A high latitude vertebrate fossil assemblage from the Late Cretaceous of west-central Alberta, Canada: evidence for dinosaur nesting and vertebrate latitudinal gradient

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ABSTRACT

This study reports on a new microvertebrate locality from the Campanian (c74 My) fluvial beds of the Wapiti Formation in the Grande Prairie area (west-central Alberta, Canada). This locality represents deposition on a low-gradient, waterlogged alluvial plain approximately 300 km to the north west of the Bearpaw Sea. Detailed sedimentological analyses suggest an environment characterized by a high-sinuosity channel system responsible for widespread oxbow lakes, bogs and marshes. A total of 260 identifiable elements were recovered from three distinct sites at the Kleskun Hill Park, documenting a diverse terrestrial and fresh-water palaeocommunity. The recovered fossils include those from hatching- to nestling-sized hadrosaurid dinosaurs, indicating the presence of a nesting ground in the area. This is the first evidence for dinosaur nesting site in the Wapiti Formation and simultaneously an extremely rare evidence of high-latitude dinosaur nesting, the northernmost in North America to date. A large number of teeth of the small theropod Troodon are associated with baby hadrosaurids in the site supporting a northern affinity of this taxon as well as a previously proposed predator–prey association. Other dinosaurs are less common at the locality and include large and small theropods (i.e. tyrannosaurid, Saurornitholestes, Richarodoestesia, Paronychodon, and dromaeosaurid) and five ornithischian taxa. Fish, squamate, turtle, and mammal elements were also identified. Collectively, the vertebrate fossil assemblage from the locality allows palaeocommunity reconstruction in the Wapiti Formation. The importance of the data collected from the new locality is twofold: first, they represent the first comprehensive report from a geographically significant area located between the well-sampled fossil localities of southern Alberta and the high-latitude localities of Alaska. Furthermore, the reconstructed vertebrate fauna support latitudinal gradient of vertebrate distribution along the Western Interior region during the Late Cretaceous.

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1. Introduction

Microvertebrate localities from both marine and non-marine deposits are a powerful tool for the study of palaeoecology and palaeobiogeography. They represent a rich source of information on local biota and are useful in addressing a variety of questions in palaeoecology (Sankey, 2008a). This study is a preliminary report on a new Campanian micro-fossil locality from the Wapiti Formation beds exposed at the Kleskun Hill Park (Grande Prairie area, west-central Alberta, Canada), and the first attempt to document the terrestrial taxa in the formation during the maximum transgression of the Bearpaw Seaway in the Late Cretaceous. High-resolution sedimentological data and an analysis of the heterogeneous fauna were combined to estimate the local biodiversity and the relative abundance of selected groups of vertebrates. In so doing, we focused primarily on faunal composition and comparison, and address implications on environmental factors that characterized the fauna also on the light of the proposed north–south biozonation of vertebrate taxa during the Campanian in western North America (Brinkman, 1990; Eberth, 1990; Eberth and Brinkman, 1997; Ryan et al., 1998; Fiorillo and Gangloff, 2000; Lehman, 2001; Sankey, 2001; Brinkman et al., 2004, 2007; Baszio, 2008; Sankey, 2008a; Wilson, 2008).

This paper consists of three parts: 1) a detailed description of stratigraphic, sedimentological, and palaeoecological signatures at the Kleskun Hill; 2) a statement of the diversity of the vertebrate assemblage recovered; and 3) a discussion on the implication of this locality on latitudinal gradient of vertebrate distribution in the Western Interior during the Late Cretaceous.

2. Geographical and geological setting

The Kleskun Hill Park area is located approximately 25 km northeast of Grande Prairie (west-central Alberta) on the left side of
the Smoky River (Fig. 1). Discontinuous badlands exposures, the most northern occurrence of this peculiar geomorphology in Alberta (Byrne, 1955), rise up to 100 m above surrounding plains over an area of 16 km². The Kleskun Hill badlands have been considered for years as the richest fossil locality in the Grande Prairie area: hundreds of disarticulated hadrosaur bones and other dinosaur remains collected in the 1940s were referred to an unknown locality within the area (Tanke, 2004). However, to date the locality has been neither mapped nor documented and a description of squamate jaws by Sternberg (1951) is the sole published work on the Kleskun Hill fossils.

The first geological report on the Kleskun Hill was made by Allan and Carr (1946) who tentatively correlated the exposures to the lower Edmonton Formation southeast to the area. However, data from geophysical well logs of exploration boreholes indicate that strata exposed at Kleskun Hill Park lie approximately 340 m above the base of the Wapiti Formation, within a lithostratigraphic unit characterized by medium to high accommodation conditions, decimetre-to-metre thick bentonitic layers, and well developed, tabular coal seams (Fanti, 2007). This unit is considered an inland equivalent of the Bearpaw shale of central and southern Alberta, rather than that of the lower Edmonton Group (i.e. Horseshoe Formation). Supporting this correlation is a 20 cm thick, olive volcanic ash layer located in the lowermost section of strata exposed in the park (Fig. 2) which yielded a \(^{40}\text{Ar}/^{39}\text{Ar}\) age of 73.77 ± 1.46 My (Eberth, in Fanti, 2007). This age is roughly equivalent to the maximum transgression of the Bearpaw Seaway in central and southern Alberta (\textit{Baculites compressus} zone, 73.4 My; Obradovich, 1993). Therefore, the Kleskun Hill palaeofauna is a rare terrestrial fossil assemblage from a stratigraphic interval represented by marine deposition elsewhere in western Canada and northwestern United States. Furthermore, the Wapiti fossil record is geographically important, as the locality is between the deposits of southern Alberta and the high-latitude fossil localities of Alaska (the present day distance is in the range of 400 km north and 3200 km south respectively; Parrish et al., 1987; Fiorillo et al., 2007). Palaeogeographic reconstruction for the late Campanian of North America place the southern Alberta localities (Belly River Group) at about 58°N palaeolatitude, the Grande Prairie localities at approximately 65°N palaeolatitude (Scotese, 1991; Brinkman, 2003), and the

![Fig. 1.](image-url)

**Fig. 1.** A, reference map of Alberta (Canada) showing the extension of the Campanian–Maastrichtian Wapiti Formation. B, location of the study area northeast of Grande Prairie. Sites A, B, and C are located within the Kleskun Hill Park area. Contour lines elevation data are expressed in metres. S–S′, cross section shown in Fig. 2.
Alaskan localities between 75° and 85°N latitude (Smith and Briden, 1977; Ziegler et al., 1983; Witte et al., 1987). Therefore, in this study the Kleskun Hill Park assemblage is referred to as high latitude.

3. Materials, methods, and institutional abbreviations

For this study, the Kleskun outcrops were prospected from 2004 to 2008. This led to the identification of three restricted areas where erosive processes and surface hydraulic transportation had concentrated vertebrate remains. These spots will be referred to in the text and figures as Sites A, B, and C. Detailed outcrop analyses resulted in a composite cross-section of the study area (S–S′, Fig. 2) that permitted to document reciprocal stratigraphic occurrence of fossiliferous sites. Colours used for sedimentological descriptions follow the Munsell Soil Colour Chart. Following discovery of fossils from the surface of the outcrop, a 4 m² area was excavated in 2004 at Site B by the field crew of Royal Tyrrell Museum of Palaeontology (Drumheller, Alberta, Canada). Sandy and silty sediments to the depth of 40 cm were collected for screen washing (sieves of 1 mm). With about 90% of the collected matrix screened and sorted, 29 specimens have been identified. In addition to this, surface collection at Sites A, B, and C yielded 231 identifiable specimens (for a total amount of 260 specimens), primarily theropod teeth and hadrosaurid postcranial and teeth fragments.

The collected specimens were primarily identified and compared with those from the well-described Campanian–Maastrichtian vertebrate fossil assemblages in southern Alberta (Brinkman, 1990; Currie et al., 1990; Brinkman and Neuman, 2002; Eberth et al., 2001; Sankey et al., 2002). Identification of hadrosaurid elements, particularly of juvenile and baby-sized individuals, is based on comparisons with *Hypacrosaurus stebingeri* (Horner and Currie, 1994), *Maiasaura peeblesorum* (Horner, 1999), and hadrosauridae indet. from the Horseshoe Canyon (Ryan et al., 1998) and Dinosaur Park formations (Tanke and Brett-Surman, 2001) of Alberta, and the Fruitland Formation (Hall, 1993) of New Mexico. Identification and terminology of the theropod teeth follow Currie et al. (1990), Baszio (1997), and Fanti and Therrien (2007).

3.1. Institutional abbreviation

UALVP, University of Alberta Laboratory of Vertebrate Palaeontology, Edmonton, Alberta, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.
3.2. Other abbreviations

BW, tooth basal width; FABL, fore–aft basal length; TCH, tooth crown height.

4. Sedimentology

Fluvial deposits exposed at the Kleskun Hill represent a medium- to high-sinuosity channel system within an alluvial plain and comprise predominantly interbedded mudstone, siltstone, and minor sandstone. Sedimentological analyses and facies associations indicate that, overall, the depositional environment was a low-energy, swampy alluvial area where a series of light coloured bentonitic sandstones, organic rich-mudstones, coal seams, thin bentonite, and ironstone beds accumulated under medium to high accommodation conditions (Fig. 2).

The presence of three discrete and laterally persistent coal beds permitted to reliably refer different outcrops and fossiliferous sites to a composite stratigraphic column; significant variations in geometries, lithology, and palaeocurrents within observed inclined heterolithic strata (IHS, sensu Thomas et al., 1987) allowed to identify two overlapping intervals in the exposed strata.

The lower interval (zone 1) is characterized by 1–4 metre thick fining-upward sequences of silt and mud with minor fine grained sandstone. Trenches through twelve outcrops show dips of bedding planes between 20° and 35° suggesting a significant component of lateral accretion. IHS consist of brownish silt and grey, organic rich mud forming a graded rhythms within individual inclined units (Fig. 3A). Vertical accretion on top of IHS is documented by oxbow and back swamp deposits that include brown and green mudstones interbedded with wet and immature paleosols, bentonitic horizons, and thin ironstone lenses (Fig. 3B). Gypsy, sideritic, and carbonaceous concretions and nodules are recurrently associated with light coloured sediments of this interval. Lastly, channel fill deposits of zone 1 are capped by reddish peat horizons, 40 cm thick on average, that gradually change into tabular coal seams up to a metre thick that deep gently westward with an angle of 10–11°. Such layers have been traced at the Kleskun Hill Park over an area of approximately 40 km² as well as in several well logs in the Grande Prairie region, thus supporting the presence of high-water table and swampy environments over a vast area. Vertebrate remains described herein were primarily recovered from fine, organic-rich deposits of zone 1.

The overlying interval (zone 2) consists of up-to 7 metre thick fining-upward sequences of low angle (5–10°) interbedded sand and silt. Sporadic pebbles and ironstone nodules occur at the base of inclined beds (Fig. 3C). Sandstones are light grey in colour, fine grained, and characterized by a pervasive carbonate cement. Mud component is nearly absent and restricted to discontinuous lenses. Fining-upward deposits are often cut by channel-base fine sands and locally topped by 10–15 cm thick, discontinuous ironstone layers. In spite the fact that silicified plant and wood remains are ubiquitous within this interval, zone 2 lacks organic-rich beds, paleosols, as well as peat and coal, suggesting higher drainage conditions and minor distance from the active channel belt. To date, few and poorly preserved vertebrate remains have been recovered from this interval.

The transition from zone 1 to zone 2 is interpreted as a shift from highly vegetated, swampy and bog-rich environments characterized by permanent high-water table conditions to the active channel belt within the alluvial plain. Differences in lithology and clinoform geometries observed in zones 1 and 2 may also reflect local variations in size, sinuosity, and pattern of the channel system and consequent extension of oxbows and back swamp areas. Palaeocurrent measurements (n = 25) taken either parallel or perpendicular to that of clinoforms from both zones 1 and 2 indicate predominant flows direction toward the northeast (average on 25 measurements N60°E). However, a certain degree of variability observed is consistent with a high-sinuosity fluvial system.

Fig. 3. Exposures of the Campanian fluvial deposits of the Wapiti Formation at the Kleskun Hill Park. A, interbedded light coloured silt and organic-rich mudstones (IHS) capped by a couplet of tabular reddish peat and coal. B, heavily rooted paleosol formed by interbedded dark grey, organic-rich mudstone and whitish, carbonaceous mudstone overlying a 45 cm thick coal bed. C, the transition from muddy, organic-rich deposits of zone 1 to overlying silty and sandy channel facies of zone 2 (see text for discussion). D, site A. E, site B. F, site C (see also Fig. 1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
Lastly, the top of the exposed interval at the Kleskun Hill is marked by a 35 cm thick, laminated, carbonate cemented sandstone that also denotes the present day prairie level morphology. The subaerial, strongly erosive nature of its basal contact and the coarser grain size of the sandstone suggest a crevasse splay origin.

5. Palaeopedology

The presence in the study area of distinctive paleosol related features provides useful information on soil acidity, precipitations, and water saturation. Pedotype are associated with specific environments (Fastovsky and McSweeney, 1987; Retallack et al., 1987; Retallack, 1994, 2001; Schaetzl and Anderson, 2005) and therefore may provide a reliable way to investigate local environmental and climatic conditions preserved within the Kleskun Hill deposits. Pedotype features observed in the study area include well developed peat deposits, tabular coal seams, ironstone layers, bentonitic heavily rooted soils, as well as sideritic, calcitic, and gyspic concretions, and discontinuous siliceous/tuffaceous horizons.

The presence of several decimetre-thick peat levels within zone 1 indicate a water-saturated environment with persistent high moisture content, such as bog or fen, characterized by acidic conditions. Peat results from decomposition of significant amount of organic matter (usually plant remains) that accumulated under swamp, marsh, or other kinds of vegetation that can tolerate permanent waterlogged ground (Histosol, Retallack, 2001). The presence of extensive vegetation and still water is also indicated by abundant plant remains within the peat layers (including coalified roots, seeds, leaves, and amber), overlaying well developed coal seams, and laminar calcitic concretions generated by flocculation processes. Tabular, decimetre-thick ironstone deposits, also support the presence of widespread bogs in the area and significant amounts of percolating water under tropical or sub-tropical climatic regimes. Acid soil conditions are also responsible for higher Fe concentrations and therefore for the formation of observed sideritic nodules and ironstone layers. The presence of siliceous nodules and tuffaceous concretions within the uppermost portion of channel fill deposits of zone 1, probably reflects intense lisciviation processes of volcanic ash soils over a period of weathering under humid climatic conditions (Podzols, Schaetzl and Anderson, 2005). In support of this hypothesis, similar processes observed today are typical of environments characterized by very humid to temperate moist climate, high water table, and associated with coniferous or mixed forests. However, such processes result in the development with possible wet–dry cycles, strongly connected with periods of prolonged subaerai exposure (Retallack, 2001; Schaetzl and Anderson, 2005). However, such crystals are most likely related to digenetic processes influenced by sulphur-rich percolating water and by intense bacterial activity within organic rich bogs (Phillips and Bustin, 1996), as also documented by high sulfur contents within the sediments (more than 600 ppm on average).

6. Vertebrate palaeontology

Dinosaur elements represent nearly 87% (n = 225) of the 260 fossils collected from the Kleskun Hill Park and consist predominantly of hadrosaur and theropod teeth (including Troodon, tyrannosaurids, Saurornitholestes, Richardoestesia, Paronychodon, dromaeosaurids, and a bird), and hadrosaur postcranial elements (Fig. 4). The remaining specimens include elements from fishes, squamates, turtles, ankylosaurids, ceratopсидs, pachycephalosaurids, and mammals, all characteristic components of Campanian terrestrial assemblages in western North America (Ryan et al., 1998; Brinkman, 2008; DeMar and Breithaupt, 2008, and references therein).

6.1. Fish

Three different taxa of fish have been collected from Site B, each represented by a single type of element: an esocoid dentary (TMP 2004.23.7), three holostean A scales (TMP 2004.23.6), and a holostean B scale (TMP 2004.23.8; Fig. 8). The esocoid dentary has C-shaped tooth bases as in those collected from the Campanian of southern Alberta, and is most similar to *Oldmanesox* sp. in that there are only one or two rows of teeth (Brinkman, 1990; Wilson et al., 1992). As in *Oldmanesox*, the tooth row is single in the posterior part of the dentary (Fig. 8A–D). The scales of holostean A are identified on the basis of a peg-and-socket joint, thin enamel cover, and absence of tab-like extension (Brinkman, 1990) (Fig. 8E–G). The holostean B scale (Fig. 8H) differs from those of a holostean A in that it has multiple tubercles on the enamelled surface (Brinkman, 1990). The fish elements are virtually indistinguishable from those described from the Campanian of southern Alberta (Brinkman, 1990; Wilson et al., 1992; Brinkman and Neuman, 2002) (Fig. 8A–M).

6.2. Non-dinosaurian reptiles

A possible turtle carapace fragment was collected from Site A (Fig. 8), but the weathering on the surface precludes possibility of identifying the element to further taxonomic level. Squamate remains are relatively abundant and well-preserved in Site A, consisting of articulated skulls and several isolated cranial and postcranial elements. Specimens were recovered exclusively from a discrete bentonitic paleosol that occurs in the organic-rich deposits of zone 1. Interestingly, squamate remains from the Cretaceous of North America are more commonly found in significantly dryer environments (Gao and Fox, 1991, 1996; Nydam, 2000; Nydam et al., 2007). These noteworthy squamate materials merit detailed systematic description elsewhere and are currently under study.

6.3. Theropoda

6.3.1. Troodontidae

The most abundant theropod teeth recovered from Site A are identified as *Troodon* for having relatively large, strongly-hooked denticles, and recurved crowns (Fig. 5A–F). A few specimens have wear facets (Schubert and Ungar, 2005) and spalled surfaces that extend from the apex of the teeth. The *Troodon* teeth from the Kleskun Hill Park are indistinguishable from other *Troodon* teeth described from deposits of Wyoming (Lance Formation), Montana (Judith River Formation), Alberta (Belly River Group, and Horseshoe Canyon Formation), and Alaska (Prince Creek Formation) (Russell, 1948; Brouwers et al., 1987; Currie, 1987; Currie et al., 1990; Fiorillo and Currie, 1994; Baszio, 1997a; Holtz et al., 1998; Ryan et al., 1998; Sankey et al., 2002; Fiorillo, 2008a; Sankey, 2008b). Based on variation in dental morphology along the dental series in *Troodon* (Currie, 1987), the Kleskun Hill specimens encompass the entire tooth series, including premaxillary, posterior maxillary, and posterior dentary teeth. *Troodon* has been reported from other stratigraphic levels and fossil localities of the Waspit Formation in the Grande Prairie region (Tanke, 2004; Currie et al., 2008) supporting a wide distribution of this taxon; however, the relative abundance of *Troodon* teeth is remarkably high at the Kleskun Hill microsites (11.9%).

6.3.2. Dromaeosauridae

Three teeth are identified as Saurornitholestes sp. (Fig. 5H–L) based on elongate and hooked shaped denticles, size differences between anterior and posterior serrations and strong labio-lingual compression (Currie et al., 1990; Baszio, 1997a; Sankey et al., 2002).
6.3.3. Dromaeosauridae indet

Although only the anterior carina has been preserved, UALVP 50640.01 is distinctive in that denticles vary greatly in size along the crown, from 2.5 to 5 per millimetre, curve slightly distally toward the tip of the tooth, and have sharp ridges of enamel along the midline (Fig. 5G). Blood grooves (sensu Fanti and Therrien, 2007, Fig. 3B) are
absent or restricted to the base of the denticles, being shallow and poorly defined. Both denticles and blood grooves are oriented perpendicularly to the longitudinal axis of the tooth. Therefore, specimen UALVP 50640.01 is assigned the taxonomic status Dro-maeosauridae indet.

6.3.4. Family unknown

One incomplete tooth (UALVP 48815) is identified as Paronychodon sp. (Fig. 5P). This specimen is the first unequivocal record of this taxon from the Wapiti Formation and is the most northern occurrence to date. The non-serrated tooth has three characteristic longitudinal ridges on both lingual and labial sides, and an elongated and slightly apically curved overall shape (FABL, 2.3 mm; BW, 1.1 mm; TCH, 3.9 mm). The flattened and ridged lingual surface becomes broader anteriorly toward the base of the tooth.

6.3.5. Tyrannosauridae

Fragments of tyrannosaurid teeth are commonly encountered in all the Kleskun Hill microvertebrate fossil sites as well as in other fossil sites in the Grande Prairie area. Denticles are wider labio-lingually than they are long proximodistally and occur 2–2.5 per millimetre in the posterior carina and 3–3.5 per millimetre in the anterior one (Fig. 5Q–S). Blood grooves are small and restricted to the base of denticles. The most complete tooth (UALVP 48773.2007.6) lacks the basal-most portion and would have exceeded 10 cm in height when complete (FABL, 34.5 mm; BW, 30 mm; TCH 95 mm). The number of denticles per millimetre on the anterior and posterior carinae is 2.5 and 2 respectively. In cross section, the tooth is compressed labio-lingually. It is similar in size and overall morphological characteristics to those of tyrannosaurids from the Campanian and Maastrichtian successions of southern Alberta (Fig. 5T).

6.3.6. Theropoda incertae sedis

A single small theropod tooth from the Site B (TMP 2004.93.3) is assigned to Richardoestesia gilmorei based on the minute denticles on the anterior carina and the small denticles on the posterior carina (Currie et al., 1990; Sankey et al., 2002). The tooth lacks the top of the crown, but the morphology is identical to those found in the Campanian deposits of southern Alberta in that it is labio-lingually compressed with a moderately recurved posterior carina, and it is relatively small compared to other theropod teeth (Fig. 5M–O).

6.4. Bird

A small, un serrated tooth from the Site B (TMP 2004.93.4) is identified as that of a bird (Fig. 5U–Z). The tooth is short and lacks denticles, but its posterior margin is blade-like and shows an incipient carina. The crown is more compressed labio-lingually than in other theropod teeth from the same locality. It has a few wrinkles on the lingual surface parallel to the anterior margin of the tooth. It also differs from the bird teeth from the Belly River Group (Campanian), southern Alberta described by Sankey et al. (2002) in that the tooth crown recruses slightly posteriorly (Hope, 2002). However, the crown tip is still anterior to the posterior margin of the tooth and the crown base expands anteroposteriorly as in other bird teeth (Sankey et al., 2002).

6.5. Hadrosauridae

More than half of hadrosaurid elements collected at the Kleskun Hill consist of adult-sized teeth and teeth fragments, tendons, and poorly preserved postcranial bones. Teeth are worn on the occlusal surfaces and have a medial carina on the lingual surface.

Other hadrosaur specimens include three dentary fragments, well preserved teeth, dorsal and caudal centra, a partially preserved pedal phalanx, and an angular and are all referable to nestling-sized hadrosaurs (Fig. 6). The dentary fragments (Fig. 6L–Q) have pitted surfaces on both sides, and the alveoli (4–5 mm in width) correspond with size of the teeth. The better preserved baby tooth (UALVP 48748) has a crown height and width of 7 and 4.5 mm respectively, which roughly compares to the largest tooth of an embryonic Hypacrosaurus stebingeri (4 mm in width; Horner and Currie, 1994). As in other juvenile hadrosaurid teeth, the tooth is compressed labio-lingually relatively to those of a typical hadrosaurid adult. It has the crown–root angle greater than 145° as in lambeosaurines (Horner et al., 2004). The tooth has a straight median carina as in hadrosaurines and some lambeosaurines, and an accessory ridge independent from the median carina on the enamelled side as in some lambeosaurine teeth (Horner et al., 2004). Teeth of embryonic or hatchling individuals of Hypacrosaurus stebingeri (Horner and Currie, 1994) and Hadrosauridae indet. (Ryan et al., 1998) lack the accessory lingual ridge observed in the Kleskun Hill specimens. Furthermore, the enamel edges have irregular and tiny denticles (papillae, after Horner, 1992) toward the apex of the tooth. Other teeth are roughly comparable to UALVP 48748 in size (Fig. 6A–C).

The baby-sized hadrosaurid vertebrae consist of a single dorsal centrum (UALVP 48816) and four caudal centra (UALVP 48751.01, 48751.02, 50636.03 and 50636.09) (Fig. 6). UALVP 48816 reaches 10 mm in transverse central width, UALVP 48751.01 is 7 mm wide, and UALVP 50636.09 is a distal caudal centrum with 4 mm in width, as wide as the teeth are. All the specimens have smooth sutureal surfaces on the dorsal side for the neural arch. The neural canal is relatively broad, being about two thirds of the centrum width. As in other hadrosaurids, immature or mature individuals, the dorsal centrum (UALVP 48816) is hexagonal when viewed anteriorly or posteriorly, and bears ventral keels. The caudal centra (UALVP 48751.01 and 48751.02) are vertically low and transversely wide relative to those of adult hadrosaurids. Ventrally, contact with a haemal arch is not clear. UALVP 48751.01 retains a notochordal pit which has previously been observed for baby hadrosaurid vertebrae from the Horseshoe Canyon Formation (Ryan et al., 1998). The pedal ungual (UALVP 48817; 9 mm in length) is relatively narrow and elongate compared to those in adult hadrosaurids, and is less constricted at the base (Fig. 6U–U).

The baby hadrosaurid materials from the Kleskun Hill compare well with those of Hypacrosaurus stebingeri from the Oldman and Two Medicine formations (Horner and Currie, 1994) and Hadrosauridae indet. from the Horseshoe Canyon Formation (Ryan et al., 1998). The baby-sized hadrosaurid materials are either not worn or with minor abrasion, whereas wear is evident in the adult hadrosaurid elements. The simple assumptions is to associate the specimens to a single hadrosaurid taxon. The accessory ridge parallel to the median carina and the relatively large crown–root angle (Horner et al., 2004) further suggest that these are from a lambeosaurine hadrosaur.

6.6. Ceratopsidae

Four ceratopsian teeth were recovered from microsites at the Kleskun Hill Park. Three of them (UALVP 50636.08, 50636.10, and 50636.11) are referred to adult individuals based on size, overall shape, and denticulate ridge (Fig. 7A). Specimen UALVP 50636.08
represents a tooth from a juvenile. It is significantly smaller than other ceratopsian teeth from the locality (FABL, 2 mm; TCH, 3 mm) and is convex in both dorsoventral and mesiodistal views. It contains a sharp, unserrated central ridge as well as less developed secondary ridges and denticles (Fig. 7B). Ceratopsian remains are often recovered within the fluvial deposits of the Wapiti Formation, usually preserved in large-scale bonebeds. Currently, all identifiable ceratopsian specimens from the formation are referred to two species of *Pachyrhinosaurus* (Tanke, 2004; Currie et al., 2007; Fanti and Currie, 2007; Currie et al., 2008). Therefore the teeth from the Kleskun Hill Park are tentatively referred to *Pachyrhinosaurus* sp.

6.7. Ankylosauridae

Two ankylosaurid teeth (UALVP 48747 and TMP 2004.23.9) were recovered from Sites A and B respectively. The teeth are weathered to the extent that the enamel surface is almost entirely gone (Fig. 7C).

6.8. Hypsilophodontidae

A pachycephalosaur tooth (TMP 2004.93.1) were collected from Site B. The base is thickened, and a robust median ridge supports the spade-shape crown with multiple denticles and ridges (Fig. 7D–G). Tentatively identified as a hypsilophodont, an ornithischian isolated tooth from the Site B (TMP 2004.93.5) is heavily worn and weathered. Even though identification of such an incomplete element is difficult, the labio-lingually flattened tooth with multiple ridges extending to the base of the crown is most likely a non-hadrosaurid ornithopod. Size of the tooth assumes an animal similar in size with *Parksosaurus* and immature *Thescelosaurus* (Fig. 7H–L).

6.9. Mammals

Two isolated mammal teeth were collected from Site B. One is a multituberculate P3 (TMP 2004.23.2; Fig. 8S–T). As in *Chulsanbataar* and others (Clemens and Kielen-Jaworowska, 1978), the premolar is plesiomorphic in having two roots. Its postero-lingual part is reduced by anterolingual expansion of the P4. The four cusps are largely conical and weakly ridged on their anterior and posterior slopes longitudinally. Of the three cusps on the labial side, the anteriormost is the smallest and more lingual than the posterior two. A transversely wide, anteroposteriorly narrow basin sits between the anteriormost labial cusp and the lingual cusp. The second labial cusp is highest, followed by the posteriormost labial cusp and then by the lingual cusp. Based on these characteristics, the premolar most closely resembles that of *Cimolodon*, but the specimen lacks the posterior lingual cusp. In addition, the only lingual cusp is displaced relatively more posteriorly, the anteriormost labial cusp is the smallest, and the posteriormost labial cusp is relatively larger and higher than in previously known species of *Cimolodon*. The tooth is tentatively assigned here to *Cimolodon* sp.

The second specimen is a double-rooted right lower molar of a marsupial, presumably RM4 (TMP 2004.23.1; Fig. 8U–Z). The molar is relatively shorter anteroposteriorly than in typical marsupial molars such as that of *Herpeotherium*, and characterized by the trigonid twice as tall as the talonid as in M4 of *Didelphodon coy* (Fox and Naylor, 1986). The roots are approximately 1.5 times deeper than height of the trigonid. The molar has stylar shelves around its anterior and posterior margins. The metaconid is more anterior than the protoconid, and reduced in size to the shortest cusp in the trigonid. Both the protoconid and paraconid are oriented slightly posteriorly than the
7. Discussion

The vertebrate diversity recovered from the Kleskun Hill sites indicates that the locality is a multidominant, high diversity microsite (following the classification and nomenclature proposed by Eberth et al., 2007). The site originated in a channel/overbank-wetland palaeoenvironment characterized by wet and humid climatic conditions. The twelve dinosaur taxa identified outnumber other vertebrates and represent 54.6% of the overall diversity. Hadrosaurid bones and teeth are 46.9% of all the recovered elements and together with theropod teeth (35.4%) constitute the bulk of the collection, with eight-branched plesiosaurs and the bulk of the collection, with eight

7.1. Possible explanation for abundance of Troodon

Hadrosaurids and small theropods (Troodon, Saurornitholestes, Paronychodon, and Dromaeosauridae indet.) represent 76.4% of all the specimens from Site A. Particularly, hatchling- to nestling-sized hadrosaurids occur at 10.9% (baby hadrosaurids account for 17.4% of all hadrosaurian elements), and Troodon occupies 16.7%. Ryan et al. (1998) suggested a non-random association between baby hadrosaurids and Troodon in a microvertebrate fossil locality in the Horseshoe Canyon Formation of southern Alberta (latest Campanian–early Maastrichtian), where other dinosaur taxa are uncommon. Barring the small sample size of Troodon and baby hadrosaurs, their relative abundance may be congruent with Ryan et al.’s finding and possibly expands this distribution of the baby hadrosaurid-Troodon association northwards. Ryan et al. (1998) explained the association with the hypothesis that Troodon hunted on either young or small sized dinosaurs, at least as a part of their diet. However, the high abundance of both baby hadrosaurids and Troodon in Site A alone does not constitute evidence of the predator–prey association in the locality. Whether or not feeding on hatching and young hadrosaurs, the abundance of small theropods at Site A is probably reflection of relatively large number of small-bodied predators in the area. The small and agile carnivores would have been more successful in a swampy, palustrine, and highly vegetated environment inaccessible to larger carnivores such as tyrannosaurids.

Beside feeding strategy of Troodon, the genus seems to show latitudinal gradient in its relative abundance within local theropod faunas. Troodon is increasingly more common northward, with 6% occurrence rate in the Judith River Formation of Montana (Currie and Fiorillo, 1994), 31.2% in the northern section of the Wapiti Formation (Fanti, 2007; this paper) and 65% in the Prince Creek Formation of Alaska (Fiorillo and Gangloff, 2000; Fiorillo, 2006). Sankey (2001) rejected the previous assignment of the theropod teeth to Troodon sp. from the Aguja Formation of Texas, and suggested that Troodon was a member of the northern dinosaur assemblages. The unusual abundance of Troodon in the Kleskun Hill locality may not accurately reflect its real abundance in the region because it may assume local environmental factors, such as food source, that favoured assembling Troodon. Another confounding problem is that compared localities are not necessarily contemporaneous to each other. Although these caveats suggest that the high Troodon occurrence in the north may be partly exaggerated, it is plausible that Troodon was more common in northern regions (Bazin, 1997a,b; Fiorillo and Gangloff, 2000).

8. Faunal comparison

In spite of the taxonomical diversity preserved at the Kleskun Hill, the limited sample size precludes a detailed and extensive statistic comparison between the local fauna and fossil association reported elsewhere in western Canada and the United States. However, the microvertebrate fossil assemblage at the Kleskun Hill locality represents 92% of the total vertebrate diversity recovered from the Wapiti Formation to date. For this reason, specimens described in this paper allow a preliminary reconstruction of the palaeocommunity in such an important temporal and geographical context (Fig. 10). Three fish taxa are recognized from the Kleskun Hill: an esocoid (Oldmanesox sp.) and holosteans A and B. They are virtually indistinguishable from their counterparts in the Belly River Group (Campa-

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occurrence in the high-latitude and polar Late Cretaceous terrestrial localities, including the Prince Creek Formation of Alaska (Buffetaut, 2004; Godefroit et al., 2008). Squamates are also interesting stratigraphically since their post-Bearpaw to early Maastrichtian record is scarce in North America (Gao and Fox, 1996). Sternberg (1951) also reported a teiid squamate jaw from the vicinity of the Kleskun Hill Park. In addition, Tanke (2004) mentions occurrences of salamander and choristoderan reptiles. However, such specimens were not relocated in the collections.

All the dinosaur taxa are known from the Campanian–Maastrichtian units of southern Alberta (the Belly River Group and Edmonton Group: Brinkman, 1990; Currie et al., 1990) and, except for Paronychodon, Richardoestesia, and the bird, also from the Prince Creek Formation of Alaska (Rich et al., 1997; Fiorillo and Gangloff, 2000; Gangloff et al., 2005). Notably, the occurrence of Paronychodon and Richardoestesia are the northernmost records of these enigmatic genera. Fiorillo (2008b) reported unusual teeth of Troodon from the Prince Creek Formation of Alaska which are twice the size of those known from southern Alberta and Montana; consequently Fiorillo suggests that Troodon increases in body size northward, possibly because of its dominance and competitive edge (e.g., increased orbit diameter) over other theropods in higher latitudes.

On the contrary, the teeth of Troodon from the Kleskun Hill Park are comparable in size to those from southern Alberta and Montana. Therefore, our results are consistent with Fiorillo’s hypothesis that Troodon increases in body size as a function of its dominance over multiple carnivorous niches, but not as a function of high latitude as predicted by Bergman’s rule. Because most taxa are only identified to the higher taxonomic levels (i.e. Tyrannosauridae, Veroceratopidae, Ankylosauridae, Hypsilophodontidae, Lambeosaurinae, Pachycephalosauridae, Paronychodontidae, Sauropitholestes, and Troodon), it would not be surprising if the dinosaur assemblages in Alaska, northern Alberta, and southern Alberta differed at species or generic level, as predicted by the hypothesis of dinosaur provincialism in western North America during the Campanian and Maastrichtian (Lehman, 1987, 1997, 2001; Sampson and Lowen, 2007). The current data from the Wapiti Formation support a wide distribution of all dinosaur families and subfamilies discussed in this paper along the Western Interior during the Campanian and Maastrichtian, although this does not necessarily refute the hypothesis of provincialism.

The mammals are tentatively identified as Cimolodon sp. and Didelphodon sp. respectively and are the northernmost occurrence for the genera. In particular, Didelphodon sp. from the Kleskun Hill is most similar to Didelphodon sp. from the Scabby Bute of southern Alberta (St. Mary River Formation, Edmonton Group: Fox and Naylor, 1986) based on the acute triangle formed by the trigonid cusps, suggesting a close phylogenetic relationship. Discovery of both a multituberculate and a marsupial is not surprising, because these mammals were already reported from Alberta (Lillegraven, 1969; Fox, 2005) and from the Prince Creek Formation (Santonian–Maastrichtian) of Alaska (Clemens and Nelms, 1993; Fiorillo and Gangloff, 2000). Pending taxonomic assignment of the Alaskan fossils, the Kleskun Hill specimens are potentially important for mammal palaeobiogeography during the Late Cretaceous of North America.

According to the most recently compiled dinosaur and other vertebrate faunal lists (Tanke, 1988; Currie, 1989; Ryan and Russell, 2001; Weishampel et al., 2004; Tanke, 2004) and in the light of recent dinosaur discoveries in the Grande Prairie area (Fanti and Currie, 2007; Currie et al., 2008; this paper) more than thirty-five species are currently known from the Wapiti Formation. Amongst these taxa, the ceratopsian dinosaur Pachyrhinosaurus lakustai (Currie et al., 2008) is the only diagnostic vertebrate taxon described from the formation. Currie et al. (2008) also confirmed that a second ceratopsian bonebed above the Campanian–Maastrichtian boundary in the Wapiti
Formation yielded a chelydrid turtle neural plate, a varanid squamate vertebra, and crocodile scutes.

9. Nesting of hadrosaurids

Hatchling- to nestling-sized hadrosaurid elements from the Kleskun Hill Park indicate that hadrosaurids nested in the area in the late Campanian (~74 My). A high-latitude record of dinosaur nesting is extremely rare. Recently, Godfrey et al. (2008) reported eggshell fragments and juvenile hadrosaur elements from a latest Cretaceous locality in northern Siberia. In North America, G. Nelms, in Carpenter (1999) mentions “Edmontosaurus” sp. bones from the Prince Creek Formation of Ocean Point, Alaska, in the global survey of baby dinosaur records. However, the supposed Alaskan baby Edmontosaurus has neither been described nor illustrated since Nelms’s personal communication to Carpenter (1999). In addition, the presence of Edmontosaurus is yet to be confirmed from Alaska (Bell and Snively, 2008). Therefore, the report on the Alaskan baby dinosaur material is considered not reliable in this study. The Kleskun Hill locality is currently the northernmost published record of a dinosaur nesting ground in North America, pending proper assessment of the Alaskan material. Fiorillo (2008a) emphasized the argument in Fiorillo and Gangloff (2001) that the juvenile hadrosaur materials from the Prince Creek Formation represent individuals younger than 1 year old. Therefore, it is likely that the hadrosaurs were year-round residents of the region, inferring that they also nested in the Arctic.

The hypothesized hadrosaurid nesting site at the Kleskun Hill is also important in a palaeoecological perspective. Previously, hadrosaurid nesting sites (referring to localities where eggshells or embryonic elements have been reported) seemed to preferentially occur in dry, upland regions (Horner, 1982; Horner and Currie, 1994). Carpenter (1982, 1992), and Fiorillo (1987, 1989) reported eggshells and baby or juvenile hadrosaur specimens from the low-land settings (the Lance and Hell Creek formations and the Judith River Formation, respectively). In Alberta, Nadon (1993) noted common occurrence of eggshells from the anastomosed fluvial deposits of the St. Mary River Formation, Ryan et al. (1998) described hatchling- to nestling-sized hadrosaurid elements from the Horseshoe Canyon Formation, and Tanke and Brett-Surman (2001) also reported hatchling- to nestling-sized hadrosaurid elements and eggshells from the low-land Dinosaur Park Formation of southern Alberta. Coupled with these previous findings, the Kleskun Hill hadrosaurid materials provide further evidences that hadrosaurids also nested in low-land settings. Nadon (1993) proposed that ornithopods preferentially selected wetland habitats as ideal reproductive site where a soft substrate and flooded conditions would have deterred large carnivores. The implications are that hadrosaurids seem to have had various strategies in nesting site selection, and that the fossil record of nesting sites is taphonomically biased against wet, lowland environment as weak acidity in groundwater would have generally enhanced dissolution of eggshells and poorly ossified elements unless buffered.

In addition to hadrosaurs, small ceratopsian elements imply that ceratopsians either nested in the region or had not migrated over long distance from the nesting site (Currie, 1989b). Interestingly, post-cranial elements ascribed to juvenile and subadult hadrosaurs have been collected from nearly coeval strata cropping out along the Wapiti River south of Grande Prairie (see also Tanke, 2004). Furthermore, Currie et al. (2008) report of an almost complete ontogenetic series of Pachyrhinosaurus lakustai (including juvenile, subadult, and adult individual) from the densely packed Pipistone Creek bone bed which has been dated 73.27 ± 0.25 My. Palaeogeographic reconstruction for the Bearpaw time (Dawson et al., 1994) place the Grande Prairie area in the order of 250–300 km from the shoreline, located approximately...
to the north and to the west of Edmonton. Sedimentological data and palaeoenvironmental reconstruction presented in this study support an extensive lowland environment (referring to the low and relatively level ground of the region, in contrast with adjacent higher country), genetically related to the maximum transgressive phase of the Bearpaw Sea.

10. Conclusion

The Kleskun Hill Park vertebrate fauna represents the first high-diversity multidominant assemblage from the Late Cretaceous of north western Canada. The fauna is also stratigraphically important being the only locality that provides a glimpse of a diverse terrestrial vertebrate fauna in western North America during the Bearpaw Sea transgressive event about 74 My. At the Kleskun Hill Park, Site A best represents the vertebrate diversity of the formation because of the larger sample size. The site is characterized by relative abundance of *Troodon* teeth and hatching- to nesting-sized hadrosaur elements. The latter suggests the presence of a hadrosaurid nesting ground in the nearby lowland area within the alluvial plain. In contrast Sites B and C, both with a smaller sample size, preserve a reworked assemblage dominated by pre-burial fluvial transportation. The Kleskun Hill vertebrate fauna preserves many taxa that are common in Campanian terrestrial vertebrate faunas in southern Alberta. The locality marks the northernmost distribution of *Paronychodon* and *Richardoestesia*. Additionally, three fish taxa (Holosteans A and B, and an escoid *Oldmanesox* sp.), squamates, and bird have not been reported from Alaska to date (Fiorillo and Parrish, 2004; Fiorillo et al., 2007). Multituberculates and marsupials have been reported from the Prince Creek Formation of Alaska (Clemens and Nelms, 1993), but it is not clear if the Kleskun Hill Park taxa (*Cimolodon* sp. and *Didelphodon* sp.) are identical to their counterparts in the Campanian of southern Alberta and Alaska. An impeding task is more sampling at the Kleskun Hill and assessment of new material from the Alaskan localities which may further result in testing the hypothesis of dinosaur provinciality (Lehman, 2001). Although the sample size remains small, the preliminary account of the vertebrate diversity demonstrates that the Grande Prairie region promise to be a key area in both stratigraphic and palaeobiogeographic contexts during the Late Cretaceous of North America.

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