, C., and Mori, H. 2013. Evidence for a distinct, early Maastrichtian polar dinosaur fauna from the Prince Creek Formation of northern Alaska. *Journal of Vertebrate Paleontology, Program and Abstracts* 2013: 117.
- Eberth, D.A., Evans, D.C., Brinkman, D.B., Therrien, F., Tanke, D.H., and

- Russell, L.S. 2013. Dinosaur biostratigraphy of the Edmonton Group (Upper Cretaceous), Alberta, Canada: evidence for climate influence. *Canadian Journal of Earth Sciences* 50: 701–726.
- Erickson, G.M. and Druckenmiller, P.S. 2011. Longevity and growth rate estimates for a polar dinosaur: a *Pachyrhinosaurus* (Dinosauria: Neoceratopsia) specimen from the North Slope of Alaska showing a complete developmental record. *Historical Biology* 23: 327–334.
- Falster, D.S., Warton, D.I., and Wright, I. J. 2006. *SMATR: Standardized Major Axis Tests and Routines. Version 2.0.* <http://www.bio.mq.edu.au/ecology/SMATR/>
- Fiorillo, A.R. 2008a. Dinosaurs of Alaska: Implications for the Cretaceous origin of Beringia. In: R.B. Blodgett and G. Stanley (eds.), *The Terane Puzzle: New Perspectives on Paleontology and Stratigraphy from the North American Cordillera. Geological Society of America Special Paper* 442: 313–326.
- Fiorillo, A.R. 2008b. On the occurrence of exceptionally large teeth of *Troodon* (Dinosauria: Saurischia) from the Late Cretaceous of northern Alaska. *Palaio* 23: 322–328.
- Fiorillo, A.R. and Gangloff, R.A. 2001. The caribou migration model for Arctic hadrosaurs (Dinosauria: Ornithischia): A reassessment. *Historical Biology* 15: 323–334.
- Fiorillo, A.R. and Tykoski, R.S. 2012. A new Maastrichtian species of the centrosaurine ceratopsid *Pachyrhinosaurus* from the North Slope of Alaska. *Acta Palaeontologica Polonica* 57: 561–573.
- Fiorillo, A.R. and Tykoski, R.S. 2014. A diminutive new tyrannosaur from the top of the world. *PLoS ONE* 9: e91287.
- Fiorillo, A.R., McCarthy, P.J., and Flaig, P.P. 2010. Taphonomic and sedimentologic interpretations of the dinosaur-bearing Upper Cretaceous Strata of the Prince Creek Formation, Northern Alaska: Insights from an ancient high-latitude terrestrial ecosystem. *Palaeogeography, Palaeoclimatology, Palaeoecology* 295: 376–388.
- Fiorillo, A.R., McCarthy, P.J., Brandlen, E., Flaig, P.P., Norton, D., Jacobs, L., Zippi, P., and Gangloff, R.A. 2007. Paleontology, sedimentology, paleopedology, and palynology of the Kikak-Tegoseak Quarry (Prince Creek Formation, Late Cretaceous), Northern Alaska. In: D. R. Braman (ed.), *Ceratopsian Symposium: Short Papers, Abstracts and Programs*, 48–49. Royal Tyrrell Museum of Palaeontology, Drumheller.
- Fiorillo, A.R., Tykoski, R.S., Currie, P.J., McCarthy, P.J., and Flaig, P. 2009. Description of two partial *Troodon* braincases from the Prince Creek Formation (Upper Cretaceous), North Slope Alaska. *Journal of Vertebrate Paleontology* 29: 178–187.
- Flaig, P.P. 2010. *Depositional Environments of the Late Cretaceous (Maastrichtian) Dinosaur-Bearing Prince Creek Formation: Colville River Region, North Slope, Alaska.* 311 pp. Unpublished Ph.D. thesis, University of Alaska Fairbanks, Fairbanks.
- Flaig, P.P., McCarthy, P.J., and Fiorillo, A.R. 2011. A tidally influenced, high-latitude coastal-plain: The upper Cretaceous (Maastrichtian) Prince Creek Formation, North Slope, Alaska. In: S.K. Davidson, S. Leleu, and C.P. North (eds.), *From River to Rock Record: The Preservation of Fluvial Sediments and Their Subsequent Interpretation*, 233–264. SEPM (Society for Sedimentary Geology), Tulsa.
- Flaig, P.P., McCarthy, P.J., and Fiorillo, A.R. 2013. Anatomy, evolution, and paleoenvironmental interpretation of an ancient arctic coastal plain: integrated paleopedology and palynology from the Upper Cretaceous (Maastrichtian) Prince Creek Formation, North Slope, Alaska, USA. In: S.G. Driese and L.C. Nordt (eds.), *New Frontiers in Paleopedology and Terrestrial Paleoclimatology: Paleosols and Soil Surface Analog Systems*, 179–230. SEPM (Society for Sedimentary Geology), Tulsa.
- Flores, R.M., Myers, M.D., Houseknecht, D.W., Stricker, G.D., Brizzolara, D.W., Ryherd, T.J., and Takahashi, K.I. 2007. Stratigraphy and facies of Cretaceous Schrader Bluff and Prince Creek Formations in Colville River Bluffs, North Slope, Alaska. *United States Geological Survey Professional Paper* 1747: 1–52.
- Frederiksen, N.O. 1991. Pollen zonation and correlation of Maastrichtian marine beds and associated strata, Ocean Point dinosaur locality, North Slope, Alaska. *United States Geological Survey Bulletin* 1990-E: 1–24.
- Frederiksen, N.O., Ager, T.A., and Edwards, L.E. 1988. Palynology of Maastrichtian and Paleocene rocks, lower Colville River region, North Slope of Alaska. *Canadian Journal of Earth Sciences* 25: 512–527.
- Frederiksen, N.O., McIntyre, D.J., and Sheehan, T.P. 2002. Palynological dating of some Upper Cretaceous to Eocene outcrop and well samples from the region extending from the easternmost part of NPRA in Alaska to the western part of Arctic National Wildlife Refuge, North Slope of Alaska. *U.S. Geological Survey Open-File Report* 02-405: 1–37.
- Gangloff, R.A. 1994. The record of Cretaceous dinosaurs in Alaska: an overview. In: D.K. Thurston and K. Fujita (eds.), *Proceedings of the 1992 International Conference on Arctic Margins*, 399–404. Alaska Geological Society, Anchorage.
- Gangloff, R.A. 1998. Arctic dinosaurs with emphasis on the Cretaceous record of Alaska and the Eurasian-North American connection. *New Mexico Museum of Natural History and Science Bulletin* 14: 211–220.
- Gangloff, R.A. and Fiorillo, A.R. 2010. Taphonomy and paleoecology of a bonebed from the Prince Creek Formation, North Slope, Alaska. *Palaio* 25: 299–317.
- Gangloff, R.A., Fiorillo, A.R., and Norton, D.W. 2005. The first pachycephalosaurine (Dinosauria) from the paleo-Arctic of Alaska and its paleogeographic implications. *Journal of Paleontology* 79: 997–1001.
- Gates, T.A. and Sampson, S.D. 2007. A new species of *Gryposaurus* (Dinosauria: Hadrosauridae) from the late Campanian Kaiparowits Formation, southern Utah, USA. *Zoological Journal of the Linnean Society* 151: 351–376.
- Gates, T.A., Horner, J.R., Hanna, R.R., and Nelson, C.R. 2011. New unadorned hadrosaurine hadrosaurid (Dinosauria, Ornithopoda) from the Campanian of North America. *Journal of Vertebrate Paleontology* 31: 798–811.
- Godefroit, P., Bolotsky, Y.L., and Lauters, P. 2012. A new saurolophine dinosaur from the Latest Cretaceous of far Eastern Russia. *PLoS ONE* 7: e36849.
- Goloboff, P.A. 2008. *Bremer Support Script. Version 1.0.* http://tnt.insect-museum.org/index.php/Main_Page
- Goloboff, P.A., Farris, J.S., and Nixon, K.C. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.
- Gryc, G., Patton, W.W., Jr, and Payne, T.G. 1951. Present Cretaceous stratigraphic nomenclature of northern Alaska. *Journal of the Washington Academy of Sciences* 41: 159–167.
- Harper, D.A.T. and Ryan, P.D. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4: 1–9.
- Horner, J.R. 1983. Cranial osteology and morphology of the type specimen of *Maiasaura peeblesorum* (Ornithischia: Hadrosauridae), with discussion of its phylogenetic position. *Journal of Vertebrate Paleontology* 3: 29–38.
- Horner, J.R. 1992. Cranial morphology of *Prosaurolophus* (Ornithischia: Hadrosauridae) with descriptions of two new hadrosaurid species and an evaluation of hadrosaurid phylogenetic relationships. *Museum of the Rockies Occasional Paper* 2: 1–119.
- Horner, J. R. and Currie, P. J., 1994. Embryonic and neonatal morphology and ontogeny of a new species of *Hypacrosaurus* (Ornithischia, Lambeosauridae) from Montana and Alberta. In: K. H. Carpenter, Karl F. and J. R. Horner (eds.), *Dinosaur Eggs and Babies*, 312–336. Cambridge University Press, Cambridge, UK.
- Horner, J.R., Weishampel, D.B., and Forster, C.A. 2004. Hadrosauridae. In: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria 2 ed*, 438–463. University of California Press, Berkeley.
- Hu, C.-C. 1972. A new hadrosaur from the Cretaceous of Chucheng, Shantung. *Acta Geologica Sinica* 2: 179–202.
- Kitching, I., Forey, P.L., Humphries, C.J., and Williams, D.M. 1998. *Cladistics: The Theory and Practice of Parsimony Analysis*. 2 ed., 228 pp. Oxford University Press, Oxford.
- Lambe, L.M. 1914. On *Gryposaurus notabilis*, a new genus and species of trachodont dinosaur from the Belly River Formation of Alberta, with a description of the skull of *Chasmosaurus belli*. *The Ottawa Naturalist* 27: 145–155.

- Lambe, L.M. 1917. A new genus and species of crestless hadrosaur from the Edmonton Formation of Alberta. *Ottawa Naturalist* 31: 65–73.
- Lawver, L.A., Grantz, A., and Gahagan, L.M. 2002. Plate kinematic evolution of the present Arctic region since the Ordovician. *Geological Society of America Special Paper* 360: 333–358.
- Lull, R.S. and Wright, N.E. 1942. Hadrosaurian dinosaurs of North America. *Geological Society of America Special Papers* 40: 1–242.
- Maddison, W.P., and Maddison, D.R. 2011. *Mesquite: a Modular System for Evolutionary Analysis. Version 2.75*. <http://mesquiteproject.org>
- Marsh, O.C. 1881. Principal characters of American Jurassic dinosaurs, IV. *American Journal of Science* 3: 167–170.
- Marsh, O.C. 1892. Notice of new reptiles from the Laramie Formation. *American Journal of Science* 3: 449–453.
- Maryańska, T. and Osmólska, H. 1981. Cranial anatomy of *Saurolophus angustirostris* with comments on the Asian Hadrosauridae (Dinosauria). *Palaeontologia Polonica* 42: 5–24.
- McKee, E., Conrad, J.E., and Tuin, B.D. 1989. Better dates for arctic dinosaurs. *Eos* 70: 74.
- Mori, H. 2014. *Osteology, Relationships And Paleoecology of a New Arctic Hadrosaurid (Dinosauria: Ornithopoda) From the Prince Creek Formation of Northern Alaska*. 333 pp. Unpublished Ph.D. Thesis, University of Alaska Fairbanks, Fairbanks.
- Mull, C.G., Houseknecht, D.W., and Bird, K.J. 2003. Revised Cretaceous and Tertiary stratigraphic nomenclature in the Colville Basin, northern Alaska. *U.S. Geological Survey Professional Paper* 1673: 1–51.
- Nelms, L.G. 1989. Late Cretaceous dinosaurs from the North Slope of Alaska. *Journal of Vertebrate Paleontology, Abstracts of Papers* 9: 34A.
- Nelson, G.J. 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. *Systematic Zoology* 27: 324–345.
- Parrish, J.T. and Spicer, R.A. 1988. Late Cretaceous terrestrial vegetation: A near-polar temperature curve. *Geology* 16: 22–25.
- Pearson, K. 1901. On lines and planes of closest fit to systems of points in space. *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science* 2: 559–572.
- Prieto-Márquez, A. 2008. *Phylogeny and Historical Biogeography of Hadrosaurid Dinosaurs*. 861 pp. Unpublished Ph.D. Thesis, Tallahassee.
- Prieto-Márquez, A. 2010a. Global phylogeny of Hadrosauridae (Dinosauria: Ornithopoda) using parsimony and Bayesian methods. *Zoological Journal of the Linnean Society* 159: 435–502.
- Prieto-Márquez, A. 2010b. The braincase and skull roof of *Gryposaurus notabilis* (Dinosauria, Hadrosauridae), with a taxonomic revision of the genus. *Journal of Vertebrate Paleontology* 30: 838–854.
- Prieto-Márquez, A. 2011. Cranial and appendicular ontogeny of *Bactrosaurus johnsoni*, a hadrosauroid dinosaur from the Late Cretaceous of northern China. *Palaeontology* 54: 773–792.
- Prieto-Márquez, A. 2012. The skull and appendicular skeleton of *Gryposaurus latidens*, a saurolophine hadrosaurid (Dinosauria: Ornithopoda) from the early Campanian (Cretaceous) of Montana, USA. *Canadian Journal of Earth Sciences* 49: 510–532.
- Prieto-Márquez, A. 2013. Skeletal morphology of *Kritosaurus navajovius* (Dinosauria: Hadrosauridae) from the Late Cretaceous of the North American south-west, with an evaluation of the phylogenetic systematics and biogeography of Kritosaurini. *Journal of Systematic Palaeontology* 12: 133–175.
- Prieto-Márquez, A. 2014. A juvenile *Edmontosaurus* from the late Maastrichtian (Cretaceous) of North America: Implications for ontogeny and phylogenetic inference in saurolophine dinosaurs. *Cretaceous Research* 50: 282–303.
- Prieto-Márquez, A., Wagner, J.R., Bell, P., and Chiappe, L.M. 2014. The late-surviving “duck-billed” dinosaur *Augustynolophus* from the upper Maastrichtian of western North America and crest evolution in Saurolophini. *Geological Magazine* 152: 225–241.
- Sampson, S.D., Loewen, M.A., Farke, A.A., Roberts, E.M., Forster, C.A., Smith, J.A., and Titus, A.L. 2010. New horned dinosaurs from Utah provide evidence for intracontinental dinosaur endemism. *PLoS ONE* 5: e12292.
- Sampson, S.D., Lund, E.K., Loewen, M.A., Farke, A.A., and Clayon, K.E. 2013. A remarkable short-snouted horned dinosaur from the Late Cretaceous (late Campanian) of southern Laramidia. *Proceedings of the Royal Society B* 280: 20131186.
- Schuyler, W.H. 2004. *Reading Statistics and Research. 4th Edition*. 544 pp. Pearson, Boston.
- Seeley, H.G. 1887. Researches on the structure, organization, and classification of the fossil reptilia. I. On *Protosaurus Speneri* (von Meyer). *Philosophical Transactions of the Royal Society of London B* 178: 187–213.
- Smith, R.J. 2009. Use and misuse of the reduced major axis for line-fitting. *American Journal of Physical Anthropology* 140: 476–486.
- Spicer, R.A. and Herman, A.B. 2010. The Late Cretaceous environment of the Arctic: A quantitative reassessment based on plant fossils. *Palaeogeography, Palaeoclimatology, Palaeoecology* 295: 423–442.
- Spicer, R.A. and Parrish, J.T. 1990. Late Cretaceous–early Tertiary palaeoclimates of northern high latitudes: a quantitative view. *Journal of the Geological Society, London Journal of the Geological Society* 147: 329–341.
- Spicer, R.A., Parrish, J.T., and Grant, P.R. 1992. Evolution of vegetation and coal-forming environments in the Late Cretaceous of the North Slope of Alaska. *Geological Society of America Special Papers* 267: 177–192.
- Sternberg, C.M. 1953. A new hadrosaur from the Oldman Formation of Alberta: discussion of nomenclature. *National Museum of Canada, Bulletin* 128: 275–286.
- Sullivan, R.M. 2006. A taxonomic review of the Pachycephalosauridae (Dinosauria: Ornithischia). *New Mexico Museum of Natural History and Science Bulletin* 35: 347–365.
- Tsuihiji, T., Watabe, M., Tsogtbaatar, K., Tsubamoto, T., Barsbold, R., Suzuki, S., Lee, A.H., Ridgely, R.C., Kawahara, Y., and Witmer, L.M. 2011. Cranial osteology of a juvenile specimen of *Tarbosaurus bataar* (Theropoda, Tyrannosauridae) from the Nemegt Formation (Upper Cretaceous) of Bugin Tsav, Mongolia. *Journal of Vertebrate Paleontology* 31: 497–517.
- Warton, D.I., Wright, I.J., Falster, D.S., and Westoby, M. 2006. Bivariate line-fitting methods for allometry. *Biological Reviews* 81: 259–291.
- Watanabe, A., Erickson, G.M. and Druckenmiller, P.S. 2013. An ornithomimosaurian from the Upper Cretaceous Prince Creek Formation of Alaska. *Journal of Vertebrate Paleontology* 33: 1169–1175.
- Witte, W.K., Stone, D.B., and Mull, C.G., 1987. Paleomagnetism, paleobotany, and paleogeography of the Cretaceous, North Slope, Alaska. In: I.L. Tailleux and P. Weimer (eds.), *Alaska North Slope Geology*, 571–579. Pacific Section, Society of Economic Paleontologists and Mineralogists, Bakersfield.
- Xing, H., Zhao, X., Wang, K. Li, D., Chen, S., Jordan, C.M., Zhang, Y., and Xu, X. 2014. Comparative osteology and phylogenetic relationship of *Edmontosaurus* and *Shantungosaurus* (Dinosauria: Hadrosauridae) from the Upper Cretaceous of North America and East Asia. *Acta Geologica Sinica (English Edition)* 88: 1623–1652.