“There is nothing like looking, if you want to find something. You certainly usually find something, if you look, but it is not always quite the something you were after.”

~J.R.R. Tolkien

University of Alberta

The occurrences of vertebrate fossils in the Deadhorse Coulee Member of the Milk River Formation and their implications for provincialism and evolution in the Santonian (Late Cretaceous) of North America

by

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Abstract

The Deadhorse Coulee Member of the Milk River Formation of southern Alberta preserves one of the oldest well-documented non-marine vertebrate assemblages in Canada. In this study, the taxonomic diversity of this member is updated, and vertebrate localities are placed in geographic and stratigraphic context. The stratigraphic provenance of specimens indicates all vertebrate material from this member is latest Santonian (83.5 Ma). A new species of turtle is described. Analyses of the rank and relative abundances of taxa support interpretations of this member as a prograding clastic wedge with localities approximately 40 km from the palaeoshoreline at time of deposition. Results support high local abundances of vertebrates in western North America, with faunal provincialism regulated by distance to the palaeoshoreline and mean annual temperatures. Morphologic changes in small theropod taxa through the latest Cretaceous of western North America act as a case study for evaluating species turnover of vertebrate microfossil material.

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List of Abbreviations

Institutional Abbreviations

AMNH, American Museum of Natural History, New York, New York

CMN, Canadian Museum of Nature, Ottawa, Ontario

LSUMG, Luisiana State University, Baton Rouge, Louisiana

ROM, Royal Ontario Museum, Toronto, Ontario

TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta

UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta

UCMP, University of California Museum of Paleontology, Berkeley, California

UMNH, Utah Museum of Natural History, Salt Lake City, Utah

Anatomical Abbreviations

bo, basioccipital

bs, basispenoid

ex, exoccipital

for. n. hypo., foramen nervi hypoglossi

for. stap., fo-ramen stapediotemporale

fr, frontal

op, opisthotic

pa, parietal

pf, prefrontal

pr, prootic

pt, pterygoid

qu, quadrate

so, supraoccipital

sq, squamosal

Other Abbreviations

3WC, “Three White Cow Site”

ADD, anterior denticle density

BW, basal width

CBS, “Clive’s Birthday Site”

CH, crown height

CI, consistency index

DCM, Deadhorse Coulee Member

DFA, Discriminant Function Analysis

DS, “Derek’s Crappy Dino Site”

FABL, fore-aft basal length

JS, “Jeff’s Site”

MANOVA, Multivariate Analysis of Variance

MR, Milk River Formation

MS, “Michael’s Site”

PDD, posterior denticle density

RA, relative abundance

RC, rescaled consistency index

RI, retention index

Chapter 1 — Introduction

Introduction

The 83.5 million-year-old uppermost Santonian Deadhorse Coulee Member (DCM) of the Milk River Formation (Payenberg et al. 2002) is the oldest of the aerially exposed non-marine clastic wedges in the Western Canadian Sedimentary Basin. The uppermost of the three members in the formation (Meijer Drees and Myhr 1981), the DCM is the only non-marine unit in the formation and the only one in which vertebrate fossil material occurs. The DCM of the Milk River Formation crops out only east of the town of Milk River in southern Alberta, although time-equivalent outcrops are known farther west from the Chungo Member of the Wapiabi Formation (Braman 2001). Although it immediately predates Campanian strata and contains many of the first and last occurrences of well-known vertebrate lineages, the DCM represents a time span that has received little scientific study relative to Campanian and Maastrichtian research in the Western Interior.

Vertebrate fossil preservation in this member is mostly restricted to isolated skeletal elements and accumulations of unassociated small bones and teeth in vertebrate microfossil bone bed (Eberth et al. 2007) assemblages. Vertebrate fossils were first described from the DCM by Russell (1935) and descriptions of new material continue to the present (Chapter 4). Previous studies have identified new species in cases where diagnostic material was available (Fox 1968, 1969, 1970, 1971a, 1971b, 1972a, 1972b, 1976, 1980, 1984a, 1984b, 1987; Gao and Fox 1996; Fox and Naylor 1982; Wu and Brinkman 1993). However, incomplete remains of many vertebrates (including fish, amphibians, turtles, lizards, snakes, crocodylomorphs, and dinosaurs) from this member can only be identified to the familial or generic level (Russell 1935; Fox 1975; Gao and Fox 1996; Baszio 1997b; Brinkman 2003; Larson 2008), or by morphotype (Eberth and Brinkman 1997; Larson 2008).

Baszio (1997a) first noted a peculiar pattern of dinosaur faunal distribution in that the Milk River fauna most closely resembled that of the Scollard Formation (latest Maastrichtian) rather than the intervening Campanian age Dinosaur Park and Horseshoe Canyon formations. Work on the mammal assemblage (Fox 1968, 1969, 1970, 1971a, 1971b, 1972a, 1972b, 1976, 1980, 1984a, 1984b, 1987) has revealed a generally primitive collection of species, which defines the Aquilan North American Land-mammal "Age" (Lillegraven and McKenna 1986). However, there has not been, to date, any detailed investigation into assemblage variation within the DCM and whether or not the assemblages from different localities are homogenous in their abundances. Perhaps related to this problem, vertebrate fossil localities have never been studied in a stratigraphic context. Moreover, the palaeoenvironments of the DCM have not been thoroughly discussed as they relate to fossil vertebrate occurrences. Descriptive works on the geology of the formation (Meyer 1998; Payenberg 2002) have likewise not discussed the provenance of vertebrate fossil material.

More recent work in other formations (Brinkman 1990; Brinkman et al. 1998, 2004; Currie and Russell 2005) has shown that when fossil material represented by sufficiently large sample sizes from constrained geographic regions is examined in stratigraphic sequence, patterns can be observed. The resulting patterns of abundance change can be used to develop hypotheses about palaeoecology, and patterns of evolution in fossil taxa. These patterns will be investigated in this study to help understand the palaeoecological, palaeoclimatological, and evolutionary significance of vertebrates in the DCM.

Objectives of Study

This study documents the vertebrate fossils of the DCM of the Milk River Formation to: **1)** place known fossil vertebrate occurrences in stratigraphic and lithologic context, **2)** assess vertebrate diversity within the assemblage and identify specimens to lowest defensible taxonomic levels, **3)** address possible causes for any noted changes in the relative and rank abundances of taxa throughout the DCM, **4)** evaluate the palaeoenvironmental and latitudinal provincialism of North American taxa of Santonian age, and **5)** compare the biodiversity, patterns of provinciality, and evolution of taxa to the younger and well-studied formations of Campanian age to further our understanding of the Santonian–Campanian faunal transitions in western North America. These objectives are met in the following chapters as follows.

1) The geology of the DCM of the Milk River and the distribution of vertebrate fossil sites within this unit are described in ***Chapter 2***. The measured sections and elevation data used in this chapter were collected over two field seasons. Past vertebrate fossil localities were relocated (historical locality data for this region is inexact by modern standards) and marked using handheld GPS (Global Positioning Satellite) units initially, followed by more accurate elevation measurements using differential GPS (MacDonald et al. 2005). ***Chapter 2*** presents the known distribution of vertebrate sites across the outcrop exposure and notes lithological associations of vertebrate localities, providing the depositional environment for these fossil assemblages. Significant fossil abundances are concentrated at distinct stratigraphic levels above the base of the DCM and are presumed to be roughly time-equivalent.

2) ***Chapters 3*** and ***4*** report the diversity of vertebrate taxa from the assemblage and describe aspects of the assemblage that have not yet been recorded. Establishing the taxa present in the assemblage is necessary to perform abundance analyses of taxa. Material from the DCM has been collected over the past 60 years and is curated at the Canadian Museum of Nature (CMN), the Royal Ontario Museum (ROM), the Royal Tyrrell Museum of Palaeontology (TMP), and the University of Alberta Laboratory of Paleontology (UALVP). All of these collections and pertinent descriptive literature were examined to establish accurate identification of specimens in terms of modern usage of valid names. ***Chapter 3*** examines the overall faunal assemblage, whereas ***Chapter 4*** looks specifically at an aspect of the testudine component of the DCM assemblage.

3) For the analyses of assemblages in ***Chapters 5*** and ***6***, vertebrate microfossil material (Eberth et al. 2007) from six major and several minor localities within the DCM was collected, identified, and counted. The fossil material from the major localities is either collected and sorted for the purpose of this study [Milk River (MR)-6, MR-12, "Derek's Crappy Dino Site" (DS), "Clive's Birthday Site" (CBS)] or counted from previously sorted material in which no taxa of interest had been removed from the sample ["Michael's Site" (MS), "Three White Cow" (3WC)].

4) In ***Chapters 5*** and ***6***, specimens are analyzed with conventional rank abundance methods (Brinkman et al. 2004), as well as the assessment of true assemblage abundance of common taxa using two different methods (Jamniczky et al. 2003; Moore et al. 2007). The two methods provide similar results, so the samples are analyzed as a proxy of true relative abundances of the assemblage. In addition, in ***Chapter 6***, vertebrate microfossil material from the John Henry Member of the Straight Cliffs Formation (Eaton 2006) is counted for two assemblages: one from a possible estuarine depositional environment (UMNH VP Loc. 99), and one from a more inland environment (UMNH VP Loc. 424). Analyses based on both the DCM alone (***Chapter 5***) and with the DCM and John Henry Member (***Chapter 6***) are done to test for provinciality of dominant taxa during the Santonian of western North America in regard to coastal, inland, northern, and southern palaeocommunities. Trends in abundances of taxa are compared to similar studies of Campanian assemblages (Lehman 1997; Brinkman et al. 2004; Demar and

Breithaupt 2008) as a test of distributions of taxa relative to mean global temperature (Wolfe and Upchurch 1987).

5) Changes between the assemblages of Santonian and successive ages are also compared to discern any time-dependent, or evolutionary, patterns. ***Chapter** 7*, a case study on small theropod teeth using pairwise discriminant function analysis, supports the distinction of several distinct species in the Western Interior Basin through the last 18 million years of the Mesozoic. Although lineages (as previously discerned by identification of vertebrate microfossils) have been hypothesized to persist through this time interval (Baszio 1997a), this turnover is expected due to the large amount of time represented (Ryan and Evans 2005). The DCM, in this analysis, serves as a starting point for comparison of later assemblages, and how these assemblages change through time.

Significance

This study reports on the diversity and palaeoenvironmental data of one of the earliest non-marine units in the Western Canadian Basin, contributing to the growing body of knowledge of biodiversity of the Late Cretaceous. Using a combination of multivariate statistical techniques, an accurate picture of the preserved assemblage can be presented. The results of this study can be used to develop and test hypotheses about the provinciality and palaeocommunities in the Late Cretaceous of Alberta, and has implications for the timing of faunal exchange with southern North America and Asia. This study also provides insight into evolutionary patterns that have previously remained undetected (Baszio 1997a).

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Chapter 2 — Vertebrate fossil distribution in the Deadhorse Coulee Member of the Milk River Formation in southern Alberta

Introduction

The Milk River Formation is a marine to non-marine siliciclastic wedge in the Western Canadian Sedimentary Basin, partially equivalent to the Telegraph Creek and Eagle formations of Montana (Payenberg et al. 2002). Named by Dowling (1916), the unit was formally subdivided by Meijer Drees and Myhr (1981), and it is this nomenclatural system that is followed here. The Milk River Formation overlies the Colorado/Alberta Group marine shales and is overlain by the marine Pakowki Formation (Payenberg et al. 2002). Although laterally extensive in the subsurface, in Alberta the formation crops out only in southernmost Alberta, east of the town of Milk River. It is at least partially equivalent to the Eagle and Telegraph Creek formations in Montana (Payenberg et al. 2002). The non-marine Deadhorse Coulee Member (DCM) of the Milk River Formation and its fossil assemblages were first described by Russell (1935, 1936), although at that time, the term "upper" Milk River Formation was applied. The deposit consists of muddy siltstone floodplain deposits with laterally discontinuous centimetre- to decimetre-scale coals, interbedded with fluvial sandstone beds. Although no single outcrop exposes the member completely, well-logs and outcrop studies estimate that it is 52 to 75 m thick in the outcrop area and thins southward (Payenberg et al., 2002; Leahy and Lerbekmo 1995).

The fauna described by Russell (1935) was collected from localities in Black Coulee (then Deadhorse Coulee), near the eastern edge of the exposed unit and an estimated 40 km southwest of palaeoshoreline as estimated from shoreface deposits in core (Payenberg 2002). Russell (1935) described mollusc, amphibian, turtle, and dinosaur material, including specimens from a macrofossil bonebed. These specimens are currently accessioned at the Canadian Museum of Nature (CMN). Subsequent undescribed vertebrate fossil collections made by Russell are curated at the Royal Ontario Museum (ROM; Russell, 1964). Fox (1968, 1969, 1970, 1971a, 1971b, 1972a, 1972b, 1975, 1976, 1980, 1982, 1984a, 1984b, 1985, 1987), Gao and Fox (1996), Fox and Naylor (1982), and Gardner (2002) worked with vertebrate microfossil bonebed material from Verdigris Coulee, near the western edge of the outcrop and an estimated 44 km southwest of the palaeoshoreline. He and others documented fish, amphibians, lizards, snakes, champsosaurs, dinosaurs, and mammals, all of which are now housed in the collections of the University of Alberta Laboratory for Vertebrate Paleontology (UALVP). Additional vertebrate microfossil and turtle material was collected by the Royal Tyrrell Museum of Palaeontology (TMP) starting in 1991, leading to the description of a mesosuchian (Wu and Brinkman 1993) and the turtle fauna (Brinkman 2003). Baszio (1997a, 1997b) studied the UALVP vertebrate microfossil collections in his comparison of Late Cretaceous North American (mostly Canadian) theropod teeth. None of these studies mentioned the lithology, distributions, depositional environments, or stratigraphy of vertebrate fossils within the DCM.

Although the ages of the strata above and below the Milk River Formation are known, the age of the DCM remains poorly constrained. The base of the Telegraph Creek Formation of Montana (the stratigraphic equivalent to the Telegraph Creek Member of the Milk River Formation) corresponds to the base of the *Desmoscaphites bassleri* ammonite zone, the latest Santonian biostratigraphic marker in the Western Interior Basin (Landman and Cobban 2007), of which the oldest known age is 84.4 Ma ± 0.8 Ma (Obradovich, 1988). The uppermost extent of this taxon is thought to coincide with the Santonion-Campanian boundary (Landman and Cobban 2007). No radiometric dates have been reported from the Milk River Formation itself. However, Leahy and Lerbekmo (1995) identified the 33r-34n magnetochron boundary, the end of the Long Cretaceous Normal, at 38.0 m above Virgelle Member within the DCM. The age of this magnetochron boundary has been assessed at 83.5 ± 0.7 Ma (Ogg and Smith 2004). Although this age has also been regarded as the age for the base of the Campanian, Braman (2001) did not detect any palynological transition to a Campanian flora above this magnetochron boundary in the DCM. None of the previous geological and index fossil studies have documented the relative ages and stratigraphy of the fossil vertebrates of the DCM. The purpose of this study is to evaluate the geologic, stratigraphic, and geographic context of the known vertebrate fossil localities of the DCM in order to understand the patterns of distribution.

Materials and Methods

A total of 17 fossil localities known to produce more than one element were closely examined during this study. The locations and elevations of nine of the localities were determined by use of differential global positioning system (GPS) technology. The remainder were positioned geographically using a single handheld commercial GPS and assessed stratigraphically with reference to the base of the DCM. The Virgelle Member – Deadhorse Coulee Member contact (Fig. 2-1) was chosen as a stratigraphic datum for purposes of determining stratigraphic position of fossil localities and correlating measured sections. This contact is used, not only because it is readily accessible in many of the outcrops of interest, but also defines a planar, minor transgressive surface of erosion (Payenberg et al. 2003), and therefore allows excellent stratigraphic and potential temporal control. The uplifted Sweetgrass Arch structural high (Podruski 1988; Payenberg et. al. 2003) has caused the beds of the Milk River Formation to dip to the NNE. Therefore, four locations along the datum were assessed using differential GPS technology (close to the mouth of Verdigris Coulee, at Writing-On-Stone Provincial Park, at Cave Coulee near section Audet 1, and at the Deer Creek Bridge Section; Fig 2-2), and the resulting data were used to calculate the strike and dip of this surface. The strike and dip was then used to estimate the elevation of the datum at different localities, and to help estimate the stratigraphic positions of fossil localities where the base of the member is not exposed. Fourteen geologic sections (Fig. 2-2) were measured that together document lithologies, stratigraphic patterns, and fossil occurrences in the lower 49.3 m of the member over an east-west distance of 25.7 km (Fig. 2-3).

Results

The locally calculated strike of the DCM is 115.25° with a dip of 0.51°, which is roughly parallel to the palaeoshoreline at the time of deposition (Fig. 2-4) as documented by the distribution of shoreface deposits in the subsurface (Payenberg 2002). The measured sections document the lithological characteristics through the member as well as variation across the lateral extent of the outcrop. The upper contact with the overlying Pakowki Formation was not preserved in any of the sections. The results of Payenberg et al. (2002) indicate a thickness of 52.0 m for the DCM, whereas those of Leahy and Lerbekmo (1995) indicate a thickness of 70.0 m, based largely on a single roadcut that has since grown over. Although the DCM thins to the south (Payenberg et al. 2002), this discrepancy in estimates is not reconcilable given that both studies (Leahy and Lerbekmo 1995; Payenberg et al. 2002) worked on outcrop only a few kilometres apart. Neither one of these unit thicknesses could be confirmed from the outcrops studied, although it is suspected that further investigation of outcrops farther north in Verdigris Coulee or farther east along the Milk River will confirm the local thickness of the DCM. Based on these published data, however, the current study deals with the lower 50.9 m or 73–98% of the DCM.

The measured sections of the DCM usually possess two distinct lithozones: a lower siltstone and mudstone-dominated zone with frequent coals and only sporadic channel sandstones, and an upper zone dominated by stacked channel sandstones with occasional siltstones and coaly beds. The division between these two zones varies according to the localized thickness of the lowest sandstone in the upper unit, but occurs minimally at 25.1 m and maximally at 27.2 m above the base of the DCM. This upper zone persists until a siltstone zone with interbedded thin sandstone beds appears in the upper 3.5 to 5.0 m of the formation before contacting the overlying Pakowki Formation (Leahy and Lerbekmo 1995; Payenberg 2002). As the DCM in this area corresponds to the Virgelle 3 allomember of Payenberg et al. (2003), this unit represents a depositional sequence. The three lithozones of the member represent, respectively, the early highstand, late highstand, and transgressive depositional system tracts (Catuneanu 2006) and indicate a localized regression in which sedimentation rate exceeded accommodation followed by the beginning of a transgression event during this time interval.

The documented productive vertebrate microfossil localities, based on stratigraphic position and correlation of facies, occur in at least three distinct stratigraphic levels (Fig. 2-5) that are interpreted as time-equivalent. These levels are referred to, in ascending order, as Levels I–III. These levels were designated for the convenience of grouping localities, as the known localities cluster at one of these four elevations, at most separated from other localities in a level by 2.9 m (within the standard deviation) and separated from other levels by at least 5.2 m.

It is important to note that these zones do not necessarily reflect laterally continuous beds, but rather, stratigraphically equivalent levels in which vertebrate fossils are common. Indeed, most of the outcrop known from these stratigraphic levels preserves no vertebrate fossils, and lithological units in which vertebrate fossils occur are often not laterally extensive. In addition to productive localities, isolated occurrences of bone have been found from 3.0 m to 27.2 m (although possibly up to 37.6 m) above the base of the DCM. No vertebrate material is known from higher than 38.0 m above the datum, constraining the age of all known fossils from the formation to older than 83.5 ± 0.7 Ma (Ogg and Smith 2004) and. Although the uppermost portion of the DCM is poorly constrained in terms of absolute age, the known vertebrate fossils from the formation all minimally range from 84.4 ± 0.8 Ma (Obradovich 1988) through to 83.5 Ma ± 0.7 Ma (Ogg and Smith 2004), placing their occurrence in the latest Santonian.

Section Descriptions

Verdigris 2 – The Verdigris 2 (Fig. 2-6) section was measured in the area of the westernmost of the localities studied and represents some of the westernmost exposures of the DCM. It is located on the southwestern slopes of Verdigris Coulee south of secondary highway 501 (Fig. 2-3). The section exposed in this area is 26 m high. In the vicinity of this section, several fossil vertebrate sites have been found, the most notable being MR-12 (a UALVP site), and the TMP localities MS and JS. JS, located 10.4 m above the datum, occurs at stratigraphic

Level I. It occurs in an organic-rich dark brown to black siltstone which is here interpreted as a crevasse splay deposit, as has been done in other formations (Eberth 1990). Mollusc shell fragments are common at this locality, indicating the presence of localized standing water. No significant collection of material has been made at this site. Both MR-12 and MS (22.0 m above the datum and within one standard deviation of each other in elevation) are within stratigraphic Level II. At both sites, vertebrate fossils are recovered from a brown, organic-rich, decimetre-thick siltstone at the base of a light grey, sandy siltstone. It is likely that these deposits also represent crevasse splays.

Verdigris 3 – Farther east, the Verdigris 3 section (Fig. 2-7a) runs through the well-known UALVP localities MR-6 and MR-9, as well as a new locality (DS) much lower in section. This section is 27.1 m thick. Localities MR-6 (26.4 m above the datum) and MR-9 are both preserved at the base of the same fining upward, yellow sandstone with trough cross-stratified beds dominating the lower portion and ripple laminations dominating the upper portion. Fossils are preserved in brown, organic-rich sandstone interbedded with light grey sandstone near the base of the yellow sandstone body, and are interpreted as channel lag deposits (Eberth 1990). These sites belong to stratigraphic faunal zone Level III. In addition to the vertebrate microfossil collection, large elements (greater than 0.3 m in length) have been quarried at MR-6. A series of blind samples similar to the methods of Eaton (2004) was collected from several discrete lithological units below MR-9 (Fig. 2-7b), including a sample in beds stratigraphically equivalent to MR-12 and MS. Low concentrations of fossil vertebrate material were recovered in only one of the samples roughly 0.5 m below the capping sandstone body, in a dark grey, organic-rich non-marine claystone. DS, located at 10.2 m above the datum, is another locality belonging to stratigraphic Level I. Similar to JS, DS preserves material in a dark grey, organic-rich siltstone with a high abundance of bivalve shells (both complete and fragmentary). In contrast to JS, larger pieces of vertebrate material (> 0.1 m long) are preserved, although these pieces are poorly permineralized and preserve few informative characters to facilitate identification. This site also represents a crevasse splay deposit with evidence of localized standing water. A large sample of matrix was removed from this site, but this material has yet to be sorted and studied. Less than 1.0 m above this locality, in a particularly organic-rich layer, leaf impressions preserved in a soft, light grey, sandy siltstone were uncovered and collected.

Verdigris 1 – Located on the northeastern side of Verdigris Coulee near the southern end of outcrop exposure, the Verdigris 1 section (Fig. 2-8) is the most extensive on the eastern side of Verdigris Coulee (20.0 m thick) and the closest measured section to the Verdigris Coulee DCM datum. On this side of Verdigris Coulee, MR-20, MR-4, 3WC (TMP locality) as well as several minor UALVP localities (including MR-29) have been sampled. MR-20, MR-4, 3WC, and many of the minor localities are located at similar stratigraphic levels, at or near the base of the capping sandstone equivalent to that at the top of Verdigris 3, and belong to the Level III stratigraphic faunal zone. Differential GPS data puts the MR-20 locality at 26.1 m above the base of the DCM. Isolated larger bones (> 0.5 m) have been found at this level and a few metres lower. MR-29 is preserved in a dark grey, organic-rich siltstone laterally equivalent to a coal bed. It is not included in any stratigraphic level based on its estimated height above the base of the DCM of 14.6 m, although it may be equivalent (albeit apparently lower in section) to stratigraphic Level II. A significant sample of matrix has been removed from this site, but this material has not been studied. No mollusc shell fragments have yet been recovered from this locality.

Weir Bridge – Outcrop (Fig. 2-9) of the Weir Bridge section is discernible in the roadcuts leading to the Weir Bridge on the Milk River. Only the northwest roadcut was measured for the section because of its proximity to the DCM datum. Although only 10.8 m thick, this section is the most substantial outcrop of the DCM between the mouth of Verdigris Coulee and Van Cleeve Coulee in Writing-On-Stone Provincial Park. There are no known fossil vertebrate remains that have been recovered from this section.

Van Cleeve – Van Cleeve (or Rocky) Coulee is the westernmost coulee branching off of the Milk River valley within Writing-On-Stone Provincial Park. The section (Fig. 2-10) was measured in a side coulee adjacent to the mouth of Van Cleeve Coulee (on the southern side) and preserves the lower 31.0 m of the DCM. Sparse fossil vertebrate fragments are known from the capping sandstone in this area and leaf impressions in ironstone were recovered from roughly 21.0 m above the base of the DCM. Although lower in absolute elevation than the sandstone bodies in Verdigris Coulee, the capping sandstone in Writing-On-Stone Provincial Park is consistent with those of Level III and is probably an equivalent unit. An isolated partial small theropod phalanx is known from the capping sandstone in adjacent Police Coulee, and a badly eroded, unidentified ornithischian limb element (Fig. 2-11) was found in a light grey siltstone 4.5 m above the base of the DCM. These are the only known dinosaur remains from Writing-On-Stone Provincial Park.

Humphreys – The Humphreys Coulee section (Fig. 2-12) matches the section from Payenberg (2002) between Humphreys and Davis coulees, and was measured in approximately the same location. It preserves the lowest 15.0 m of the DCM. Nearby vertebrate fossil fragments are known from roughly 3.0 m above the base of the DCM.

Davis – The Davis Coulee section (Fig. 2-13) was taken on the east branch of Davis Coulee near the eastern border of Writing-On-Stone Provincial Park in the vicinity of the section from Payenberg (2002). This section illustrates more outcrop than that of Payenberg (2002) with 39.0 m preserved, the base of which was measured as 9.0 m above the datum. Exposures here are quite sheer relative to other outcrops of the DCM, and detailed examination of the rock is often hampered by slumped sediment. The steep rock faces also make prospecting difficult, both here and in the west branch of Davis Coulee. There are no known fossil vertebrate remains recovered from this area.

Audet 1 – Roughly 1.5 km east of Writing-On-Stone Provincial Park, one of the most complete and well-exposed outcrops of the DCM occurs in a small tributary coulee of the Milk River Valley locally known as Cave Coulee. Between Audet 1 and Audet 2 sections, both of which are located on the north wall of the coulee, 43.5 m of outcrop is exposed, starting at the DCM datum. The Level III sandstone is up to 7.0 m thick. The Audet 1 section (Fig. 2-14) is equally close to the localities discussed under the Audet 2 section description. It is also close to Fan Coulee, a coulee that opens up roughly 0.2 km to the west, in which abundant fossil vertebrate remains were observed during preliminary prospecting. Two sandstone bodies (one of which is in the zone equivalent to the capping sandstone of Verdigris 3), interpreted as palaeochannels, pinch out between sections Audet 1 and Audet 2 (Fig. 2-15).

Audet 2 – The Audet 2 section (Fig. 2-16), roughly 0.5 km to the east of Audet 1, preserves the upper portion of the Cave Coulee outcrop. Close to this section, many fossil vertebrates have been recovered from stratigraphic zone Level III at the base of a trough cross-stratified sandstone. The specimens include an almost complete *Neurankylus* shell found 26.9 m above the base of the DCM and a partial, non-associated *Neuranklus* skull. On the south wall of the coulee, a Level II locality known as CBS is located 20.9 m above the DCM datum. The fossils preserved at CBS include vertebrate microfossil material as well as well-preserved elements > 0.1 m long, including a pachycephalosaurid frontoparietal dome. The fossils are preserved in a dark grey, organic-rich siltstone interpreted as a crevasse splay deposit.

Deer Creek Bridge – The Deer Creek Bridge section (Fig. 2-17) likely corresponds to the basal part of Leahy and Lerbekmo's (1995) section at Deer Creek Bridge, which is an estimated 0.2 km away. As mentioned, this roadcut on secondary Highway 500 has since grown over, although an equivalent representation crops out adjacently, and it is represented here by sections Audet East 1 and Audet East 2. The Deer Creek Bridge section is 12.5 m thick. No known fossil vertebrate remains have been recovered from this section.

Audet East 1 – Roughly 1.0 km to the southeast of Deer Creek Bridge, the Audet East 1 section (Fig. 2-18) is located on the west side of a tributary coulee on the south side of the Milk River Valley. This section is correlated with the Deer Creek Bridge section based on the coal beds present in both, the observed relative elevation, and the elevation of a trough cross-stratified sandstone similar to those of other sandstones at Level III. This section preserves 28.9 m of outcrop. Fragmentary fossils, including a weathered small pachycephalosaurid dome, from this area are all associated with the base of the Level III sandstone.

Audet East 2 – The Audet East 2 section (Fig. 2-19), a 33.0 m thick section, is located on the east side of the same tributary coulee as Audet East 1, and is adjacent to secondary Highway 500. Vertebrate fossils are known from 27.5 m above the base of the DCM, at the base of a yellow, trough cross-stratified channel sandstone, again at Level III. At 38.0 m above the base of the DCM in this section, a palaeomagnetochron boundary equivalent to that of Leahy and Lerbekmo (1995) is expected to be preserved. This section does not reach the elevation of the section measured by Leahy and Lerbekmo (1995), and based on their measurements, a further 24.0 m of sandstone should be expected to overly this section. However, this section may only lack the top 11.3 m of the DCM according to the estimates of Payenberg et al. (2002).

Black 2 – The section Black 2 (Fig. 2-20) on the northwest wall of Black Coulee, measured 3.5 km east of the Deer Creek section, preserves 22.6 m of section. This section is in close proximity to Locality 10 of Russell (1935) and a new, unnamed locality, both at the base of a trough cross-stratified sandstone. The Locality 10 quarry has long since been obscured by fallen sandstone, and other Russell (1935) localities are inaccessible. Locality 10 differs in elevation from the other channel lag deposits of Level III, with differential GPS measurements placing the locality at 37.6 m above the DCM datum. This difference in elevation is enough to consider this assemblage at a distinct stratigraphic level. However, Black 2, along with Black 1, are both located down-dip from other relatively complete DCM exposures, and it is possible sedimentation rates were higher in these two areas, creating a situation in which these sites may be temporally equivalent to other localities, but at a higher stratigraphic level. More investigation into outcrops on the south side of Black Coulee are necessary to evaluate the time-equivalency of these localities. All of the fossil vertebrates recovered from both of these sites have been quarried or surface collected. No vertebrate microfossil matrix collection has been made from these localities. The differential GPS assessment indicates that this section (the top of which is 49.3 m above the base of the DCM) preserves the stratigraphically highest point in the DCM measured in the current study.

Black 1 – The Black 1 section (Fig. 2-21) is 3.5 km northeast of Black 2. This section is the easternmost section measured for this study, and although it lacks any differential GPS data or proximity to the DCM datum, the section has been represented as at least partially equivalent with the Black 2 section. Further confirmation of such a high elevation for this section is provided by the proximity of the section to the type section of the Milk River shoulder (Meijer-Drees and Myhr 1981) where the DCM contacts the overlying Pakowki Formation, roughly 5.0 km to the northeast. Vertebrate fossils were surface collected from a silty, fine-grained sandstone that is an estimated 30.8 m above the base of the DCM. No elements were found in situ. If this site does correlate with those of Level III at other localities, it may be of interest as it seems to preserve fossils of this layer in a different depositional environment (probably a crevasse splay). No vertebrate microfossil matrix samples have been taken from this locality. Further work in Black Coulee is needed to evaluate the stratigraphic provenance of fossil vertebrate specimens from these localities.

Conclusions

Geographic and stratigraphic data from known vertebrate fossil localities allow the first documentation of the distribution and geologic associations of vertebrate fossils from the DCM. Vertebrate fossils are known from 3.0 m to 27.2 m above the base of the DCM, with at least four particularly productive, stratigraphically equivalent zones. Large concentrations of vertebrate fossils are more common in mudstone, crevasse splay deposits in the lower part of the member, and in channel sandstones in the higher part of the member. This change is most likely due to a general increase of channelization due to decelerating base level rise. The lowest accumulations host abundant invertebrate material, suggesting the presence of localized standing water. The most productive and consistent level occurs as a channel lag deposit in roughly the middle of the member, with vertebrate remains likely reworked from the surrounding crevasse splay mudstones. It is from this level that most of the published specimens from the Milk River Formation are derived. At least one additional channel lag deposit is present higher in section, but this may be an artefact of differential sedimentation. None of the known fossil occurrences occur above 38.0 m above the base of the DCM (the 33r-34n magnetochron boundary), and all are latest Santonian in age. These three levels, if adequately sampled, may provide the resolution to observe patterns in relative abundances of taxa during deposition of this latest Santonian non-marine unit.

The actual thickness of the DCM around Writing-On-Stone Provincial Park has not been confirmed, and there has been little done in the stratigraphic placement of the easternmost vertebrate fossil localities. Both of these points make further study of the uppermost DCM necessary.

Fig. 2-1. Contact between cliff forming Virgelle Member and recessive Deadhorse Coulee Member of the Milk River formation at Writing-On-Stone Provincial Park.

Fig. 2-2. Fourteen measured sections along transect 1-1’. Known elevations of fossil vertebrate material are indicated.

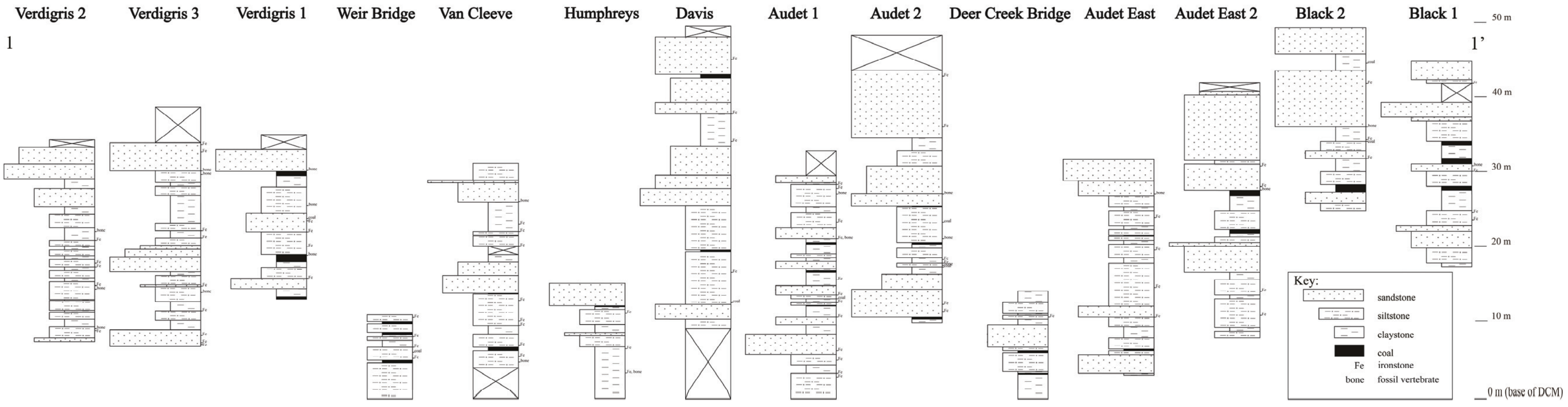


Fig. 2-3. Locations of measured sections 1-1’. Map modified from Braman (2001). A) Verdigris Coulee datum, B) WOS datam, C) Cave Coulee datum, and D) Deer Creek Bridge datum.

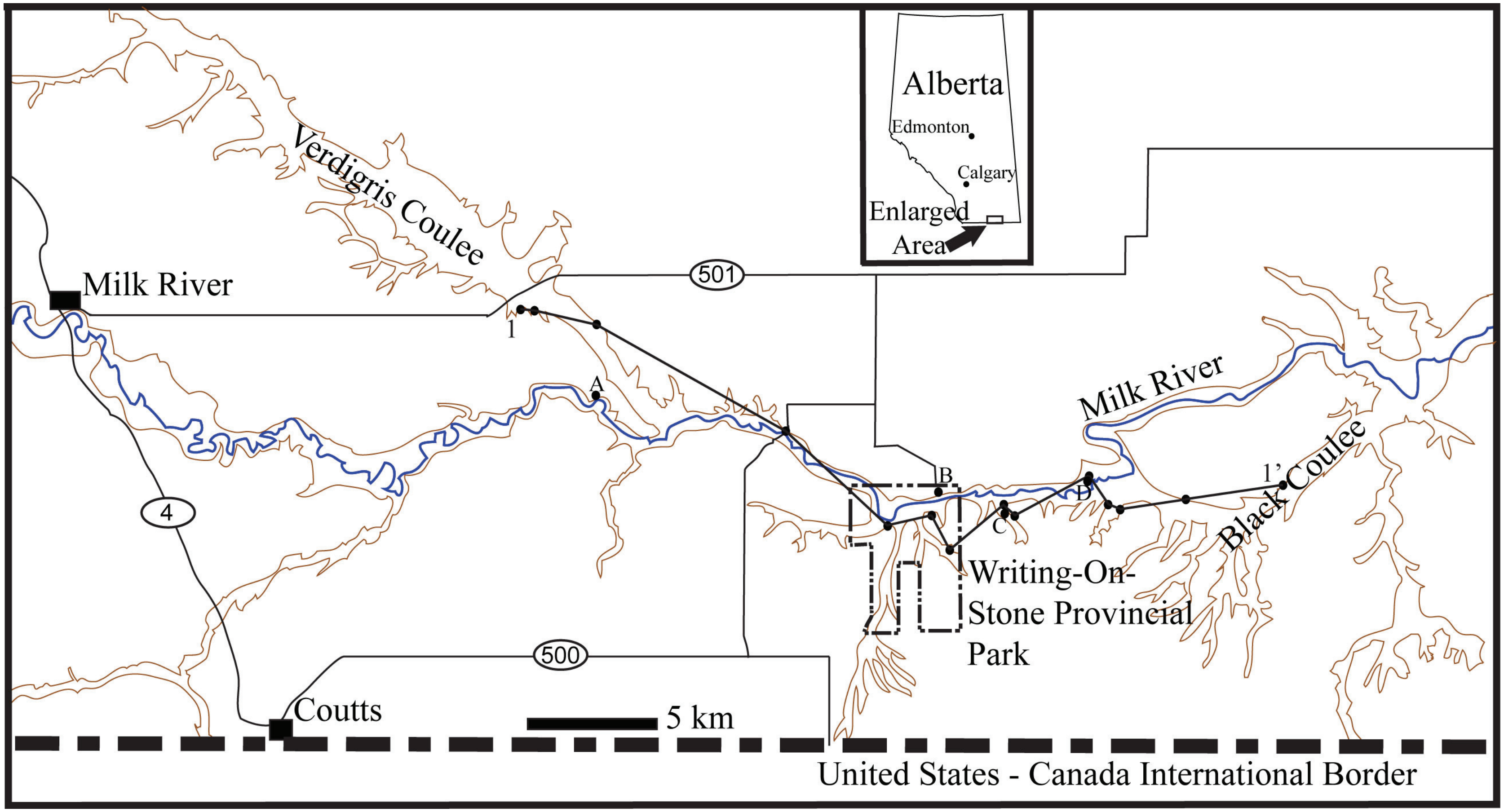


Fig. 2-4. Position of palaeoshoreline (estimated from shoreface deposits in well logs) at the time of depostion of the Deadhorse Coulee Member relative to measured sections and other landmarks. Dots represent location of sections. Map modified from Payenberg (2002).

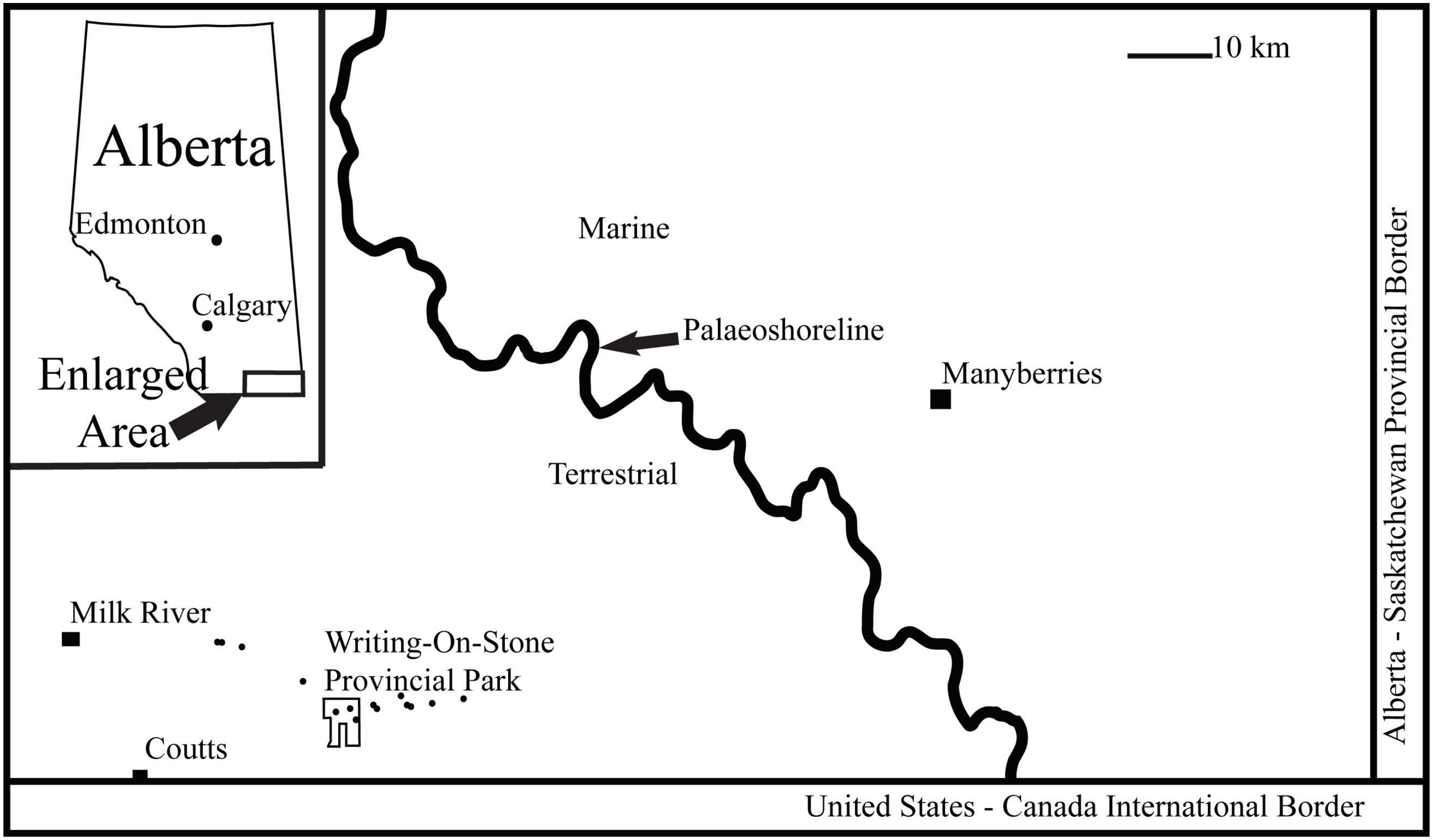


Fig. 2-5. Stratigraphic time-equivalent vertebrate microfossil levels within the lower 73−98% of the DCM with vertebrate localities marked.

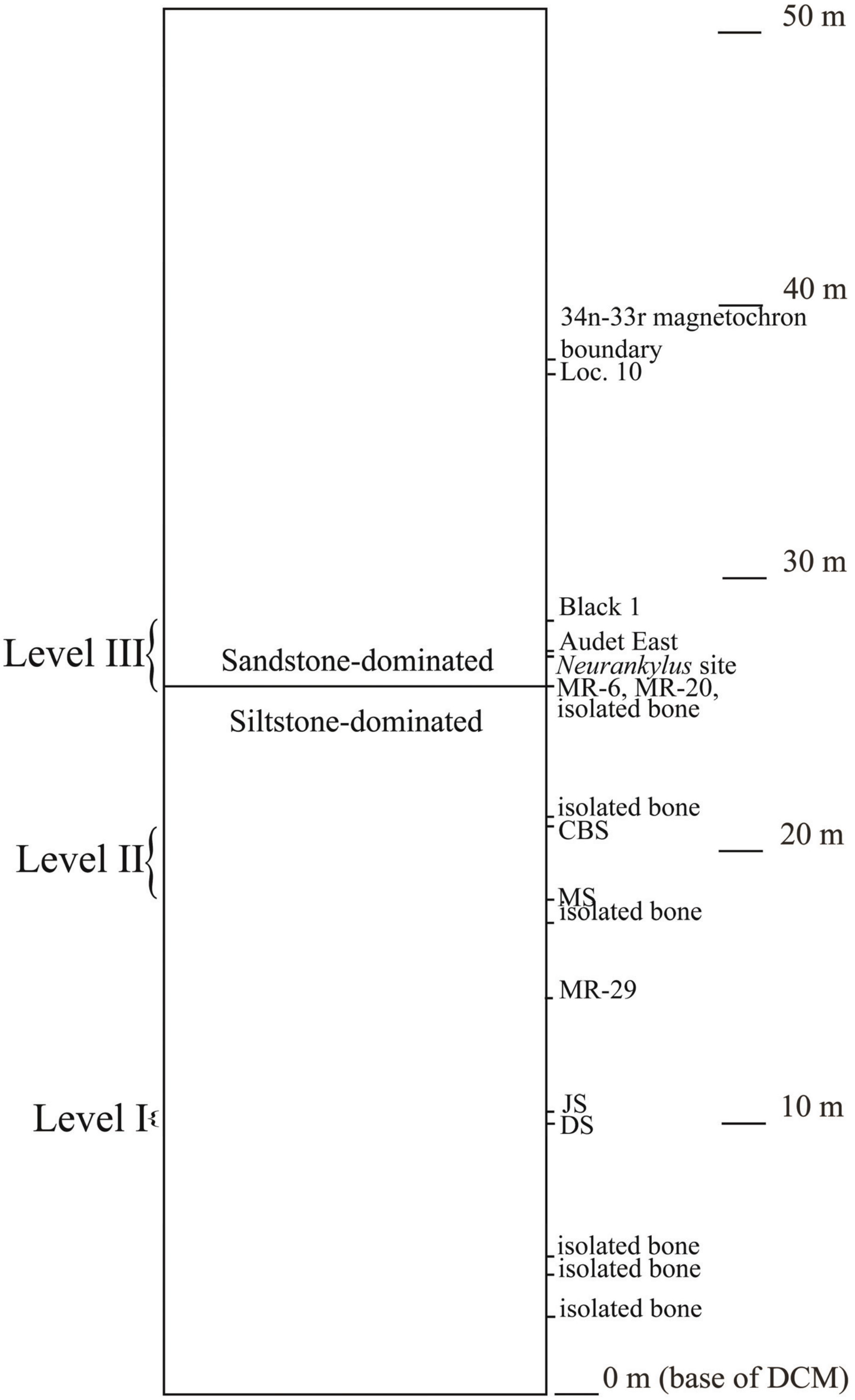


Fig. 2-6. Outcrop near Verdigris 2 measured section, Verdigris Coulee. MR-12 is seen on the right.

Fig. 2-7. Outcrop at Verdigris Coulee MR-6, Verdigris Coulee A) Verdigris 3 section with MR-6 at the top, B) blind sample localities adjacent to white sacks with MR-9 above and MR-6 to the left. Person is roughly 1.8 m.

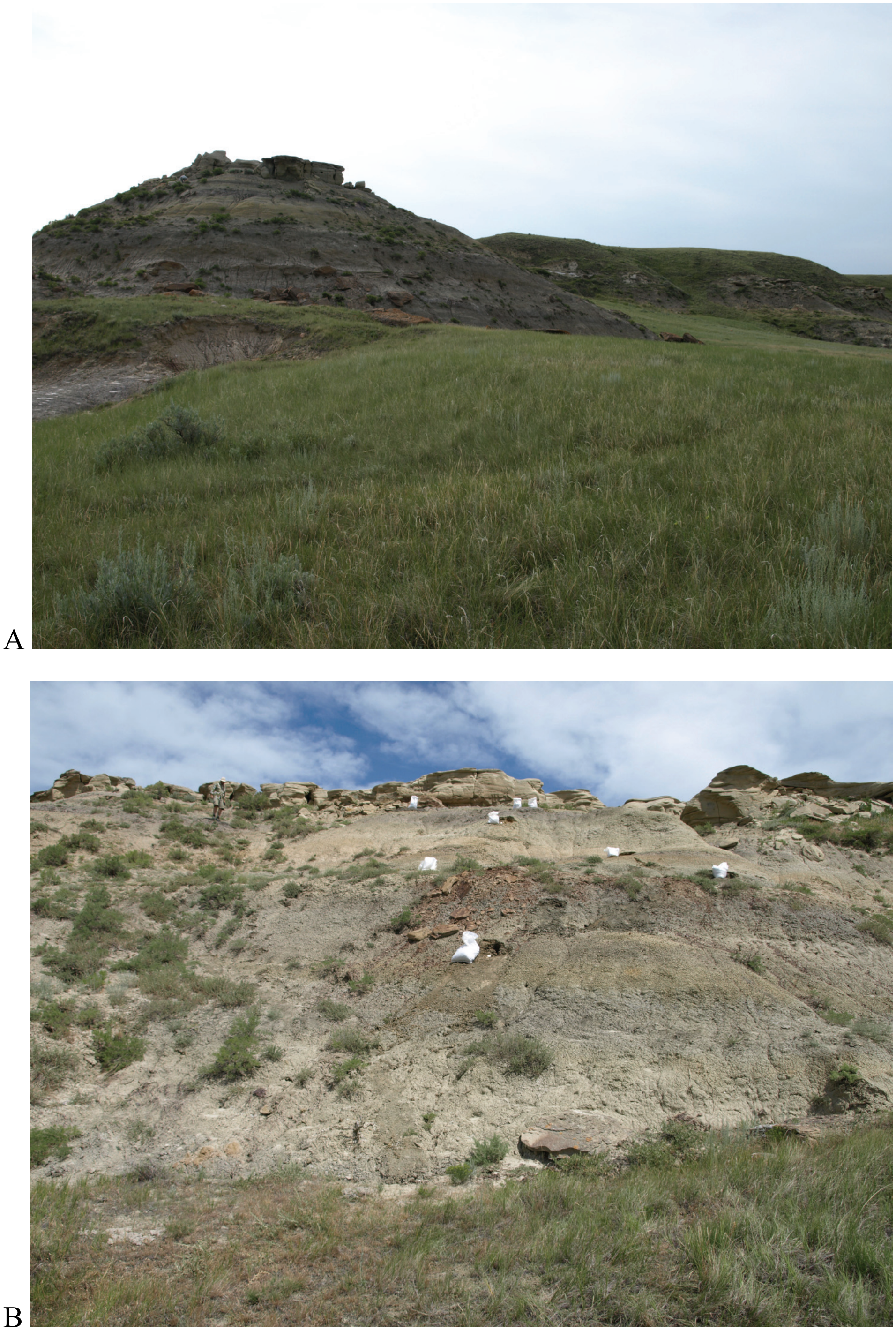


Fig. 2-8. Outcrop at Verdigris 1 section, Verdigris Coulee. Jacob’s staff is 1.5 m.

Fig. 2-9. Outcrop at Weir Creek Bridge section, Milk River Valley. People in photo roughly 1.8 m.

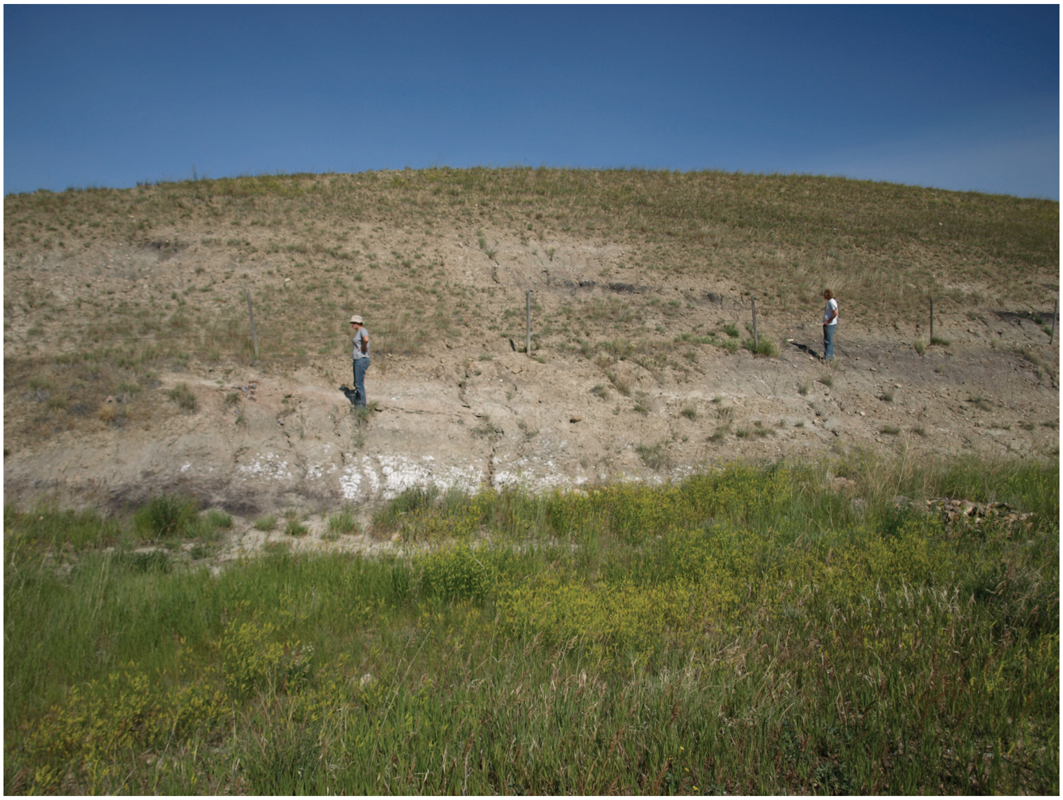


Fig. 2-10. Outcrop at Van Cleeve section, Van Cleeve (Rocky) Coulee, Writing-On-Stone Provincial Park A) bottom, B) middle, C) top. Jacob's staff 1.5 m.

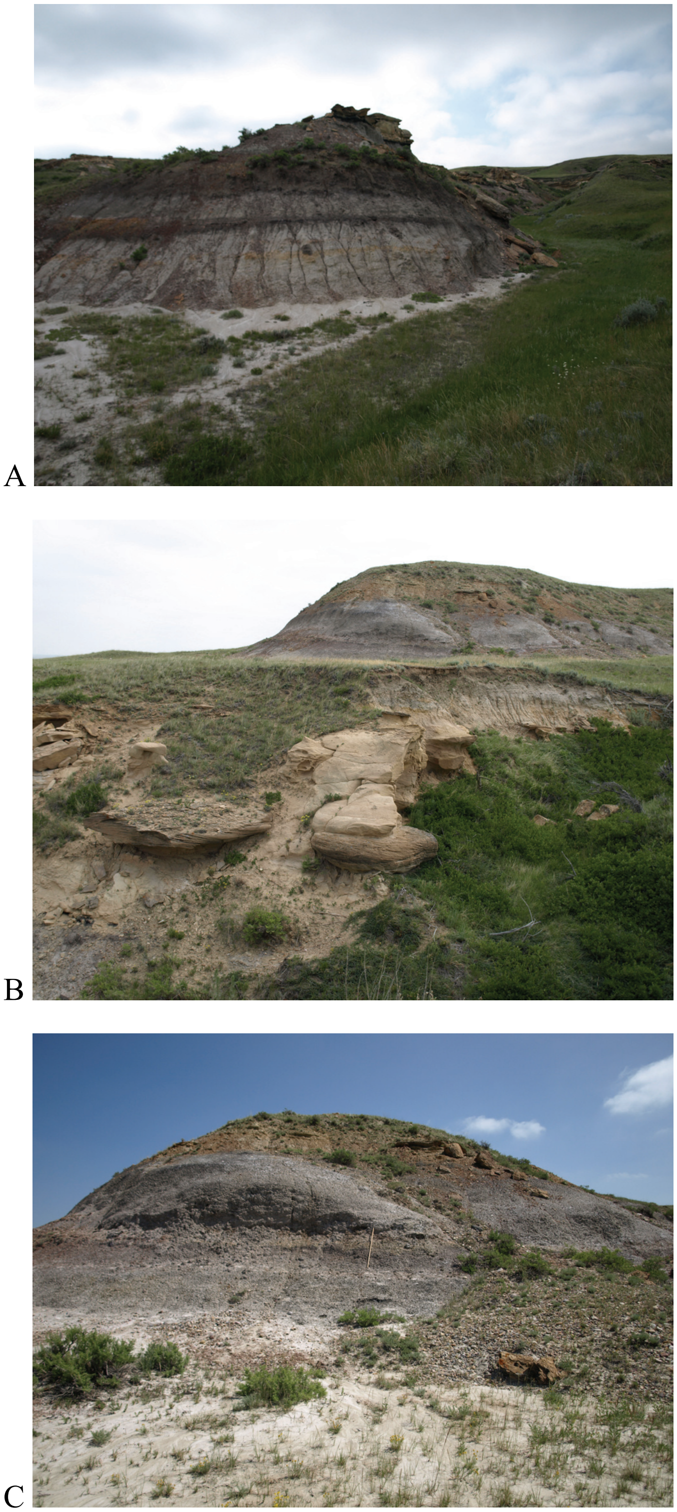


Fig. 2-11. Unidentified ornithischian limb element near Police Coulee in Writing-On-Stone Provincial Park. Scale bar 10 cm.

Fig. 2-12. Outcrop at Humphreys section, Humprheys Coulee, Writing-On-Stone Provincial Park. Jacob's staff is 1.5 m.

Fig. 2-13. Outcrop at Davis section, east branch of Davis Coulee, Writing-On-Stone Provincial Park. Jacob's staff is 1.5 m.

Fig. 2-14. Outcrop at Audet 1 section, Cave Coulee, east of Writing-On-Stone Provincial Park. Jacob's staff is 1.5 m.

Fig. 2-15. Outcrop between Audet 1 and Audet 2 sections illustrating a discontinuous channel sandstone, Cave Coulee, east of Writing-On-Stone Provincial Park. The lower sandstone body in the bottom left pinches out towards the right.

Fig. 2-16. Outcrop at Audet 2 section, Cave Coulee, east of Writing-On-Stone Provincial Park. Jacob's staff (in the middle left) is 1.5 m.

Fig. 2-17. Outcrop at Deer Creek Bridge section, Milk River Valley. Jacob's staff is 1.5 m.

Fig. 2-18. Outcrop at Audet East 1 section, south of Deer Creek Bridge, Milk River Valley.

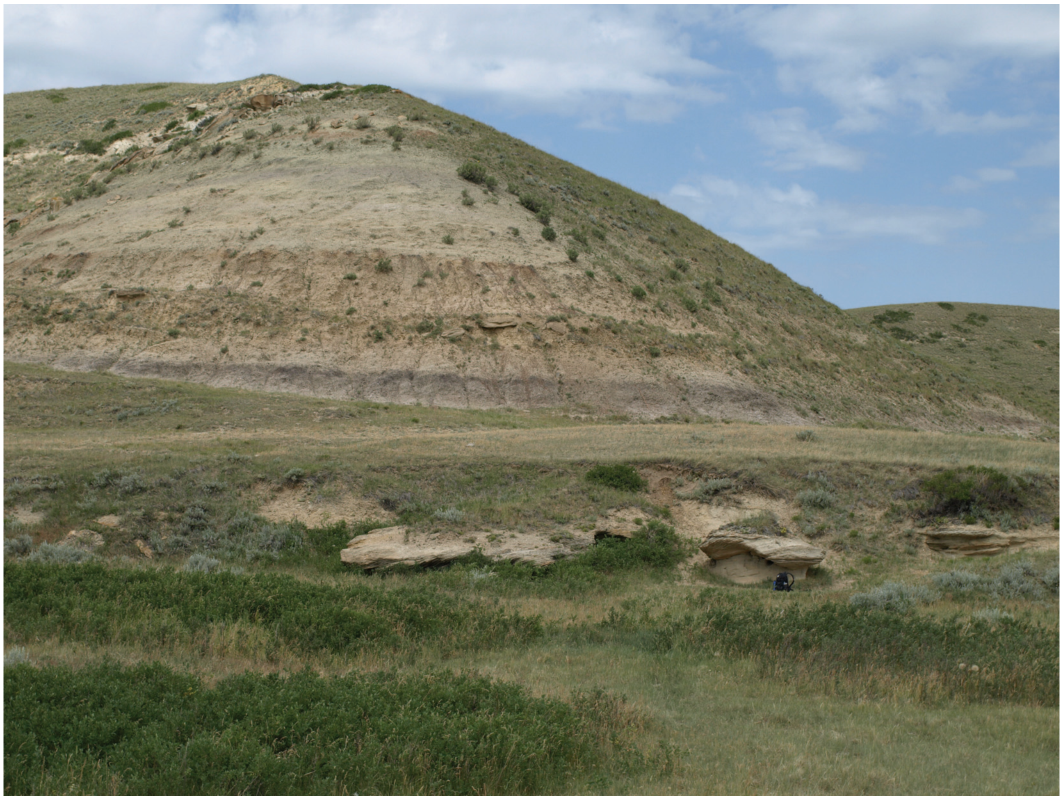
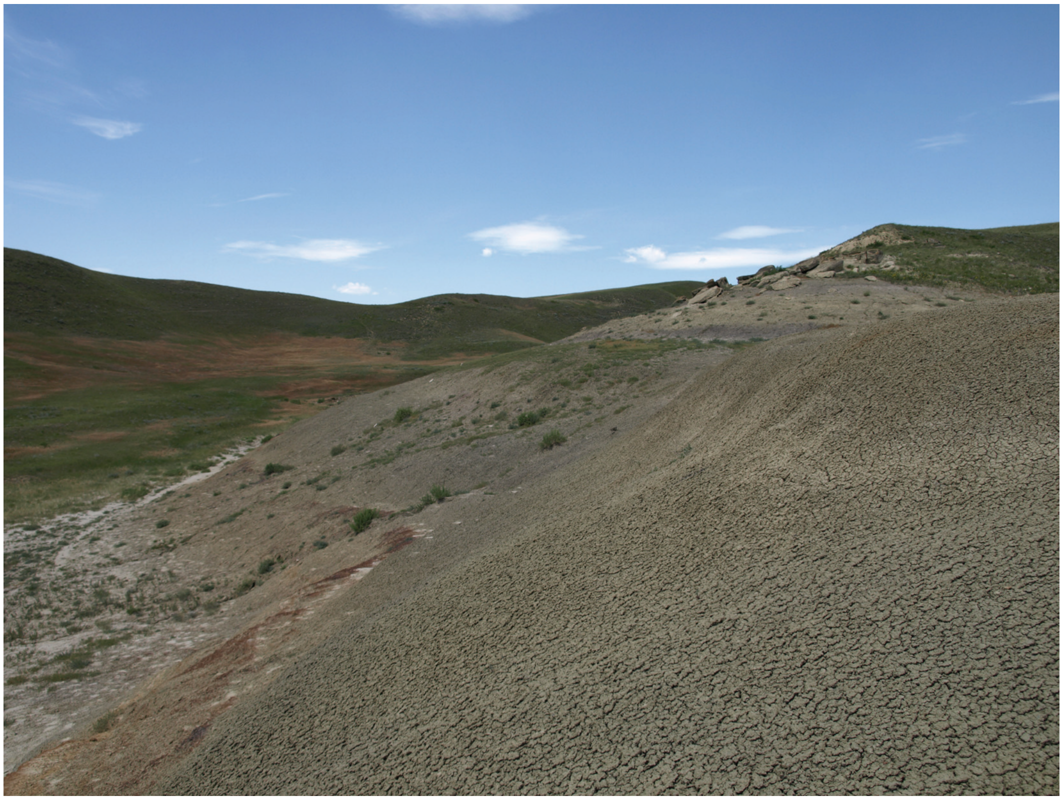


Fig. 2-19. The well-exposed bottom portion of outcrop at Audet East 2 section, south of Deer Creek Bridge, Milk River Valley. Jacob's staff is 1.5 m.

Fig. 2-20. Outcrop at Black 2 section, Deer Creek Ranch, Black Coulee. Jacob's staff (in bottom centre) is 1.5 m.

Fig. 2-21. Outcrop at Black 1 section, Deer Creek Ranch, Black Coulee.



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Chapter 3 — The vertebrate assemblage of the Deadhorse Coulee Member of the Milk River Formation, Alberta

Introduction

The non-marine Deadhorse Coulee Member of the Milk River Formation preserves an assemblage from the relatively poorly known Santonian (Eaton 2006). Many aspects of the fauna have been described over the last four decades of intense study (Fox 1968, 1969, 1970, 1971a, 1971b, 1972a, 1972b, 1976, 1980, 1984a, 1984b, 1987; Fox and Naylor 1982; Gao and Fox 1996; Johanson 1993, 1994; Wu and Brinkman 1993; Baszio 1997; Brinkman 2003; Larson 2008). However, only rarely have complete faunal lists been published (Fox 1976). As well, with increased collection and study of this member in recent years (Chapter 2) and our increased confidence in identifying vertebrate microfossil elements (Brinkman et al. 2004), our understanding of the assemblage diversity is improving, and an updated faunal survey can be undertaken. In addition to collecting this information into one source for aid in future study, this study was necessary for evaluating the relative abundances of these taxonomic groups. A faunal list, as well as systematic palaeontology of a restricted list of newly recognized taxa from this member will be dealt with in this chapter.

Materials and Methods

Specimens are curated at the University of Alberta Laboratory for Vertebrate Paleontology (UALVP), Royal Tyrrell Museum of Palaeontology (TMP), Royal Ontario Museum (ROM), and Canadian Museum of Nature (CMN). Specimens from the Deadhorse Coulee Member of the Milk River Formation were identified to their lowest taxonomic identification, usually family, species, or morphotype (Table 3-1).

Systematic Palaeontology

Chondrichthyes Huxley 1880

Hybodontoidea Owen 1846

Lonchidiidae Herman 1977

Lonchidion Estes 1964

Lonchidion sp.

Fig. 3-1

Comments — *Lonchidion* is known from transversely wide and ridged tooth crowns. Although not identified to species, the teeth resemble the type species, *L. selachos*, from the Maastrichtian of North America in that the transverse ridge has a slight flexture (Rees and Underwood 2002). Although this genus had been synonymized with *Lissodus*, Rees and Underwood (2002) concluded the genus is valid and distinct, with the genus ranging from the Triassic to the end of the Cretaceous in North America and Europe.

Rajiformes Berg 1940

Rhinobatoidei Fowler 1941

Family incertae sedis

Myledaphus Cope 1876

Myledaphus sp.

Fig. 3-2

Comments — *Myledaphus* sp. teeth were first identified as being distinct from *Myledaphus bipartitus* by Brinkman et al. (2004). Frampton (2006) noted that this species occurred in the Foremost and Milk River formations from Alberta, as well as the Wahweap, John Henry, and Dakota formations of Utah. *Myledaphus* teeth from the Deadhorse Coulee Member match those documented for the Foremost Formation (Frampton 2006; Brinkman et al. 2004). They are characterized by a lack of prominent ornamentation, and possess only a single transverse ridge on the occlusal surface. They have the same distinct variations in morphology according to position within the jaws noted by Frampton (2006). That being said, the range in morphology appears to be greater than that noted for Foremost specimens.

Many teeth from the Deadhorse Coulee Member possess pronounced, blade-like transverse ridges on the occlusal surface (Fig.3-2g).

Osteichthyes Huxley 1880

Acipenseriformes Berg 1940

Polyodontidae Bonaparte 1838

Gen. et sp. indet.

Fig. 3-3

Comments — “Microctenoid” scales from an indeterminate polyodontid, characterized by a denticulate dorsal plate and a pair of ventral projections (Grande et al. 2002) have been recovered from the Level III Deadhorse Coulee Member localities. Scales are indistinguishable from those of *Palaeopsephurus wilsoni* from the Maastrichtian of Montana (Grande and Bemis 1991). These scales are the oldest known North American polyodontid remains, and only the second-oldest of the family after *Protopsephurus liui* (Grande et al. 2002). The occurrence of this taxon may reflect an important immigration of this taxon from Asia prior to the latest Santonian. Remains of Polyodontidae are unknown in contemporaneous (Chapter 6) or Campanian (Eaton et al. 1999) deposits in Utah.

Amiiformes Hay 1930

Amiidae Bonaparte 1837

Vidalamiinae Grande and Bemis 1998

Melvius Bryant 1987

Melvius sp.

Fig. 3-4

Comments — *Melvius* is the largest known amiid fish with the only named species known from the Campanian and Maastrichtian of North America (Grande and Bemis 1998). It is poorly known and diagnosed, but one of the defining characteristics of the genus is the uniquely shaped vertebrae with lateroventral constrictions. Teeth characteristic for the subfamily, Vidalamiinae, with distinct ridged acrodin caps (Grande and Bemis 1999) are also locally abundant within the member. As the teeth of *Melvius* are not identifiable below the subfamily level, remains from vertebrate microfossil localities are only identified to this higher level.

Semionotiformes Arambourg and Bertini 1958

Semionotidae Woodward 1890

Lepidotes Agassiz 1832

?*Lepidotes* sp.

Comments — Squat, cylindrical teeth with distinctly curved tips are here tentatively referred to the genus *Lepidotes*. This occurrence would be the first occurrence of this taxon in Canada, but is only tentative until unequivocally diagnostic material becomes available.

Lepisosteiformes Hay 1929

Lepisosteidae

Gen. et sp. indet.

Fig. 3-5

Comments — Ganoid scales referred to the family Lepisosteidae differ from known specimens of *Lepisosteus* (whose scales are also present). Lepisosteidae gen. et sp. indet. often possess the overlapping tabs characteristic for the family; however, the scales also possess an internal longitudinal ridge that lies between peg-in-socket articulations. This peg-in-socket morphology is more similar to scales referred to the morphotaxon holostean A, although the prominence of these features in Lepisosteidae gen. et sp. is often less pronounced.

Reptilia Laurenti 1768

Testudines Linnaeus 1758

Solemydidae Lapparent de Broin and Murelaga 1996

Naomichelys Hay 1908

cf. *Naomichelys* sp.

Fig. 3-6

Reference material — CMN 52992, complete right xiphiplastron; UALVP 45552, peripherals, costals, and partial suprapygal.

Other occurrences —possibly Foremost Formation (middle Campanian; CMN uncatalogued, TMP 2009.037.0008), southern Alberta.

Comments — None of the recovered material for *Naomichelys* sp. is the same as that of the type specimen of *Naomichelys speciosa*. However, when compared to the Trinity Formation specimen (Hirayama et al. 2000), which is likely referable to *N. speciosa*, the following features are shared: a straight posterior xiphiplastral margin, a medially inclined femoral-anal sulcus relative to anterior xiphiplastral border, a relatively narrow first suprapygal, and probably greatly reduced extragulars relative to gulars and a posterolaterally inclined epi-hyoplastral contact (both characteristics seen in Foremost specimens). Because of the disparate ages of the *N. speciosa* and the Milk River taxon, they are not likely conspecific; however, because of the fragmentary nature of the Milk River specimens, no autapomorphies were observed. Isolated fragments of shell are only identifiable to family Solemydidae, which is characterized by the unique pustulate ornamentation of shell (Lapparent de Broin and Murelaga 1999).

Diagnosable North American representatives of the Solemydidae are rare. The only named North American species, *Naomichelys speciosa* from the Cloverly Formation, is based on a single entoplastron and two referred epiplastra (Ostrom 1970). Other specimens, including a mostly complete specimen from the Trinity Formation and scores of shell fragments from many Lower and Upper Cretaceous localities have been referred to this species. Family Solemydidae is identifiable from shell fragments because of diagnostic pronounced granulated shell ornamentation, making it the most easily identified turtle in microvertebrate assemblages.

Canadian specimens pertaining to this family have been previously identified as Solemydidae indet. (Brinkman 2003; Rylaarsdam et al. 2006) based on the fragmentary or unprepared nature of the remains. A few new more complete Canadian specimens have shed light on the diversity of North American solemydids. All known Canadian specimens are Late Cretaceous in age, unlike the Early Cretaceous *Naomichelys speciosa*.

Archosauria Cope 1870

Crocodylomorpha Hay 1930 sensu Walker 1970

Neosuchia Clark in Benton and Clark 1988

Goniopholididae Cope 1875

Gen. et sp. indet.

Fig. 3-7

Comments — Specimens referred to Family Goniopholididae from the Deadhorse Coulee Member include teeth and osteoderms. Tooth crowns are up to 31 mm tall and 12 mm in diameter and exhibit the closely-spaced longitudinal ridges and round cross-section characteristic for this group (Owen 1841). The osteoderms are included in this identification largely because of their size and distinct morphology. Osteoderms are rectangular with ornamentation that is both larger and more closely spaced than the ornamentation documented for *Denazinasuchus kirklandicus* (Lucas et al. 2006). No known osteoderms have keels. Skull fragments (Fig. 3-7C) are also referred to this taxon based on similar-sized alveolae and ornamentation consistent with that of the osteoderms; however, the fragmentary nature of the specimen does not facilitate comparison with other goniopholidid taxa. There has been little published in the way of good diagnostic characteristics of Family Goniopholididae, and North American specimens referred to *Goniopholis* are in need of revision (Salisbury et al. 1999). It is, therefore, difficult to establish to what taxonomic level the Deadhorse Coulee Member material is identifiable. Referral to the family was supported by the aforementioned characteristics, allowing for tentative identification.

Family incertae sedis

Gilchristosuchus Wu and Brinkman 1993

cf. *Gilchristosuchus palatinus* Wu and Brinkman 1993

Fig. 3-8

Comments — Tooth crowns and osteoderms from vertebrate microfossil assemblages in the Deadhorse Coulee Member are tentatively referred to *Gilchristosuchus palatinus*. Teeth come in two morphotypes: a blunt, bulbous tooth crown (Fig. 3-8A), and a stout but pointed tooth crown (Fig. 3-8B). Osteoderms (Fig. 3-8C) are small and often keeled with ornamentation that greatly resemblance the pattern of ornamentation on the skull roof of the holotype specimen. Little work on this species has been done since its initial description, but it is believed to be closely related to the Early Cretaceous *Bernissartia fagesii* (Wu and Brinkman 1993). The teeth referred to *Gilchristosuchus palatinus* in the current study bear a great deal of resemblance to the teeth described for *Bernissartia fagesii* (Buffetaut and Ford 1979). However, the eusuchian *Hylaeochampsa vectiana* is also hypothesized to have posterior teeth that display this same morphology (Clark and Norell 1992). Indeed, these teeth also resemble the posterior teeth of Alberta eusuchians (Wu 2005). Tooth crowns of cf. *Gilchristosuchus palatinus* were differentiated from those of globidontan eusuchians on the basis of size.

Ornithischia Seeley 1888

Ornithopoda Marsh 1881

Family indet.

Gen. et sp. indet.

Fig. 3-9

Comments — The ornithopod teeth from the DCM are phylloform in labial view and have one primary apical cusp and distinct cusps along their margins. There is no prominent medial ridge, and the crown is distinctly mesiodistally longer than the root. These are characteristics noted by Butler et al. (2007) in their phylogenetic character description. It is perhaps noteworthy that the cusps of these teeth often posses smaller accessory cusps at the base and between cusps.

This has not, to the author's knowledge, been noted for any other ornithopod tooth. These ornithopod teeth were first identified by Baszio (1997a) but were not figured or described. Identification more specific than Ornithopoda is, at this time, impossible.

Pachycephalosauria Maryańska and Osmólska 1974

Pachycephalosauridae Sternberg 1945

Gen. et sp. nov.

Fig. 3-10

Comments — A complete pachycephalosaurid frontoparietal dome (Fig. 3-10A) was recovered from stratigraphic Level II of the Deadhorse Coulee Member. Along with other domes in the ROM collection, this specimen represents a new species of pachycephalosaurid dinosaur, the oldest from North America. It is being described by Evans et al. (in prep.). Also, teeth from vertebrate microfossil localities first reported by Baszio (1997b) are possibly referable to this taxon and have been documented here.

The premaxillary teeth (Fig. 3-10B) are small (1.6–3.3 mm in basal crown length, 2.5 mm average), caniniform, and lack mesial carinae. The distal carina is denticulate, with 4.5 to 6.8 denticles/mm (average 5.5 denticles per millimetre). Maxillary teeth (Fig. 3-10C) of a primitive pachycephalosaur from the Milk River Formation are identified by comparison to described material from other marginocephalians. They exhibit an average crown length of 3.4 mm (2.4–4.7 mm range), and possess on average three mesial and one distal ridges. The mesial dentary teeth (Fig. 3-10D) average 3.4 mm in basal crown length (ranging from 2.3–4.6 mm) and also have relatively few denticles, averaging five on the mesial carina and four on the distal carina. The distal dentary teeth of the pachycephalosaurid (Fig. 3-10E) have been previously described by Baszio (1997). They are low and triangular and bear three to five denticles on the distal carina, and four to eight denticles on the mesial carina.

Three of the pachycaphalosaur tooth morphs not only share qualitative similarities in pattern, but also have a consistent quantitative size. From measurements of the referred teeth, the basal crown lengths (used as a proxy for crown size) do not differ in between maxillary and dentary teeth (p=0.47) or between dentary and premaxillary teeth (p=0.12), although a significant difference in size is noted between maxillary and premaxillary teeth (p=0.02).

Relatively few pachycephalosaur taxa have known premaxillae. Compared to those known, the premaxillary teeth most closely resemble those of *Goyocephale lattimorei* (Perle et al. 1983), and *Prenocephale prenes* (Maryańska and Osmólska 1974), in that they possess minute denticles on the distal carina and lack a mesial carina. Another feature shared between the premaxillary teeth of these three taxa is the wear pattern, which is vertical and restricted to a broad, and sometimes quite high, area on the lingual side of the teeth. Premaxillary teeth of the Deadhorse Coulee Member taxon more closely resemble those of *Goyocephale lattimorei* than those of *Prenocephale prenes* in that the denticle count is more in line with the six denticles per millimetre reported for the former than the 8 denticles per millimetre for the latter. Also, both the Deadhorse Coulee Member taxon and *Goyocephale lattimorei* lack the multiple longitudinal ridges present on *Prenocephale prenes*. The premaxillary teeth are also similar in shape and denticulation to those of some basal neoceratopsians, such as *Yamaceratops dorngobiensis* and *Liaoceratops yanzhiguouensis* (Mackovicky and Norell 2006). These teeth strongly contrast with those of the non-caniniform premaxillary teeth of *Stegoceras validum*, which possess both mesial carinae and denticles, and large distal denticles measuring about 3 denticles per millimetre. The wear pattern also differs, which in *S. validum* is concentrated on the tips. *Pachycephalosaurus wyomingensis* (including *Stygimoloch spinifer* and *Dracorex hogwartsia*; Horner et al. 2007) has an edentulous premaxilla.

The maxillary teeth referred to the Deadhorse Coulee Member pachycephalosaurid were first described by Baszio (1997b) as Protoceratopsian ‘B’ teeth. The teeth bear little resemblance to maxillary teeth described for *Stegoceras validum* or for *Pachycephalosaurus wyomingensis* (Sues and Galton 1987; Brown and Schlaikjer 1943), which are triangular in lateral view, display only a weak primary median ridge, and possess small denticles only on their basal distal carina, with larger denticles and ridges on the apical distal carina and all along the mesial carina. The maxillary teeth of this taxon more closely resemble the teeth of ceratopsians in the possession of a leaf-shaped crown, both mesial and distal denticles on the vertical portion of the carinae, and a strong labial median ridge confluent with a basal cingulum, forming the characteristic labial pockets on each side of the median ridge. In more heavily worn teeth, so much of the apical portion of the tooth is missing that the median ridge seems weakly developed and most of the mesial carina is removed. Such teeth are indistinguishable from the figured maxillary tooth of *Goyocephale lattimori* (Perle et al. 1983). *Tylocephale gilmorei* and *Homalocephale calathocercos* (Maryańska and Osmólska 1974), based on the written descriptions of the two specimens and a research-quality cast of GIN SPS 100/51, probably also exhibit this pattern, although the condition in *Prenocephale prenes* is unclear. These teeth differ from those of the Neoceratopsia (Sereno 1986), as they exhibit a cylindrical root with no mesiodistal compression, thereby retaining a tooth crown that is longer mesiodistally than labiolingually wide (Sereno 1984), and enamel that is not restricted to the labial side of the crown (Sereno 1986). The mesiolabial wear is oblique to the parasagittal plane of the tooth and straight, such that any median ridge on the lingual side of the crown has been removed. This is more reminiscent of the pattern seen in basal Neoceratopsians, and not in *Stegoceras validum*, which displays double wear facets from occluding in an interlocking pattern with dentary teeth. Pachycephalosaurs that have a documented similar wear pattern to the Deadhorse Coulee Member taxon include *Goyocephale lattimorei*, *Tylocephale gilmorei*, and *Homalocephale calathocercos*. The wear pattern in maxillary teeth of *Prenocephale prenes* (Maryańska and Osmólska 1974) is noted as being distinct. The maxillary tooth wear pattern in *Pachycephalosaurus wyomingensis* is undescribed.

The mesial dentary teeth of this taxon bear great similarity to the mesial dentary teeth of *Stegoceras validum* as well as a dentary referred to *Sphaerotholus goodwini* (Williamson and Carr 2002) in that the base of the swollen crown angles upward mesially so that the base of the mesial carina is well above the base of the distal carina. The only differences between this taxon and the dentary teeth of the other two taxa are the paucity of denticles, and the fact that the mesial denticles do not have associated ridges. There is no indication of an enlarged first dentary tooth as in *Goyocephale lattimorei* based on the tooth sizes represented, and these teeth differ considerably from the caniniform mesial dentary teeth of *Goyocephale lattimorei* and *Wannanosaurus yansiensis* (Butler and Zhao 2009). The mesial dentary teeth are unknown in all other pachycephalosaurs.

The denticle counts of the referred distal dentary teeth are lower than the condition seen in *Stegoceras validum* and that documented for *Wannanosaurus yansiensis*. The wear pattern is such that the weak median ridge on the labial surface of the crown is the first part of the crown to wear, unlike the condition seen in *Stegoceras validum* and cf. *Sphaerotholus goodwini* (Williamson and Carr 2002), in which wear is concentrated on the labial sides of the carinae. This pattern is consistent with the wear of referred maxillary teeth. The same wear pattern seen in this taxon is also seen in *Goyocephale lattimorei* and possibly *Tylocephale gilmorei*.

Discussion

The descriptions provided here, as well as the faunal list, demonstrate the unique character of the Deadhorse Coulee Member of the Milk River Formation. As initially noted by Fox (1968), this member preserves an assemblage distinct from those of the Campanian with several relictual or putatively ancestral taxa. The presence of *Myledaphus* sp., ?*Lepidotes*, solemydids, goniopholidids, *Gilchristosuchus palatinus*, *Alticonodon lindoei*, *Iqualadelphis lactea*, and *Apistodon exiguus* document this trend. However, the Milk River Formation also hosts some of the earliest occurrences of taxa that would later characterize North American assemblages. This can be seen in the early occurrences of Polyodontidae, *Melvius* sp., several teleost lineages, *Neurankylus*, tyrannosaurids, pachycephalosaurids, and several mammal families. This assemblage will be crucial in understanding the order and timing of faunal turnover in western North America.

Conclusion

This study further documents our knowledge of the fauna of the DCM, and provides a starting point for comparisons of assemblages in the Late Cretaceous of Alberta. In addition to the previously published occurrences, an additional 11 taxa are documented. As well, several previously published occurences have been confirmed and updated in accordance with our current understanding of diagnostic elements. Where diagnostic material is known, the DCM preserves a mostly unique assemblage of species. Higher level taxonomy indicates the presence of both older, relictual taxa, as well as younger, Campanian−Maastrichtian groups. Understanding the mechanism of a changing fauna will be an interesting topic that can be addressed in the future with the Milk River Formation providing a unique insight into the predecessor of the well-studied Campanian assemblages of Alberta.

Table 3-1. Taxa identified from the Deadhorse Coulee Member of the Milk River Formation. For identifications verified during the course of this study, specimen numbers of exemplar specimens are given in brackets.

Taxa	Material	Source (specimen)
Chondrichthyes		
Hybodontoidea		
Lonchidiidae		
Lonchidion sp.	teeth	Fox 1972a, this study (TMP 2008.090.0020)
Rhinobatoidei		
Family incertae sedis		
Myledaphus sp.	teeth, denticles, vertebrae	Russell 1935, Frampton 2006, this study (TMP 2008.090.0009)
Osteichthyes		
Polyodontidae		
Polyodontidae indet.	scales	this study (TMP 2008.093.0010)
Aspidorhynchidae		
Belonostomus sp.	scales	Fox 1972a, this study (UALVP52756)
Amiidae		
Amiinae		
Amiinae indet.	teeth, tooth plates, vertebrae	this study (TMP 2008.090.0019)
Vidalamiinae		
Melvius sp.	teeth, vertebrae	this study (ROM 56610)
Semionotidae		
?*Lepidotes* sp.	teeth, jaws	this study (TMP 2008.090.0018)

Lepisosteidae		
Lepisoteidae indet.	skull elements, vertebrae	this study (TMP 2000.001.0006)
Lepisosteus sp.	scales, teeth	Russell 1935, this study (TMP 2000.001.0001)
Gen. et sp.	scales	this study (TMP 2008.090.0022)
Teleostei		
Teleostei indet.	vertebrae	this study (TMP 2000.001.0028)
Elopiformes		
Albulidae		
Paralbula sp.	teeth	Fox 1972a, this study (TMP 2000.001.0042)
Esocoidei		
Esocidae		
Estesesox foxi	jaws	Wilson et al. 1992
Lissamphibia		
Allocaudata		
Albanerpetontidae		
Albanerpetontidae indet.	parietals, vertebrae	Gardner 2000, this study (TMP 2008.090.0056)
Albanerpeton galaktion	jaws, frontals	Fox and Naylor 1982
Albanerpeton nexuosus	jaws, frontals	Gardner 2000
Caudata		
Caudata indet.	jaws	Fox 1972a, this study (TMP 2008.091.0027)
Scapherpetontidae		
Scapherpeton tectum	atlantes	Fox 1972a, Gardner 2005
Batrachosauroididae		
Opisthotriton kayi II	atlantes	Gardner 2005
Gen. et sp. nov. B	atlantes, trunk vertebrae	Gardner 2005

Anura		
Anura indet.	jaws, skull elements	Fox 1972a, Gardner 2005, this study (TMP 2008.090.0054)
Reptilia		
Testudines		
Solemydidae		
Naomichelys sp.	shell fragments	Brinkman 2003, this study (CMN 52992)
Baenidae		
Neurankylus lithographicus sp. nov.	partial skull, partial shells	this study (TMP 2007.035.0045)
?*Boremys* sp.	shell fragments	Brinkman 2003
Plesiobaena sp.	partial shells	Brinkman 2003, this study (TMP 1994.377.0003)
Pleurosternidae		
?*Compsemys*	shell fragment	Brinkman 2003
Chelydridae		
Chelydridae indet.	shell fragments	Brinkman 2003
Trionychoidea		
Family incertae sedis		
?Kinosternoidea indet.	shell fragment	Brinkman pers. comm. (UALVP49045)
Adocidae		
Adocus sp.	shells	Brinkman 2003, this study (TMP 1992.069.0001)
Nanhsiungchelyidae		
Basilemys sp.	shell fragments	Russell 1935, Brinkman 2003
Trionychidae		
Trionychinae indet.	shell fragments	Brinkman 2003
Plastomeninae sp. nov.	partial shells	Head et al. 2009

Squamata		
Lacertilia		
Lacertilia indet.	osteoderms	this study (TMP 2008.091.0040)
Iguania		
Iguanidae		
Cnephasaurus locustivorus	maxillae	Gao and Fox 1996
Iguanidae gen. et sp. nov.	dentary, maxilla	Gao and Fox 1996
Scincomorpha		
Scincomorpha indet.	maxilla	Gao and Fox 1996
Teiidae		
Chamops sp.	dentary, maxillae	Gao and Fox 1996
Spenosaigon simplex	dentaries	Gao and Fox 1996
?*Glyptogenys ornata*	dentaries	Gao and Fox 1996
Scincidae		
Penemabuya antecessor	dentaries	Gao and Fox 1996
Aocnodromeus currugatus	dentaries	Gao and Fox 1996
Anguimorpha		
Xenosauridae		
Xenosauridae indet.	maxillae, premaxilla, jugals	Gao and Fox 1996
Anguidae		
Anguidae indet.	dentaries, maxillae, osteoderms	Gao and Fox 1996, this study (TMP 2008.090.0035)
Necrosauridae		
Necrosauridae gen. et sp. nov.	dentaries	Gao and Fox 1996
?*Parasaniwa* sp.	jaw fragments	Gao and Fox 1996
Serpentes		
Aniliidae		

Aniliidae indet.	vertebra	Fox 1975
Coniophis cf. *C. precedens*	vertebrae	Fox 1975
Choristodera		
Champsosauridae		
Champsosaurus sp.	vertebrae	Fox 1972a, this study (UALVP52757)
Crocodylomorpha		
Neosuchia		
Goniopholididae		
Goniopholididae indet.	teeth, skull elements, osteoderms	this study (UALVP52748)
Family incertae sedis		
Gilchristosuchus palatinus	partial skull, teeth, osteoderms	Wu and Brinkman 1993, this study (UALVP52749)
Eusuchia		
Family incertae sedis		
Eusuchia indet.	teeth, osteoderms	this study (TMP 2000.001.0003)
Ornithischia		
Ankylosauria		
Ankylosauridae		
Ankylosauridae indet.	teeth	Baszio 1997b, this study (TMP 2000.001.0041 part)
Nodosauridae		
Nodosauridae indet.	teeth	Baszio 1997b, this study (TMP 2000.001.0041 part)
Ornithopoda		
Family incertae sedis		
Ornithopoda indet.	teeth	this study (UALVP52752)
Hadrosauridae		
Hadrosauridae indet.	teeth, skull elements, postcrania	Russell 1935, this study (TMP 2008.090.0038)

Marginocephalia		
Pachycephalosauridae		
Pachycephalosauridae gen. et sp. nov.	frontoparietal domes, teeth	Russell 1964, Sullivan 2003, Baszio 1997b, this study (TMP 2008.045.0001)
Leptoceratopsidae		
Leptoceratopsidae indet.	teeth, dentary	Baszio 1997b, this study (TMP 2000.001.0025)
Ceratopsidae		
Ceratopsidae indet.	teeth, postcrania	Russell 1935, this study (TMP 2008.090.0037)
Saurischia		
Ornithomimidae	phalanges	Russell 1935
Tyrannosauridae		
Tyrannosauridae indet.	teeth	Baszio 1997b, Larson 2008
Dromaeosauridae		
Dromaeosauridae indet.	teeth	Larson 2008
Dromaeosaurinae		
Dromaeosaurinae indet.	teeth	Larson 2008
cf. *Zapsalis* sp.	teeth	this study (UALVP49582)
Saurornitholestinae		
Saurornitholestinae indet.	teeth	Larson 2008
Troodontidae		
cf. *Paronychodon lacustris*	teeth	Baszio 1997b, Larson 2008
Family incertae sedis		
cf. *Richardoestesia gilmorei*	teeth	Baszio 1997b, Larson 2008
cf. *Richardoestesia isosceles*	teeth	Larson 2008
Aves		
cf. Aves indet.	teeth	Larson 2008

Mammalia		
Triconodonta		
Triconodontidae		
Alticonodon lindoei	dentary fragment with molars, molar	Fox 1969
Multituberculata		
Ptilodontoidea		
Ectypodontidae		
Mesodma senecta	premolars	Fox 1971b
?*Mesodma* sp.	molar	Fox 1971b
Paracimexomys magister	premolars, molar	Fox 1971b, Lillegraven and McKenna 1986
Cimexomys antiquus	premolars, molar	Fox 1971b
Ptilodontidae		
Cimolodon electus	premolars, molars	Fox 1971b
Cimolodon similis	premolars, molars	Fox 1971b
Cimolodon sp.	molars	Fox pers. comm.
Taeniolabidoidea		
Cimolomyidae		
Cimolomys sp. nov. A	premolars, molars	Fox 1971b
Cimolomys sp. nov. B	premolars	Fox 1971b
Meniscoessus ferox	premolar	Fox 1971b
Family incertae sedis		
Viridomys orbatus	premolars	Fox 1971b
Theria		
Spalacotheriidae		
Symmetrodontoides canadensis	dentary fragment with molars	Fox 1976
?Tinodontidae		
Mictodon simpsoni	molar	Fox 1984b

Family incertae sedis		
Potamotelses aquilensis	molars	Fox 1972a
Picopsis pattersoni	molars	Fox 1980
cf. *Picopsis* sp.	molars	Fox 1980
Metatheria		
Family incertae sedis		
Apistodon exiguus	molars	Fox 1971a, Davis 2007
Iqualadelphis lactea	molars, maxilla with molars	Fox 1987, Johanson 1993
Varalphadon creber	molars	Fox 1971a, Johanson 1996
Varalphadon wahweapensis	molars	Johanson 1996
"Alphadontidae"		
Turgidodon nov. sp.	molars	Fox 1971a, Cifelli 1990
Turgidodon sp.	molars	Fox 1979, Cifelli 1990
Albertatherium primus	molars	Fox 1971a
Albertatherium secundus	molars	Johanson 1994
Stagodontidae		
Eodelphis sp.	molars	Fox 1971a
Aquildelphidae		
Aquiladelphis incus	molars	Fox 1971a
Aquiladelphis minor	molars	Fox 1971a
Eutheria		
Nyctitheriidae		
Paranyctoides maleficus	dentary with molars	Fox 1984a
?*Paranyctoides* sp.	molars	Fox 1972a; Fox pers. comm.

Fig. 3-1. *Lonchidion* sp. indet. tooth. A) labial view, and B) occlusal view. TMP 2008.090.0020.

Fig. 3-2. *Myledaphus* sp. teeth. A) hexagonal tooth (UALVP52746), B) symphysial tooth (TMP 2008.090.0001), C) indistinct rhombic tooth (TMP 2008.090.0002), D) distinct rhombic tooth (TMP 2008.090.0004), E) transitional tooth (TMP 2008.090.0005), F) lateral tooth (TMP 2008.090.0006), G) tooth with pronounced ridge (TMP 2008. 094.0001), H) vertebra (TMP 2008.090.0003), I) denticle (TMP 2008.090.0007), and J) possible denticles (TMP 2008.090.0008). Tooth forms A−F after Frampton (2006). Scale bars represent 1 mm.

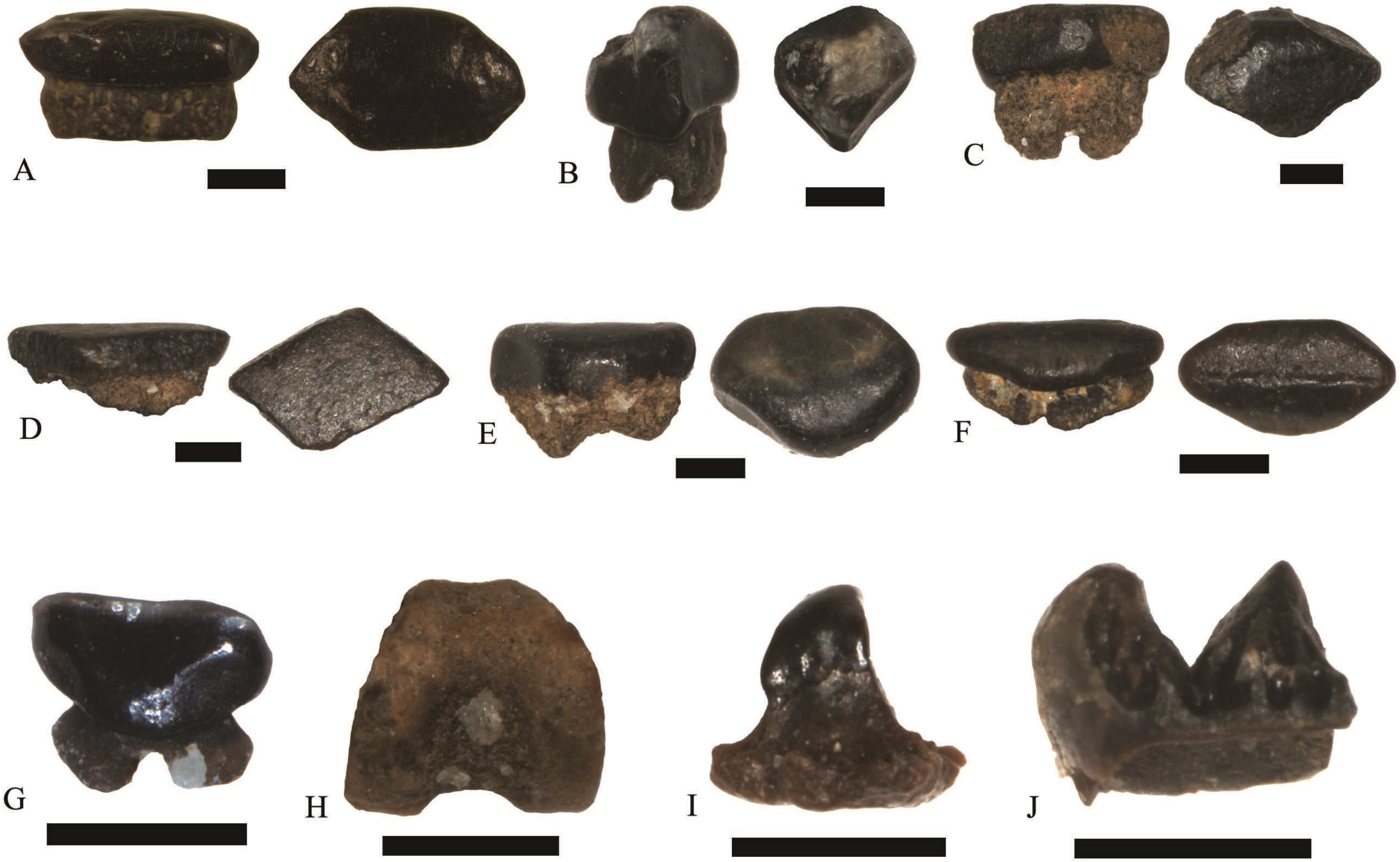
A
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Fig. 3-3. Polyodontidae scale. TMP 2008.093.0010. A) external view, and B) internal view.

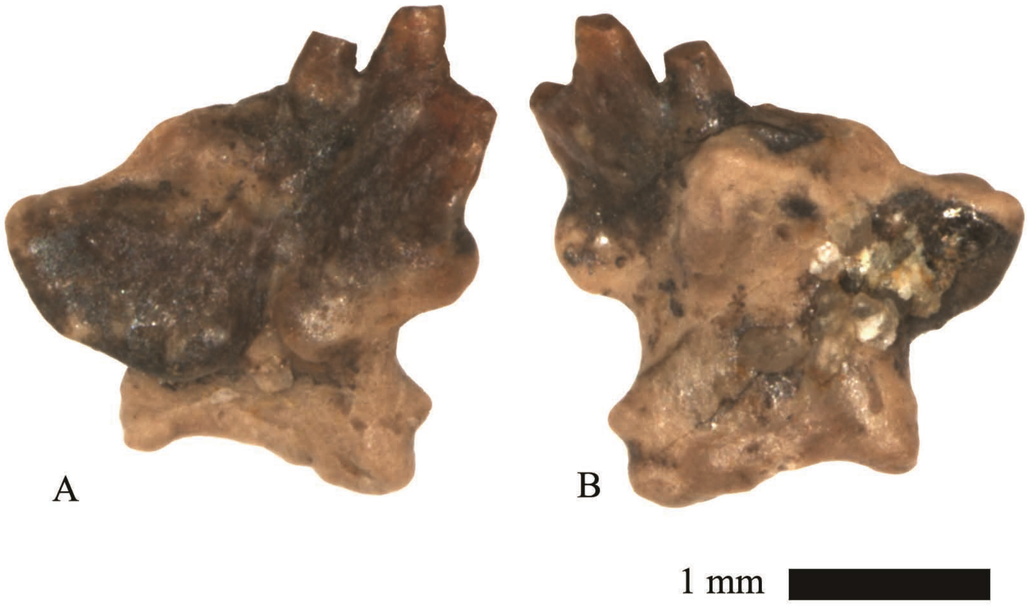


Fig. 3-4. Vidalamiinae remains. A) *Melvius* sp. vertebra, ROM 56610, B−C) Vidalamiinae tooth B) labial view, and C) lingual view, TMP 2008.091.0001.

Fig. 3-5. Holostean A scale. TMP 2008.090.0022.

Fig. 3-6. Milk River cf. *Naomichelys* sp., A) CMN 52992, complete right xiphiplastron, B) UALVP45552, peripheral, and partial costals and suprapygal.

Fig. 3-7. Goniopholididae A) osteoderm, UALVP52747, B) tooth crown, UALVP52748, C) skull fragments, ROM 56648.

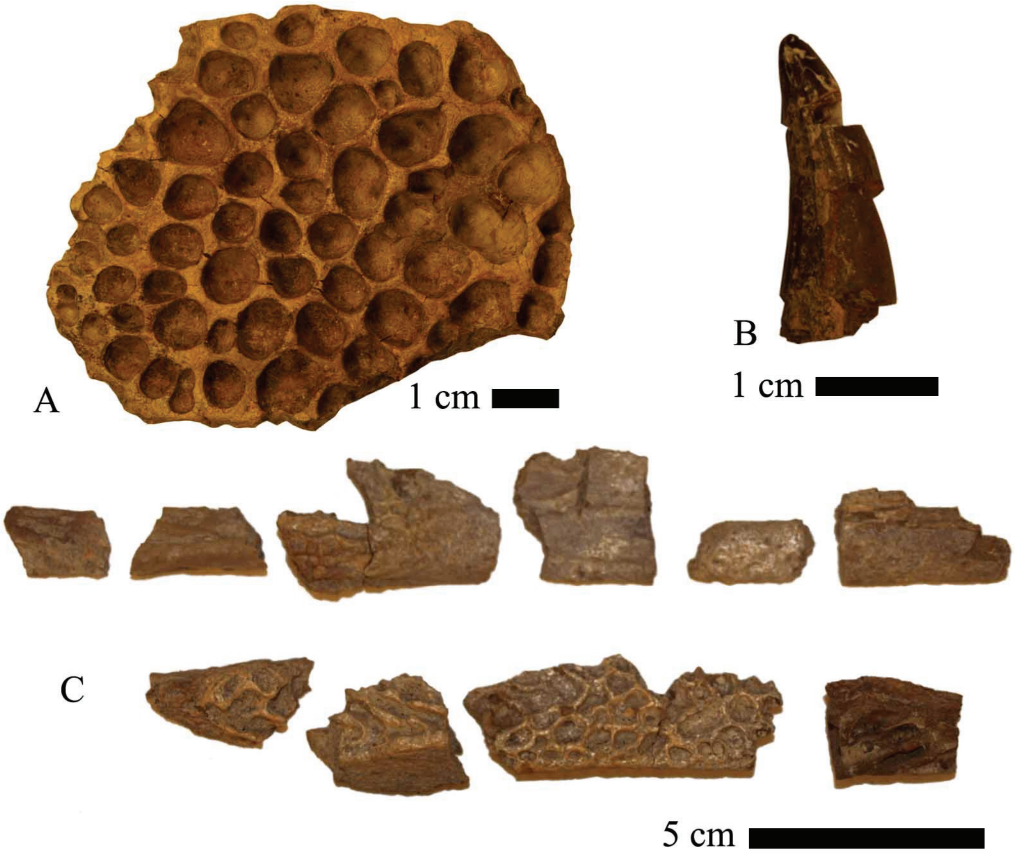


Fig. 3-8. cf. *Gilchristosuchus palatinus* A) bulbous morph (UALVP52749), B) pointed morph (UALVP52750), C) osteoderm (UALVP52751).

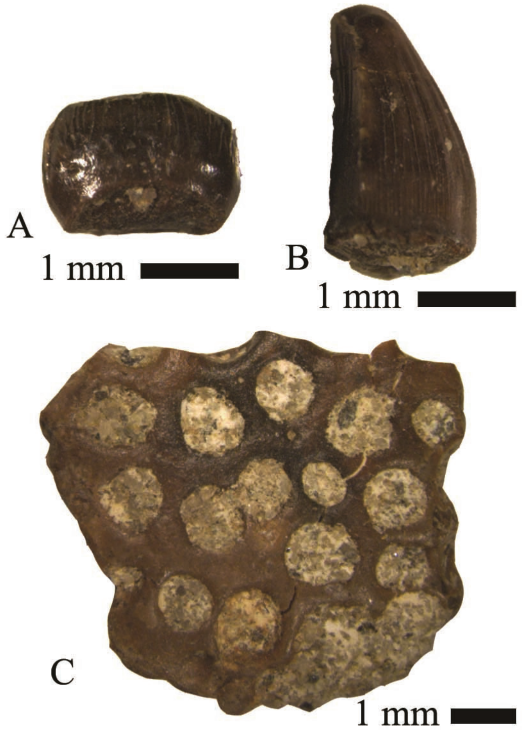
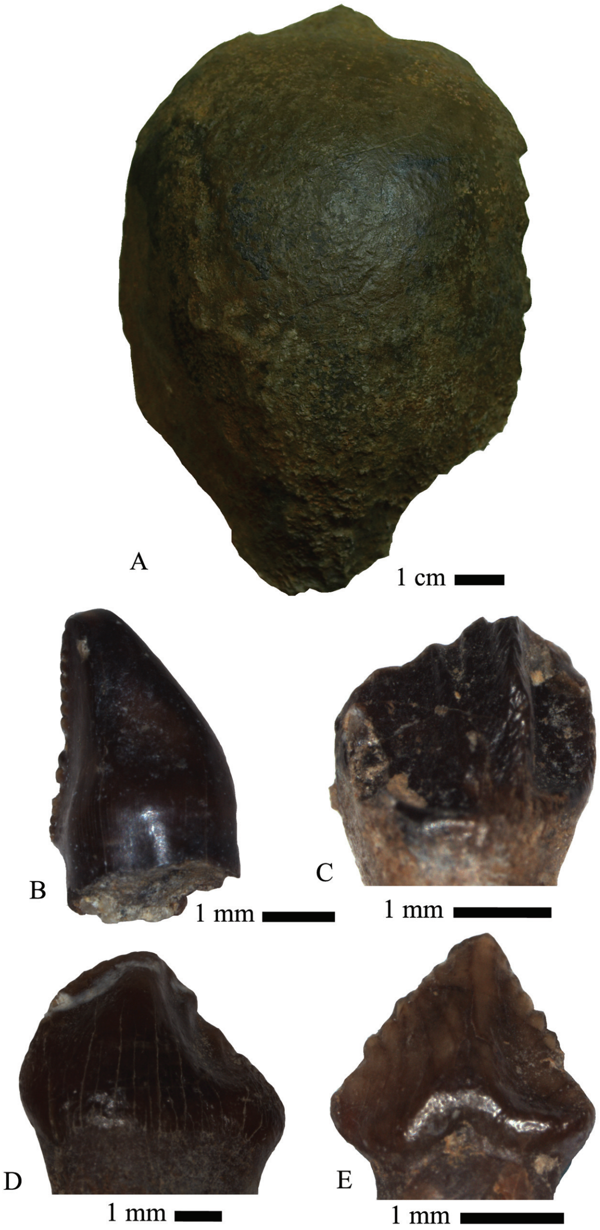


Fig. 3-9. Tooth crown from an indeterminate ornithopod. UALVP52752.

Fig. 3-10. Remains of Pachycephalosauridae gen. et sp. nov. A) frontoparietal dome, TMP 2008.045.0001, B) putative premaxillary tooth, UALVP 50634, C) putative maxillary tooth, UALVP52753, D) putative mesial dentary tooth, UALVP52754, and E) putative distal dentary tooth, UALVP52755.



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Chapter 4 — A new species of *Neurankylus* from the Milk River Formation (Cretaceous: Santonian), Alberta, and a revision of *N. eximius*[1]

Introduction

During the Late Cretaceous, North America hosted a remarkably diverse fauna of turtles. This fauna included a number of taxa that are familiar today, including softshell turtles (Trionychidae) and snapping turtles (Chelydridae). However, it also included a number of extinct families, including the terrestrial Nanhsiungchelyidae, and the aquatic Solemydidae, Adocidae, and Baenidae (Brinkman 2003, 2005; Holroyd and Hutchison 2002). The Baenidae are medium-to-large freshwater turtles that are characterized by fusion of the elements of the carapace and plastron, thick shells, and adaptation of the jaws for crushing (Gaffney 1972; Gaffney and Meylan 1988; Joyce 2007). Baenids were endemic to North America and formed a major part of North America’s aquatic fauna from the Cretaceous through the Paleogene. Although the derived baenid taxa, the Baenodda (phylogenetically defined as all baenines more closely related to *Baena arenosa* than *Hayemys latifrons*; Gaffney 1972), are well-represented from the

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[1] A version of this chapter has been submitted for publication. Larson, D.W., Longrich, N.L., Evans, D.C, and Ryan, M.J. A new species of *Neurankylus* from the Milk River Formation (Cretaceous: Santonian), Alberta, and a revision of *N. eximius* Vertebrate Paleobiology and Paleoanthropology Book Series. Springer Publishing. D.L. contributed to analyses, writing, and figures 1, 2, 4, 5, and 6. N.L. contributed to editing, and figures 1 and 3. D.E. and M.R. expended resources for the collection of the specimens and contributed to editing.

Campanian through Eocene in North America (Gaffney 1972; Sullivan et al. 1988; Brinkman 2003, 2005; Holroyd and Hutchison 2002; Hutchison and Holroyd 2003; Lyson and Joyce 2009a, 2009b, 2010), comparatively little is known about the earlier and more basal members of the group.

Neurankylus eximius Lambe, 1902, was named from a partial carapace of a juvenile individual collected from the Campanian Belly River Group along the Red Deer River of Alberta. A partial skull from the Dinosaur Park Formation, likely the same formation that produced the type, was subsequently referred to this species (Brinkman and Nicholls 1993). Since its initial description, additional material has increased the known occurrences of the genus from Campanian through Danian time, ranging from southern Alberta to New Mexico (Hutchison and Archibald 1986; Sullivan et al. 1988; Holroyd and Hutchison 2002; Hutchison and Holroyd 2003).

Gilmore (1916) erected a second species of *Neurankylus*, *N. baueri*, from the Fruitland and Kirtland formations, which was subsequently subsumed under *N. eximius* by Gaffney (1972). However, Sullivan and Lucus (2006) continued to recognize *N. baueri* as distinct on the basis of its shorter and wider first suprapygal and the coincidence of its posterior costal and posterior neural sutures. Gilmore (1919) erected *N. wyomingensis* on material collected from Wyoming, though this taxon was regarded a nomen dubium by Gaffney (1972). However, it too appears to possess a unique combination of features as revealed from the description and figures, and has been included in the phylogentic analysis. These three species are currently the only formally named species of *Neurankylus*.

Brinkman (2003) was the first to recognize *Neurankylus* from the Santonian stage on the basis of material recovered from the Milk River Formation. He regarded these specimens as distinct from *N. eximius* based on smaller shell size and a proportionately longer, more squared posterior lobe of the plastron, but did not name the taxon due to the fragmentary nature of the material available at the time. Here, a description is provided for recently collected material of *Neurankylus* from the Milk River Formation of southern Alberta. The two new specimens, an almost complete shell and a partial skull, confirm that this material represents a new species, which is here described and named *Neurankylus lithographicus*, sp. nov. In an effort to put this new taxon into its evolutionary context, the phylogeny of baenid turtles is revised.

Systematic Palaeontology

Order Testudines Linnaeus 1758

Parvorder Paracryptodira Gaffney 1975

Superfamily Baenoidea Williams 1950

Family Baenidae Cope 1882

Subfamily Neurankylinae Williams 1950

Genus *Neurankylus* Lambe 1902

Type species — *Neurankylus eximius*.

Revised diagnosis —Large relative to other baenid turtles (carapace averaging 500–600 mm long, skull more than 74 mm long in adult individuals); dorsolateral gutters along the posterolateral peripherals of the carapace; shell ornamentation consisting of subtle parallel ridges and fine, low-density pitting; foramen stapediotemporale bordered by the opisthotic, quadrate, and prootic, but not the supraoccipital; posteriorly rounded short supraoccipital ridge consisting of only the paired parietals in dorsal view.

Discussion — Some of the characters listed as diagnostic for the genus may, in fact, be diagnostic for a more inclusive Neurankylinae (here defined as all baenids closer to *Neurankylus eximius* than to *Baena arenosa* or *Trinitichelys hiatti*), such as the position of the foramen stapediotemporale, also seen in *Arundelemys dardeni* (Lipka et al. 2006). However, such conclusions are hampered by the incomplete nature of described material (Lipka et al. 2006) and a general paucity of known basal baenids. *Neurankylus wyomingensis*, known only from the posterior portion of a single shell, may not be referable to the genus *Neurankylus* based on the above diagnosis, although the known material is insufficient for diagnosis of a distinct genus. The ornamentation of this species, which consists of small nodes with shallow anastomosing channels, is distinct (more primitive) from that in other *Neurankylus* species, but the species does share large size and dorsolateral gutters with *Neurankylus*.

In addition to the diagnostic characters, many basal paracryptodire characters can be used in differentiating the genus *Neurankylus* from other Late Cretaceous baenids. Members of this genus also have primitively wide vertebral scutes bordered posteriorly by marginal scutes, and a lack of deep anterior emargination. The plastron is primitive in the roughly parallel anterior free borders, intergular scutes separating the gulars, and an anal scute that seldom overlaps the hypoplastron. The skull has prefrontals with large dorsal lappets.

Phylogenetically, the genus can be defined as a stem-based clade whose members are more closely related to *Neurankylus eximius* than to *Arundelemys dardeni*, *Trinitichelys hiatti*, or *Thescelus insiliens*. Morphologic differences between identified species of *Neurankylus* are subtle, but among the most useful appears to be the scute morphology on the anterior lobes of the plastra (Fig. 4-1). Specimens referred to *N. eximius* have been documented from Paleocene deposits in Montana and New Mexico (Hutchison and Archibald 1986; Sullivan et al. 1988); however, these specimens have neither been illustrated nor described in sufficient detail to permit comparison. Based on the descriptions, referral to *Neurankylus* is here accepted, although the species designation remains doubtful.

Neurankylus eximius Lamb 1902

Type specimen — CMN 1504, partial carapace including left costals 3, 5-9, right costals 3, 4, neural 8 (fused to first suprapygal), and both suprapygals.

Occurrence — Dinosaur Park Formation (?), Dinosaur Provincial Park, Alberta, Canada; Judith River Formation, Montana. The type comes from the Belly River Group, but there is no information as to whether it comes from the Dinosaur Park Formation or the underlying Oldman Formation. Given that the Dinosaur Park Formation is more fossiliferous, outcrops over a larger area, and that collecting has tended to focus on this formation, the specimen is probably from the Dinosaur Park Formation. The Dinosaur Park Formation is late Campanian in age (Eberth 2005).

Synonomies — *Charitemys captans* Hay 1908, pp. 98−100, figs. 93−95; *Baena fluviatilis* Parks 1933, pp. 19−25, figs. 1, 2, pl. 7.

Referred material (based on synapomorphies) — AMNH 6098, type of *Charitemys captans*, fragmentary skull, carapace, and plastron from the Judith River Formation of Montana; ROM 854, type of *Baena fluviatilis*, partial carapace and plastron probably from the Dinosaur Park Formation of Alberta; ROM 1943, complete carapace and plastron from the Dinosaur Park Formation of Alberta; TMP 1989.036.0112, anterior portion of anterior plastral lobe from the Dinosaur Park Formation of Alberta; TMP 1999.055.0134, complete carapace and plastron from the Dinosaur Park Formation of Alberta; TMP 2003.012.0171, complete carapace and plastron from the Dinosaur Park Formation of Alberta; UALVP 30824, partial skull including much of skull roof and braincase from the Dinosaur Park Formation of Alberta.

Revised diagnosis — *Neurankylus eximius* is here rediagnosed on the basis of the following autapomorphies: posterior neurals hexagonal with short sides anterior, eighth neural and first suprapygal fused (even in the lack of such fusion in other elements of the carapace) with coincidence of fourth-fifth vertebral scute sulcus along this fusion, fifth vertebral wider than second suprapygal, plastron length exceeding carapace width, intergulars only barely separating gulars with virtually no shared sulcus with humerals, and sigmoid intergular-gular sulcus oriented anterolaterally to posteromedially, creating heart shape (Figs. 4-1, 4-2). *N. eximius* differs from *N. baueri*, *N. lithographicus*, and the Lance *Neurankylus* in that the anterior margin of the carapace is squared off, the posterior margin of carapace smooth and not scalloped as in *N. wyomingensis*, and the carapace possesses a dorsal median keel as in *N. baueri*. The skull differs from that of *N. lithographicus* in being wedge-shaped, with the opisthotic posterior width exceeding 1.5 times the dorsoventral height, the stapedial foramen more than half of the anteroposterior length of the otic region away from the quadrate-squamosal suture, and the foramen nervi hypoglossi directed posteriorly.

Discussion — *Neurankylus eximius* is recognized in the current study only on the basis of material recovered from middle-Upper Campanian strata of Alberta and Montana. The presence of a dorsal median keel on the carapace, although noted to be polymorphic for the species (Gaffney 1972), is present on all known material of *N. eximius* sensu stricto, and on specimens of *N. baueri* (Gilmore 1916). All of the known Dinosaur Park Formation material lacks a scalloped posterior margin of the carapace. Other features thought to be variable within the species, such as the scute morphology on the anterior lobe of the plastron (Gaffney 1972), upon investigation, occur only in specimens from the Dinosaur Park and Judith River formations, illustrating the distinctiveness of this species. Referral of AMNH 6098 to *N. eximius* (Gaffney 1972) is accepted here, although the fragmentary nature of the material restricts comparison to only portions of the shell. The diagnostic value of the skull of *N. eximius*, and thereby the diagnosis of the entire genus, is hampered by the fragmentary preservation of the only described cranial specimens. Although most of the skull roof, braincase, and otic regions are preserved, large proportions of the facial region remain unknown. It is also unknown whether or not a squamosal-parietal contact is present. However, further preparation of UALVP 30824 after its initial description reveals the true ventral extent of the quadrates and mandibular condyles (Fig. 4-5). The mandibular condyles are comparable in relative size to those of most other baenids with the exception of *Palatobaena* (Lyson and Joyce 2009).

Neurankylus lithographicus, species novum

Holotype — TMP 2007.035.0045, nearly complete carapace and plastron.

Type occurrence — Deadhorse Coulee Member of the Milk River Formation (latest Santonian), 26.5 m above the Virgelle Member contact, 1.5 km east of

Writing-On-Stone Provincial Park, Alberta, Canada. Detailed locality information on file at the TMP.

Synonomies — *Neurankylus* sp. (Brinkman 2003, pp. 560, 561).

Provisionally referred material — TMP 1991.113.0001, fragmentary carapace and plastron; TMP 1994.377.0001, carapace fragment; TMP 1998.102.0014, carapace fragment and skull fragment including portions of basioccipital, basisphenoid, pterygoids, and palatines; TMP 2007.036.0001, partial skull, including portions of pterygoid, basisphenoid, basioccipital, exoccipital, opisthotic, prootic, quadrate, and squamosal.

Etymology — Specific epithet derived from Greek *lithos*, stone, and Greek *graphikos*, of writing, referring to Writing-On-Stone Provincial Park, the closest major landmark to the locality.

Diagnosis —Autapomorphies: intergular scutes larger than gular scutes; distinctly first marginal scutes medially narrowing; first-second costal sutures greatly anterolaterally directed such that the angle between the suture and the anterior midline of the shell is less than 70°; anterior rim of the carapace thickened.

Description — TMP 2007.035.0045 (Figs. 4-3, 4-4) and TMP 2007.036.0001 (Fig. 4-5), together with other referred material from the Milk River Formation, preserve a morphology distinct from all published descriptions and illustrations of *Neurankylus*. The species displays a unique combination of features, some of which are present in various other specimens referred to *Neurankylus*. The shell

(Figs. 4-3, 4-4) is referred to the genus *Neurankylus* based on wide vertebral scutes bordered posteriorly by marginal scutes, a lack of deep anterior emargination, dorsolateral gutters along the lateral peripherals, intergular scutes separating the gulars, and an anal scute that does not overlap the hypoplastron. All elements exhibit the large size typical of the genus. *Neurankylus lithographicus* possesses a dorsoventrally thickened anterior rim of the carapace relative to the overall thickness of the carapace. The anterior rim of the carapace is also anteriorly tapered and resembles that of *N. baueri* and the Lance *Neurankylus*, contrasting with the broader shell *N. eximius*. As well, the fourth marginal scute widens posteriorly, again resembling the state in *N. baueri* and not *N. eximius*, in which the scute widens halfway along its length. The first marginal scute narrows rapidly medially, producing a first vertebral scute with a medial anterior projection, an autapomorphy of the species. The posterior rim of the carapace, from what is preserved, does not appear to be scalloped, similar to *N. eximius* but not *N. baueri*. On the anterior lobe of the plastron, the intergular surface area is larger than the gular surface area, and the intergular-gular sulcus is straight and oriented anteroposteriorly. Like other non-baenine paracryptodires, the gular scutes are completely separated from each other by the intergulars. However, unlike in *N. eximius*, these intergulars are not heart-shaped with restricted contact with the humeral scutes. The holotype (TMP 2007.035.045) carapace has a reconstructed width of 472 mm and an estimated length of 623 mm. The anterior lobe of the plastron has a median length of 115 mm and a bridge length of 204 mm. The plastron is not complete posteriorly; however, plastron length is estimated to be 450 mm (based on the preservation of the femoral-anal sulcus), which is less than the carapace width, unlike *N. eximius*, but similar to other specimens of *Neurankylus* for which measurements are known. Most of the characters mentioned by Brinkman (2003) to differentiate the species, namely a smaller shell size and a more squared off posterior lobe of the plastron, do not serve to diagnose the species. TMP 2007.035.0045 has an estimated length comparable to referred shells of *N. eximius* and the type and referred material of *N. baueri*, and the taper of the posterior lobe appears similar to that of *N. baueri*, and more tapered than that of *N. eximius*. However, based on the preserved portion of the posterior lobe, which preserves a complete femoral-anal sulcus, the lobe appears to have been longer relative to the bridge in *N. lithographicus* than that in *N. eximius* or *N. baueri*.

The skull (Fig. 4-5) is identified as *Neurankylus* based on the foramen stapediotemporale bordered by the opisthotic, quadrate, and prootic, but not the supraoccipital, the relatively large size, and the presence of the foramen posterius canalis caroticum internus along the basisphenoid-pterygoid suture. In the skull, the mediolateral width of opisthotic is less than 1.5 times the dorsoventral height of the element. The foramen stapediotemporale is less than half of the anteroposterior length of the otic region away from the quadrate-squamosal suture. As well, the foramen nervi hypoglossi is directed posterolaterally and is not visible in posterior view. All of the cranial characters indicate a more elongate skull, unlike the wedge-shaped skull typical of most other baenids, including *Neurankylus eximius* (Fig. 4-5), but more similar to the condition seen in

Arundelemys dardeni (Lipka et al. 2006). The skull characters mentioned are likely primitive for the genus, but due to a paucity of comparable material, this is not known.

Discussion — Both the holotype, TMP 2007.035.0045, and TMP 2007.036.0001 were found at a similar stratigraphic level (roughly 26.5 m above the base of the Deadhorse Coulee Member) 185 metres apart. The specimens both possess autapomorphies of *Neurankylus*, and are provisionally regarded as belonging to the same species on the basis of provenance. TMP 1991.113.0001 is estimated to have been deposited roughly 8.0 m above the base of the Deadhorse Coulee Member in Verdigris Coulee, making it the farthest west and lowest known occurrence of this taxon. Other more fragmentary specimens have less precise stratigraphic data, but all occur within the Deadhorse Coulee Member east of Milk River, and are referred to this species largely because of provenance.

In many shell characters, such the morphology of the intergular scutes and fourth marginals, the shape of the carapace, and relative size of the plastron, *N. lithographicus* more closely resembles the shells of later and more southern taxa, such as *N. baueri* and the Lance *Neurankylus*, although neither of these taxa have described skull material, or, in the case of the Lance form, a preserved anterior lobe of the plastron. All three of these taxa appear markedly different from the morphology exhibited in the type species, *N. eximius*.

Phylogenetic analysis

To assess the systematic position of species of *Neurankylus*, maximum parsimony and Bayesian phylogenetic analyses were conducted based on a modified baenid character-taxon matrix of Lyson and Joyce (2009). Thirty-four characters and 12 taxa were added to the matrix, two characters were deleted, and three were modified or rescored (Appendix 1). Fifteen characters represented sequential or continuously variable morphological series and were treated as ordered in the parsimony analysis. Phylogenetically uninformative characters used in the Bayesian analysis were also removed for the parsimony analysis. For the purposes of this analysis, seven operational taxonomic units of *Neurankylus* with the best morphological data were included: *N. eximius*, *N. baueri*, *N. wyomingensis*, *N. lithographicus*, an unkeeled Fruitland specimen (ROM 864), two Ojo Alamo specimens, and a Lance specimen (Appendix 2). Specimens from the Hell Creek, Tullock, and Nacimiento formations referred to the genus were not examined and could not be coded from the literature. It is possible that the states coded for *Dorsetochelys delairi*, *Thescelus insiliens*, and the Ojo Alamo taxon represent chimeric taxa; however, this combination of character states is justified by comments from previous authors (Milner 2004; Lyson & Joyce 2010) and the fact that separation of specimens in these taxa does not result in changes to tree topology. The unnamed specimens that have been referred to *Neurankylus* may represent distinct species, but these specimens have not been systematically described or studied in detail by the authors.

The maximum parsimony analysis using the modified character matrix (Appendix 3) was conducted in PAUP* 4.0b10 (Swofford 2001). A heuristic search with 1000 random sequence addition replicates and tree-bisection reconnection (TBR) swapping produced 102 most parsimonious trees of 298 steps, and the majority rule consensus of these trees can be seen in Fig. 4-6b. Each tree had a CI (consistency index) of 0.413, RI (retention index) of 0.639, and an RC (rescaled consistency index) of 0.264. To evaluate support, a bootstrap analysis was performed. The bootstrap consisted of 10 000 bootstrap replicates using a 100 random sequence addition replicates heuristic search and TBR swapping.

The Bayesian analysis was conducted in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003) with default priors. Two runs of four Markov Chains were run for 1 x 10^6 generations and sampled every 100 generations. Burn-in was determined by noting when cold chain probabilities stopped increasing sharply in both runs. In this case, the first 2000 generations (20 samples) were discarded as burn-in. The results of the analysis are presented in Fig. 4-6c.

Similarities in topologies calculated from different search methods suggest a robust phylogenetic signal in the dataset (Brooks et al. 2007). A preferred topology was constructed using the Bayesian analysis and (in one instance) stratigraphic consistency to evaluate the topologies in the most-parsimonious trees (Fig. 4-6a). Constraining the parsimony analysis to topologies supported by the Bayesian analysis yielded only 56 most-parsimonious trees, 24 of which placed *N.*

eximius as the most basal member of *Neurankylus*, excluding *N. wyomingensis*, whereas 16 trees placed *N. lithographicus* and the Lance *Neurankylus* in this position. Due to the stratigraphic provenance of *N. lithographicus* as the second-earliest species, and because all of the most parsimonious trees are, naturally, equally parsimonious, topologies with *N. lithographicus* in a basal position are preferred. The figured topology (Fig. 4-6a) is a strict consensus of these 16 topologies. It is similar to the second maximum posterior probability tree in the Bayesian analysis, and represents the best available hypothesis of relationships between the species of *Neurankylus*, pending the description of more complete material.

Dorsetochelys delairi, which has been placed as a sister taxon to the Paracryptodira (Joyce 2007), is here found to be closely associated with pleurosternids. As this species does not possess the single apomorphy known for Family Pleurosternidae (a basisphenoid-palatine contact) inclusion in this family is not supported. However, a similar maximum parsimony analysis including the taxon *Kallokibotion bajajidi* as an outgroup (not shown) placed *Dorsetochelys delairi* closer to the pleurosternids than to the baenids. In the Bayesian analysis, *Dinochelys whitei* was found in a polytomy with *Dorsetochelys delairi* at the base of Baenidae, although this may be attributable to the large amount of missing data coded for *Dinochelys whitei*.

The placement of "*Dorsetochelys*" *buzzops* with *Uluops uluops* as basal baenids with a sister-group relationship to those taxa traditionally known as baenids was unexpected, although this finding is similar to the relationships initially proposed by Carpenter and Bakker (1990) and Bakker (1998). Another novel taxon placement is that of *Arundelemys dardeni* as sister to *Neurankylus* within the Neurankylinae. A previous analysis of this taxon (Lipka 2006) placed it as the sister group to Baenoidea (sensu Williams 1950: combined Baenidae and Pleurosternidae) within a more inclusive Paracryptodira. This placement seems to result from the unique configuration of elements around the foramen stapiotemporale, excluding the supraoccipital and including the opisthotic.

Neurankylus was supported as a monophyletic clade with low Bayesian posterior probability support, although this and other basal nodes were better supported when *N. wyomingensis* (a specimen consisting of only the posterior portion of the shell examined only from figures) was pruned from the analysis. The basal-most member of the genus (and also the oldest) is *N. wyomingensis*. *N. lithographicus*, the second oldest member of the genus, is placed as the sister taxon to the Lance specimen, which is also supported in the Bayesian analysis. Assuming that the *N. lithographicus*-Lance specimen grouping is basal to the remainder of *Neurankylus* species due to the stratigraphic provenance of *N. lithographicus*, the other species form a monophyletic clade with ROM 864 from the Fruitland Formation at its base. The last three taxa, *N. eximius*, *N. baueri*, and the Ojo Alamo specimens, form a polytomy, with both *N. eximius* and *N. baueri* being most closely related to the Ojo Alamo specimens in 50% of the remaining most-parsimonious trees.

Trinitichelys hiatti, in this analysis, as in Brinkman and Nicholls (1993) but unlike Lyson and Joyce (2009b, 2010), is found to be more closely related to the Baeninae, and this is supported by moderate Bayesian support. As in other analyses (Joyce 2007; Lyson and Joyce 2009a, b), the Baeninae and the Baenodda are well-supported in both bootstrap and Bayesian analyses. *Thescelus insiliens*, here including *Hayemys latifrons* (Lyson & Joyce 2010), was well-supported as the basal-most baenine, unlike in the classification of Holroyd and Hutchison (2002), which treated *Hayemys latifrons* as a neurankyline. The latter position was not supported in the current study, and even when these two taxa were separated in the parsimony analysis, *Hayemys latifrons* and *Thescelus insiliens* occupied the same position in the cladogram.

Discussion and implications

A reevaluation of *Neurankylus eximius* reveals numerous characters specific only to the type material and other specimens from the Dinosaur Park Formation of Alberta and the Judith River Formation of Montana, and absent in all other known specimens of *Neurankylus*. Thus, all known specimens of *N. eximius* are known exclusively from the mid Campanian of Alberta and Montana. *N. lithographicus* is represented by specimens exclusively from the latest Santonian Deadhorse Coulee Member of the Milk River Formation. It is interesting that closer examination of this genus reveals differences in the biogeographic distributions of some of the species (*N. eximius* and *N. baueri*, for example), with penecontemporaneous specimens from different regions yielding consistent differences in morphology. As well, similarities in temporally disjunct specimens in spatially similar localities (*N. baueri* and Ojo Alamo specimens, *N. lithographicus* and the Lance specimen) indicate strong paleobiogeographic partitioning of these species. This implies that closer studies of turtles are likely to show complex biogeographic, biostratigraphic, and evolutionary patterns. These patterns may eventually help elucidate distribution pathways and patterns of extinction in the vertebrate fossil record of North America.

Neurankylus lithographicus, along with other specimens that are poorly known (most often regarded as nomina dubia) or whose phylogenetic relationships remain poorly resolved, serves to fill in the ghost lineage between the well-known mid-Campanian baenids and their purported sistergroup, the pleurosternids (Fig. 6a). *Trinitichelys hiatti* is known from one specimen whose age can be newly interpolated as about 105.6 Ma (Jacobs et al. 1991; Gradstein et al. 2004). Interpolating the age of “*Glyptops*” *pervicax*, which may be conspecific with *T. hiatti* (Ostrom 1970), from the Cloverly Formation of Montana, yields an age of at least 101.6 Ma. *Neurankylus wyomingensis*, reported from the Colorado shale near Cody, Wyoming, was likely recovered from the Cody Shale of current usage, which in that region contains the biostratigraphic zones of *Scaphites ventricosus* and *Schaphites depressus* (Dyman et al. 1997), giving a conservative age estimate of middle to late Coniacian (87.88–85.85 Ma; Gradstein et al. 2004). *Arundelemys dardeni*, here hypothesized to be a basal neurankyline, occurs in the Arundel Clay facies of the Potomac Group, which was dated to middle Aptian by palynological biostratigraphy (Doyle 1992). The middle Aptian was dated by Ogg et al. (2004) to range from 115–121 Ma, pre-dating the age estimate of *T. hiatti*.

The placement of *Neurankylus wyomingensis* as the basal-most *Neurankylus*, and *Trinitichelys hiatti* as the basal-most member of the lineage leading to the Baenodda, suggests that both lineages independently lost the coarse shell ornamentation. Also, the presence of narrow-skulled species in both lineages (*N. lithographicus* and *T. hiatti*, respectively), as well as the basal occurrence of "*D.*" *buzzops* and *U. uluops*, indicates that the evolution of broad skulls within the Baenidae may have several different origins. It also indicates a certain degree of parallelism between the Neurankylinae and the lineage leading to the Baeninae.

The convergent evolution of derived baenid characters of these two lineages has implications for defining the Family Baenidae. Previous analyses have placed the group as the descendants of the node which leads both to *Neurankylus* and *Baena* (Joyce 2007), or *Trinitichelys* and *Baena* (Gaffney and Meylan 1988). Based on the morphological diagnosis of the family presented in Gaffney (1972), it is more consistent to regard Family Baenidae as the least inclusive clade containing both *Uluops uluops* and *Baena arenosa* as has been similarly suggested previously (Bakker 1998).

Conclusions

Neurankylus eximius has previously been regarded as the longest-lived baenid species (Gaffney 1971; Lyson and Joyce 2009a, b). Description of the new species and a re-examination of the type species have shown its range to be greatly restricted both chronologically and geographically. Comparison of *N. lithographicus* and *N. eximius* allows for diagnostic characters of the latter species to be identified and may serve as guidelines for identifying characters, both in the shells and skulls, of other specimens putatively identified as, but now not referable to, *N. eximius*.

This study provides evidence for previously undocumented morphological variation in the genus *Neurankylus*. Such variation suggests other consistent, though subtle, differences may be overlooked in other taxa. The degree of morphological similarity between species of *Neurankylus* may also indicate that baenid turtles were well adapted for relatively stable ecological niches. Many of the changes that are seen in turtle faunas appear to result from shifting patterns of geographic ranges in response to climate change (Brinkman 2003) rather than faunal turnover. These patterns of diversification and extinction may help in the elucidation of such patterns in other organisms living at the same time. With this information, in turn, one will be better able to understand the ecological shifts in these ancient faunas and the mechanism of how these shifts occurred.

Fig. 4-1. Variation present in the sulci of the ventral anterior plastral lobe in *Neurankylus*. A) TMP 2007.035.0045, *N. lithographicus* B) TMP 2003.012.0171, *N. eximius*, C) USNM 8344, *N. baueri* (modified from Gilmore 1916), and D) ROM 864, *Neurankylus* sp. Drawn to a constant length anterior of the humeral-pectoral sulcus.

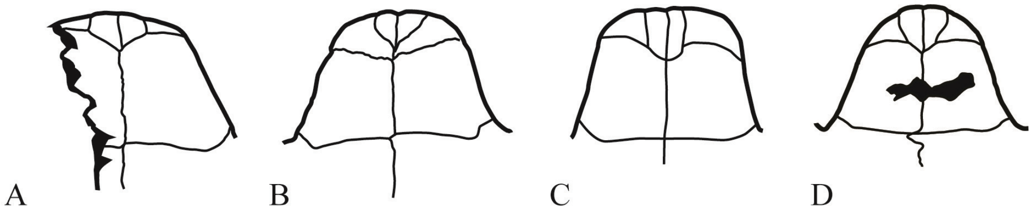

Fig. 4-2. Reconstruction of *Neurankylus eximius* referred carapace and plastron, TMP 1999.055.0134, in A) dorsal and B) ventral views. Sulci in grey.

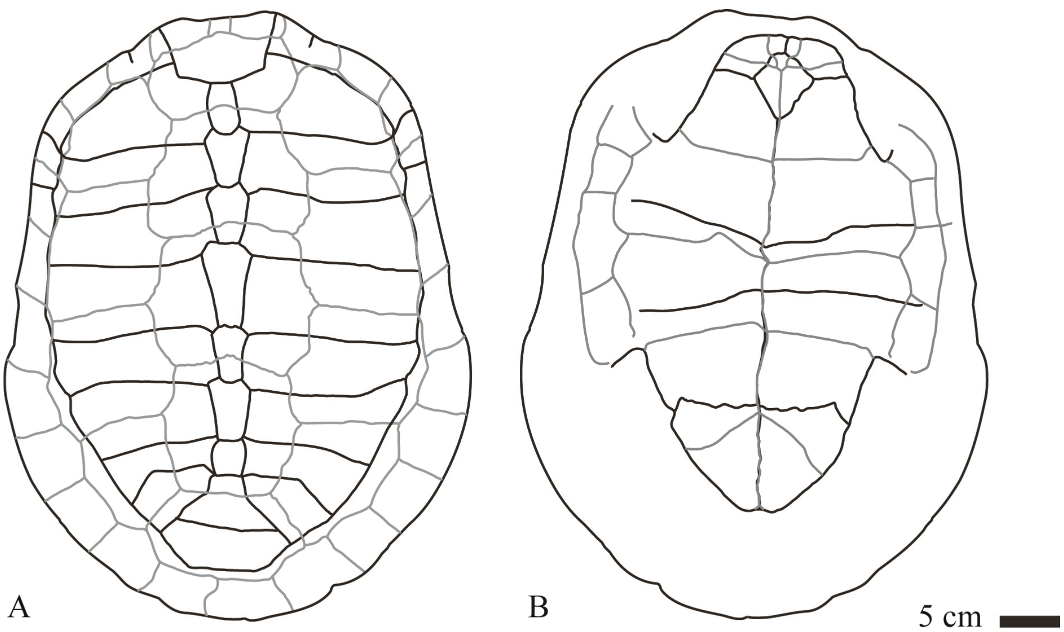

Fig. 4-3. Photographs of *Neurankylus lithographicus* holotype carapace and plastron, TMP 2007.035.0045, in A) dorsal and B) ventral views.

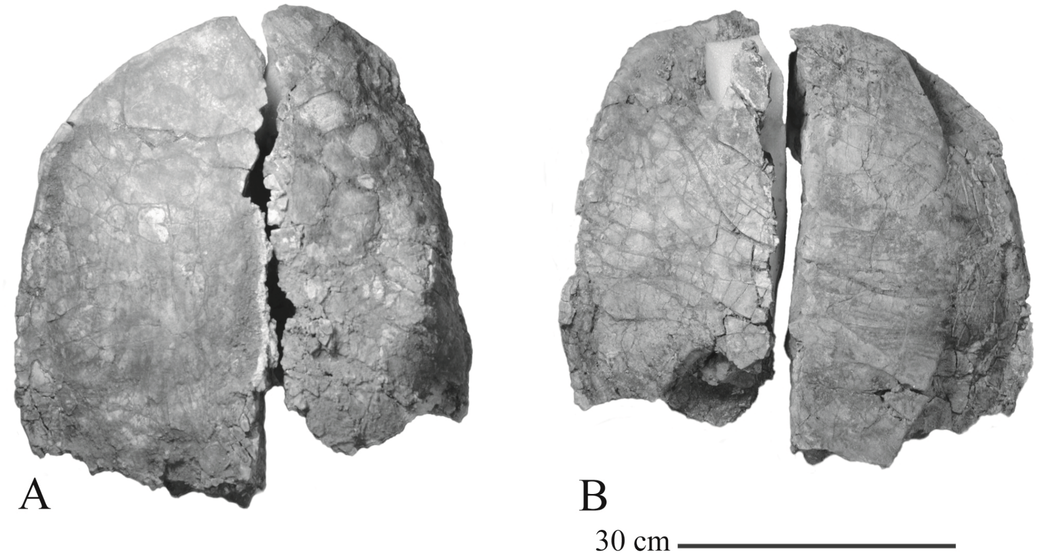

Fig. 4-4. Reconstruction of *Neurankylus lithographicus* carapace and plastron in A) dorsal and B) ventral views, based on specimens TMP 2007.035.0045 (holotype) and TMP 1994.377.0001. Sulci in grey.

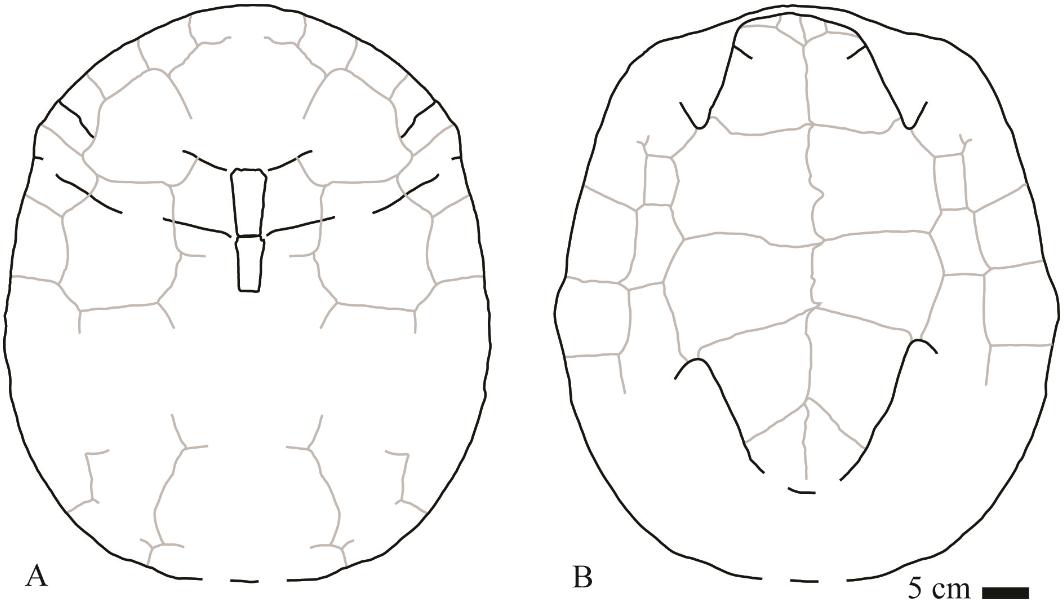

Fig.4- 5. *Neurankylus* skulls. A), C), E), and G) *Neurankylus lithographicus*, TMP 2007.036.0001, and B), D), F), and H) *Neurankylus eximius*, UALVP 30824. Specimens are in A) and B) posterior, C) and D) dorsal, E) and F), left lateral and G) and H) ventral views. Note the proportionally narrower skull and more laterally directed foramen nervi hypoglossi of *Neurankylus lithographicus*. Hatching represents broken areas. Abbreviations: bo, basioccipital; bs, basispenoid; ex, exoccipital; for. n. hypo., foramen nervi hypoglossi; for. stap., foramen stapediotemporale; fr, frontal; op, opisthotic; pa, parietal; pf, prefrontal; pr, prootic; pt, pterygoid; qu, quadrate; so, supraoccipital; sq, squamosal.

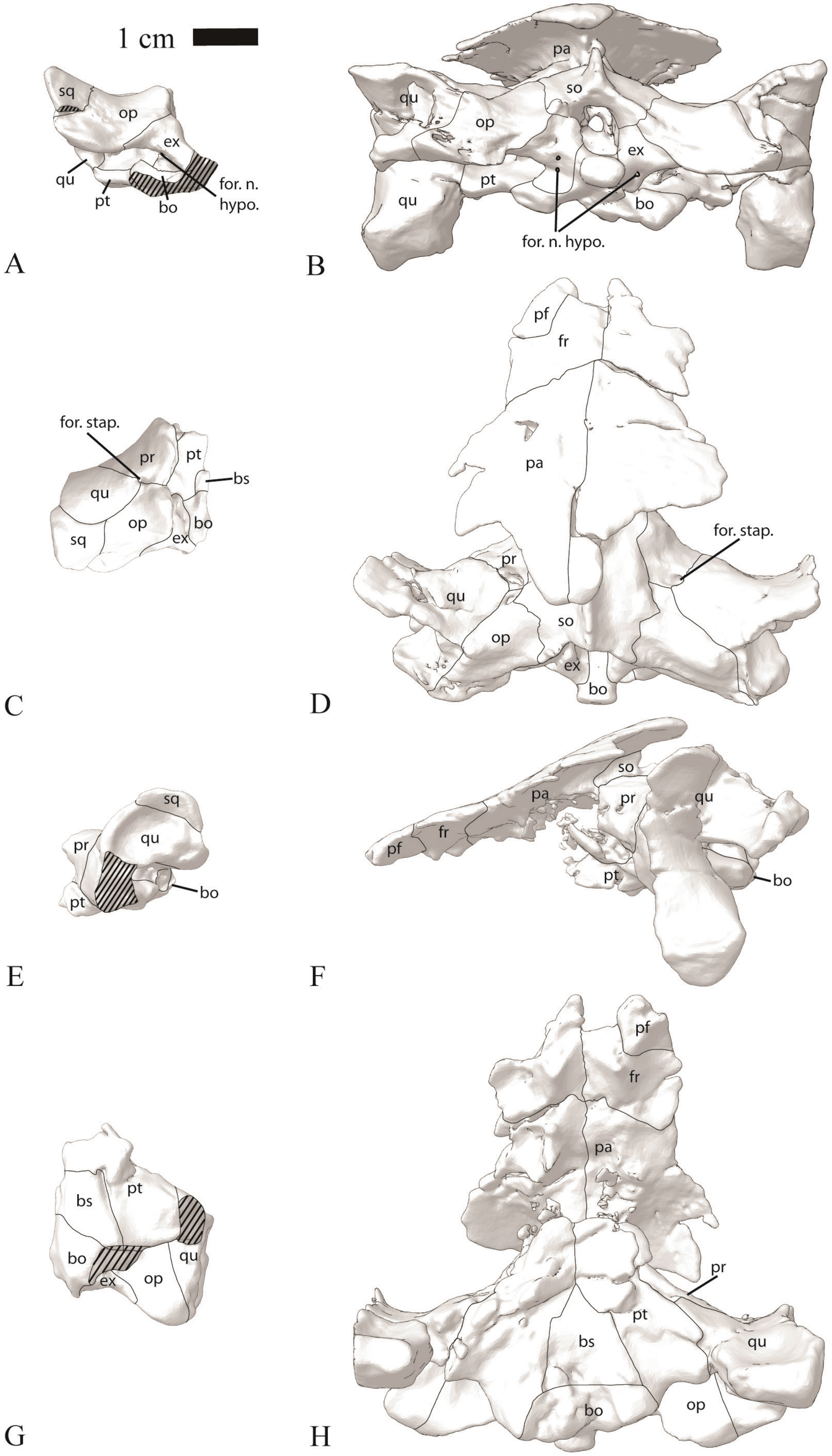
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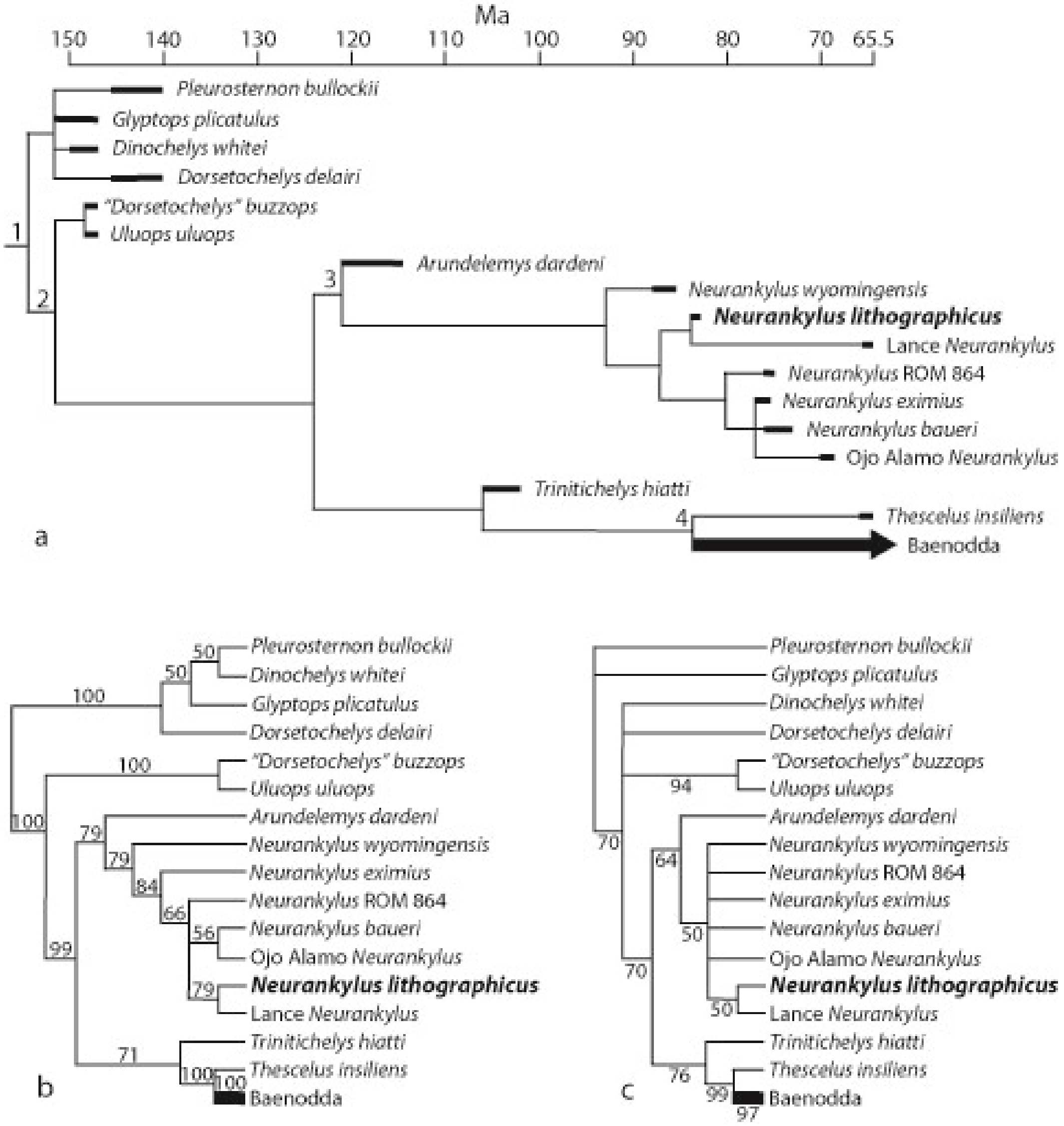
Fig. 4-6. Phylogenetic results for basal baenids. A) Time-calibrated preferred phylogeny based on a strict consensus of 16 of the 56 most parsimonious trees constrained by the Bayesian analysis which placed *N. lithographicus* basal to *N. eximius*. Numbers correspond to the following clades 1) Baenoidea, 2) Baenidae, 3) Neurankylinae, and 4) Baeninae. B) Majority-rule consensus of 102 most parsimonious trees using a heuristic search with 1000 replicates and tree-bisection reconnection. Majority rule percentages are above the branch left of the clade to which they pertain. C) Bayesian analysis using two runs of four Markov Chains run for 1 x 10^6 generations greatest likelihood tree with posterior probabilities below the branch. Baenodda taxa are summarized as one terminal taxon for emphasis on the base of the tree.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Arundelemys dardeni
Neurankylus wyomingensis
Neurankylus lithographicus
Lance Neurankylus
Neurankylus ROM 864
Neurankylus eximius
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Chapter 5 — Variation in the relative abundances of vertebrate microfossils from the Deadhorse Coulee Member of the Milk River Formation

Introduction

Vertebrate microfossil (Eberth et al. 2007) material has been collected from the Santonian Deadhorse Coulee Member of the Milk River Formation for almost 80 years (Russell 1935). This member preserves the oldest well-sampled non-marine assemblage in Canada and represents a relatively poorly-documented time in the Late Cretaceous. Since its initial description, many important vertebrate fossil sites have been identified, most notably the vertebrate microfossil localities worked initially by Fox (1968). Previous studies of the vertebrate fossil assemblage from the member (Fox 1976; Gao and Fox 1996; Brinkman 2003) have regarded the assemblage to be uniform throughout its thickness without providing evidence to support this assumption. Brinkman (1990) and Brinkman et al. (2004) demonstrated changes in the relative abundances of taxa in the Belly River Group associated with palaeogeographical preferences of taxa and changes in relative sea level. Taxa with affinities to a coastal or inland environment show shifts in their relative abundance as these environments shift through time (Brinkman 1990). It has not been noted previously in what manner the localities of the Deadhorse Coulee Member relate to each other stratigraphically, or what the occurrences and relative abundances of taxa recovered are at a single site or how these might differ between these sites.

Detailed sections were conducted to place these vertebrate microfossil sites in their stratigraphic context (Chapter 2), and this stratigraphic data was used to compare the relative abundances and occurrences of vertebrate taxa within the Deadhorse Coulee Member. Brinkman (1990) preferred the rank analysis method for determining changes in relative abundance, as fluctuations of abundance of common taxa can cause dissimilarity of relative abundances of other taxa. Moore et al. (2007) developed a multinomial modeling method by which confidence intervals of true relative abundances of taxa in an assemblage could be calculated from the relative abundances of a sample from that assemblage. Using the formula $\alpha = 1.0975e^{-2.3152\,d^{2}n}$ where α is the probability that relative abundances of a sample are similar to the relative abundances of the true assemblage, *n* is the sample size, and *d* is the degree of similarity the assemblage relative abundances are around the sample relative abundances (Moore et al. 2007), confidence intervals of true relative abundances can be calculated for samples and compared. For the analysis in this study, both methods were used to provide a more confident assessment of the true rank of the assemblage. Another method used for assessing patterns of relative abundance within a formation is that of the R-mode and Q-mode hierarchical cluster analysis (Brinkman et al. 2004) in which taxa (R-mode) and sites (Q-mode) are grouped according to the distribution ranks of taxa at these sites. These analyses provide a means of assessing an assemblage cohort of cooccurring taxa and the sites with the most similar faunal assemblages, respectively. The current study aims to use these various methods of assemblage analysis to assess any predominant trends in the vertebrate microfossil assemblage of the Deadhorse Coulee Member.

Material and Methods

Material was collected from the Deadhorse Coulee Member from a number of different localities, with material accessioned at the UALVP and TMP. Although at least four separate stratigraphic levels with abundant fossil vertebrates have been identified (Chapter 2, this thesis), vertebrate microfossils have only been processed in enough abundance from sites at two stratigraphic levels (Level II and Level III). Material collected previously that was used for this study was wet-screen washed by hand with largest screen openings measuring 1.2 mm (18x16 openings/linear inch) and 0.85 mm (20 openings/linear inch). Material collected in this study was wet-screen washed in an automated agitation system with the smallest screen size with openings measuring 0.85 mm (20 openings/linear inch).

Only some localities had enough identifiable elements recovered from them to provide accurate relative abundance data. Other sites were included for preliminary analysis, to increase stratigraphic coverage, and provide a test of variation in relative abundances at the same level. Common elements were analyzed from the following well-sampled (≥255 identifiable specimens, the amount necessary to achieve a 75% probability percentage abundances are within 5% similarity of true assemblage abundances; Moore et al. 2007) Level II sites: MR-12 (UALVP), MS (TMP), and CBS (TMP). Common elements from the following well-sampled sites from Level III were also analyzed: MR-6 (UALVP), MR-20 (UALVP), and 3WC (TMP). For the whole fauna, the poorly-sampled sites (<255 identifiable elements), DS and JS (Level I), MR-23 and MR-29 (Level II), and MR-4 (Level III) and MR-9 (UALVP), were added to the analysis. For this study, 59 distinct taxa were recognized from the vertebrate microfossil localities. Absolute and rank abundances for these sites are shown on Table 5-1 and Table 5-2. Specimens were counted using the minimum element method (Badgely 1986; except in the case of dermal bone identification, such as turtle shell, crocodilian osteoderms, or anuran cranial elements, unless the pieces could be reassembled).

For three sites (MR-6, MR-9, and MR-12), new material was collected, and diversity and abundance recorded through sorting, in a manner similar to Jamniczky et al. (2008). Numbers of identifiable vertebrate material were recorded and removed, and diversity was calculated additively. These samples approximate a rarefaction curve (Figs. 5-1a, 5-1b, 5-1c). Conservatively, after patterns of taxonomic richness stabilize using the additive method, an equal number of subsamples must be counted to ensure actually stabilization. This was not usually possible in the recently collected samples. More sorting from these sites is needed to properly support the stability of this richness. Using these methods with previously partially-sorted material present in both the UALVP and TMP collections was not deemed appropriate.

To confirm the validity of the richness taken from these three samples, as well as those sorted in the conventional means, the multinomial method of Moore et al. (2007) was utilized to ensure that taxa of not dissimilar sample abundances were given the same rank. A 75% probability was used in calculating the degree of similarity allowed for each sample, and this similarity was used to calculate a possible range of the true abundance of each taxon. Taxa were considered to be common when their relative abundances were within the similarity range of 0. This method, like the analyses of Jamniczky et al. (2008), only provides support of relative abundances of common taxa. In addition to tests of significance, the combined range in relative abundances between the two stratigraphic levels was compared to determine if any taxa display differing abundances.

Spearman's rho analysis was conducted in the statistics program JMP Version 5 (2002) to determine if supported ranks of taxa differed significantly (Brinkman 1990). The seven well-sampled sites with their elevations and supported ranks were compared to determine any trends in rank. A Spearman's rho analysis was also performed on the 36 taxa that appeared in more than two sites with differing relative abundances, with different sites included as a sensitivity test of including the poorly sampled localites. Combined relative abundances at Levels II and III of taxa from well-sampled localities were also compared using the calculation of range of abundance method (Moore et al. 2007). Again, the abundances were calculated to a 75% confidence interval.

To observe distribution patterns in taxa and site date, R-mode and Q-mode hierarchical cluster analyses (Brinkman et al. 2004) with average linkage as the dissimilarity metric (Kovach 1989) were performed on the data.

Results

Results (Table 5-3) for the largest sample (MR-6) examined using the modified method of Jamniczky et al. (2008), show that richness stabilized (began to asymptote) at 139 out of 523 specimens. At this point, 21 taxa of 30 are represented in the sample. The ranks of the top six taxa stabilize at 274 specimens, except for a switch near the end of sampling of Solemydidae with cf. *Gilchristosuchus*. This switch can be accounted for by counting individual tubercles of solemydids separately, and the nature of counting the specimens, in which smallest elements were often concentrated and poured out last. Although these changes in rank and the fewer specimens counted, strictly speaking, violate the conditions presented in Jamniczky et al. (2008), the spirit of the test is upheld, in which only those taxa with relatively stable and well-sampled abundances are considered for interpretation. The richness of taxa stabilizes in MR-9 at specimen 74 of 199, at which point 22 of 24 taxa are recognized. Except for brief ties, the additive sample MR-9 stabilizes in rank at specimen 161 of 199 for the top seven taxa. This sample is not large enough to be considered well-sampled. Though more data are needed for the robustness of these results, the current results provide a good comparison between stratigraphically-equivalent sites MR-6 and MR-9, which are laterally separated by 30.0 m. MR-12 stabilizes in richness at 26 of 30 taxa at specimen 156 of 321. The ranks of the top seven taxa stabilize, except for rare instances of ties in rank, at specimen 279.

Most of the common taxa found in the additive samples were supported as accurate abundances by the calculation method (Table 5-4) of Moore et al. (2007), and confidently ranked accordingly (Table 5-4, Table 5-5). In this analysis, uncommon taxa have similar relative abundances to zero, so they are essentially not present.

The results of the Spearman's rho analysis of the common taxa from the well-sampled sites showed that only the indeterminate teleosts were significantly different (p=0.02), and significantly decrease between the lower (Level II) and upper (Level III) sites (Fig. 5-2). The remaining twelve common taxa show no such significant trends.

When the whole assemblage is analyzed, the rare element abundances can be taken into consideration, although abundances and presence/absence data are questionable, as the abundances of these elements are not mathematically dissimilar to 0. Nonetheless, patterns do occur, and these have been documented here. Taxa that appear in at least one Level III locality, and not known in any Level I or Level II localities include Polyodontidae, *Coniophis*, Ankylosauridae, and Nodosauridae, although only two well-sampled sites were analyzed from Level II and none from Level I.

A Spearman's rho analysis of all of the taxa result only in significant increases (p=0.02 for both) in rank for Polyodontidae and Teiidae between the lower and upper levels when only the well-sampled localities were considered. When all sites were considered, *Lepisosteus* had a significant increase (p=0.01) in abundance. This is likely due to the fact that *Lepisosteus* does not occur in some of the lower, poorly sampled localities, as can be seen by the probability values when those localities are removed (p=0.13 with Level I sites removed, p=0.06 with well-sampled localities). When Level I samples are removed, Anguidae shows a significant decrease in abundance (p=0.00) between Levels II and III. Even when Level I is included, and with only well-sampled localities, p-values remain low (p=0.08 and p=0.05, respectively). With this dataset, indeterminate teleosts did not show a significant change in rank. In a combined evaluation of possible range of abundance for Levels II and III (Table 5-5), six taxa did not overlap in relative abundance between the two levels. *Myledaphus*, Lepisosteidae indet., and Solemydidae showed an increase in abundance, whereas *Lepisosteus*, Vidalamiinae, and Hadrosauridae showed decreases in abundance.

The R-mode analysis clustered taxa into three distinct groups (Fig. 5-2). The first group (Fig. 5-2a) contains many of the coastal taxa documented by Brinkman et al. (2004) in his R-mode cluster analysis and is interpreted as a coastal-preferring assemblage. The third group (Fig. 5-2c) contains mostly documented inland assemblage members (Brinkman et al. 2004) and is interpreted as an inland assemblage cluster. The other cluster, to which most of the specimens belong, is tentatively interpreted here as taxa dominating in a transitional assemblage.

The Q-mode analysis also clustered sites into three groups (Fig. 5-3). However, one of these groups (Fig. 5-3b) consisted entirely of poorly-sampled localities and is probably an artefact of sampling. The other two groups of sites, all except MR-9 were well-sampled, consisted of two of the Level II localities (Fig. 5-3a) and a group containing one Level II locality and the Level III localities (Fig. 5-3c). Within this Level III group, the closest sites were MS and 3WC, the best sampled sites, and a group containing MR-6, MR-9, and MR-20. The similarity of MS (a Level II site from a crevasse splay) and 3WC (a Level III site from a channel lag) illustrates that depositional environment and stratigraphic level are not solely responsible for determining what taxa are preserved.

Discussion

The similar results of the additive subsample method of vertebrate microfossil sorting and the similarity confidence calculations of samples confirm that the common taxa found from these sites are representative of their rank abundance in the assemblage. These results also support the use of similarity confidence calculations in determining the true abundance of an assemblage when no other data are available.

The results of all of the various analyses generally indicate that there are few differences between samples collected at Level II and Level III. This is not surprising when the chronostratigraphic relationship between the two levels is calculated. The time interval between these two levels probably represents very little time compared to time in which the relative abundance changes in the Belly River Group (2 million years) occurred (Brinkman et al. 2004).

The minor differences noted in the results indicate that there may be a slight signal of a more inland environment in the upper part of the sections. This is consistent with the geological interpretation (Chapter 2) of a transition between Level II and Level III from an early to late highstand systems tract and a prograding palaeoshoreline. The analyses and taxa supporting a more inland trend in the assemblage are the absence of Polyodontidae (Grande and Bemis 1991; Demar and Breithaupt 2008) from Level I and Level II localities and presence in Level III, the significant increase of abundance in the Spearman's rho analysis of the whole dataset for Polyodontidae, an increase in the abundance range of Lepisoteidae indet., and a decrease in the abundance ranges of *Lepisosteus* and Vidalamiinae. The R-mode cluster analysis placements of *Myledaphus*, *Lepisosteus*, and Solemydidae in the coastal group, and Lepisosteidae indet., indet. teleosts, *Albanerpeton*, and Caudata in the inland group also support this trend.

The interpretation of a small shift to a more inland environment is not supported by significant decrease in indeterminate teleost abundance among common elements, a significant increase in *Lepisosteus* in the Spearman's rho of all of the localities, the increased range of abundance of *Myledaphus* and Solemydidae in the combined analysis, and the R-mode analysis placement of Anura in the coastal group, and *Paralbula*, Eusuchia, Ceratopsidae, and *Adocus* in the inland group. As mentioned earlier, the apparent increase in *Lepisosteus* through the section is likely an artefact of sampling. It is hypothesized that apparent distribution patterns of three of these taxa (indet. teleosts, *Adocus*, and Solemydidae) are due to taphonomic overprinting. Teleost vertebrae are fragile and susceptible to breakage (Brinkman 2004) and many seemingly unconnected pieces can be broken from a single turtle shell (especially in Solemydidae in which the pustulose granulations are frequently broken off yet remain identifiable); therefore, the unexpected distribution patterns of these taxa can be explained by increased transport and breakage, causing a decrease in abundance in the former, and an increase in the latter two. This is consistent with the hypothesis that the Level III beds are reworked from surrounding mudstones.

These results suggest that taxa in addition to those documented by Brinkman et al. (2004) may display some minor changes in abundance through the member that is likely associated with distance from the palaeoshoreline, but may be attributed to other confounding factors, like temperature change or poorly understood taphonomic processes. These taxa should be scrutinized closely in further study. If related to distance from the shoreline, the following trends are observed: Anguidae, Hadrosauridae, and Metatheria are more dominant in coastal environments in this member, whereas *Coniophis*, Ankylosauridae, Nodosauridae, Teiidae, indet. lizard, and indet. lizard ossicles are hypothesized to have inland affinities. It is reassuring that Teiidae and indet. lizard are placed as sister taxa on the dendrogram (Fig. 5-2), as at least some of the latter specimens probably actually belong to the former. *Coniophis* (Caldwell 2005), and *Adocus* (Brinkman et al. 2004) possibly track temperature changes (Chapter 6), and the increased abundances of these taxa (some unexpected) may be linked to a warming temperature between these time intervals, although other metrics of average global temperature (Wolfe and Upchurch 1987) do not indicate any such trend at this time period.

Conclusions

Although well-sampled vertebrate microfossil localities are of a restricted stratigraphic range, some uncommon taxa indicate a pattern of more inland assemblages becoming more dominant. This pattern is consistent with the prograding sedimentological model hypothesized for the system. Other factors (change in depositional environment, or an increase in palaeotemperature) may also play a role in determining relative abundance changes. Taxa, additional to those documented by Brinkman et al. (2004), that may exhibit a preference for either coastal or inland environments include anguids, hadrosaurids, and metatherians (coastal), and ankylosaurids, nodosaurids, teiids, other lizards, and possibly *Coniophis* (inland). These conclusions, however, are tenuous because of subtle relative abundance changes and incomplete stratigraphic coverage, with which this study would greatly benefit. Both additive sampling of localities and calculation of confident ranges of abundance provide comparable and reconcilable determination of common taxa, and these taxa show no significant difference in abundance throughout the localities sampled.

This work illustrates that regarding the vertebrate fossils thus far recovered from the formation as belonging to a single assemblage (with both common coastal and somewhat less common inland elements) is justified. Although slight changes in relative abundances do occur, they are not well-supported, and further study is needed to support these trends. The Deadhorse Coulee Member non-marine vertebrate assemblage is tentatively supported as roughly the same throughout the member, and this will ease comparison of the assemblage with comparable assemblages in North America.

Table 5-1. Absolute abundances of all taxa at all counted sites.

Site	DS	JS	MR29	MR23	MR12	MS	CBS	MR20	MR4	3WC	MR6	MR9
Elevation (m)	10.2	10.4	14.6	14.6	18.1	18.1	20.9	26.1	26.1	26.1	26.4	26.4
Myledaphus	2			4	102	179	65	51	4	420	126	26
Lonchidion					7	22		1		1		
Belonostomus								1				
?*Lepidotes*					5		1	2		8	2	
Lepisosteus			30	10	53	618	38	147	36	404	142	58
Lepisosteidae					25	149	9	136		71	27	9
Polyodontidae								1		1	1	
Amiinae					7		4	3		2	3	1
Vidalamiinae	1					88	2	2				
Paralbula				1		1	1	3		10	1	
Esocoidea						2				4	1	
indet. teleost					45	61	46	7	2	35	6	6
Albanerpeton					9	9	22	10	1	10	5	8
Caudata					11	8	15	6	2	48	12	5
Anura		1	3		17	43	28	11	2	24	17	18
indet. lizard					4	13	4	10		5	1	3
Teiidae					2	18	2	3		20	2	2
Varanoidea						2				5		
Auguidae		1	1	1	5	15	5	1		10	1	4
lizard ossicles						6	2	1		6	15	10
Coniophis								1				1
indet. turtle			1					1		1		3
Adocus				1		32		5		27	8	10

Solemydidae			5	1	2	28	1		2	172	52	7
Baenidae			1			45	1	1		19		
Trionychidae					4	34		1		7		
Gilchristosuchus	1		1	3	8	398	27	32	2	346	44	7
Eusuchia				1	3	53	3	12		111	12	
Goniopholididae						21	1			20		3
Crocodylomorpha						4	1					
Ankylosauridae										3		
Nodosauridae										2		
Hadrosauridae			2	15	6	536	1	26	1	250	34	15
Leptocertopsidae						1				1		
Ceratopsidae				5	8		2	8		4	9	6
Pachycephalosauridae					1					8	1	
Tyrannosauridae					1	15	1	3		23	4	
cf. *R. gilmorei*	1					4	4	2		11		
cf. *R. isosceles*						26		3		16	4	
Dromaeosaurinae						7		2		9		
Saurornitholestinae				1		5	2	4	2	18		
Dromaeosauridae						1						
cf. *P. lacustris*						3		1		2	1	
cf. Aves	1				1		1				4	2
indet. theropod								1				1
Metatheria		1			2	5	4		1	10	2	
Multituberculata						30	2			18	1	
"thumb" beast							1					
indet. Mammalia				1			5	1		5		

Table 5-2. Rank abundances of all taxa at all counted sites. Ties are averaged.

Taxon	DS	JS	MR29	MR23	CBS	MR12	MS	MR6	MR9	MR 20	MR 4	3WC
Myledaphus	1	31.5	34.5	4	1	1	4	2	2	3	2	2
Lonchidion	32.5	31.5	34.5	35.5	49	11.5	16	45	41.5	29.5	36	38.5
Belonostomus	32.5	31.5	34.5	35.5	49	44.5	47.5	45	41.5	29.5	36	50
Polyodontidae	32.5	31.5	34.5	35.5	49	44.5	47.5	26.5	41.5	29.5	36	38.5
?*Lepidotes*	32.5	31.5	34.5	35.5	10	7	47.5	20.5	22	12	36	25.5
Lepisosteus	32.5	31.5	1	2	2	2	1	1	1	1	1	1
Lepisosteidae	32.5	31.5	34.5	35.5	8	4	6	6	7	2	36	7
Amiinae	32.5	31.5	34.5	35.5	17	21	47.5	45	41.5	29.5	36	35
Vidalamiinae	3.5	31.5	34.5	35.5	23	44.5	5	45	41.5	21	36	50
Paralbula	32.5	31.5	34.5	8.5	32.5	44.5	34	26.5	41.5	17.5	36	21.5
Esocoidea	32.5	31.5	34.5	35.5	49	44.5	31.5	26.5	41.5	48	36	33
indet. teleost	32.5	31.5	34.5	35.5	5	3	7	13	13.5	12	36	9
Albanerpeton	32.5	31.5	34.5	35.5	6	8	22	15	8	8.5	10	21.5
Caudata	32.5	31.5	34.5	35.5	7	6	23	9.5	12	12	5	8
Anura	32.5	2	3	35.5	3	5	10	7	3	7	5	11

indet. turtle	32.5	31.5	7	35.5	49	44.5	47.5	45	16	29.5	36	38.5
Adocus	32.5	31.5	34.5	8.5	49	44.5	12	12	5.5	14	36	10
Solemydidae	32.5	31.5	2	8.5	32.5	21	14	3	9.5	48	5	5
Baenidae	32.5	31.5	7	35.5	32.5	44.5	9	45	41.5	29.5	36	15
Trionychidae	32.5	31.5	34.5	35.5	49	16	11	45	41.5	29.5	36	27
indet. lizard	32.5	31.5	34.5	35.5	13	16	21	26.5	16	8.5	36	29.5
Teiidae	32.5	31.5	34.5	35.5	23	21	18	20.5	19	17.5	36	13.5
Varanoidea	32.5	31.5	34.5	35.5	49	44.5	31.5	45	41.5	48	36	29.5
Anguidae	32.5	2	7	8.5	11	14	19.5	26.5	13.5	29.5	36	21.5
lizard ossicles	32.5	31.5	34.5	35.5	23	44.5	25	8	5.5	29.5	36	28
Coniophis	32.5	31.5	34.5	35.5	49	44.5	47.5	45	22	29.5	36	50
Gilchristosuchus	3.5	31.5	7	5	4	9.5	3	4	9.5	4	5	3
Eusuchia	32.5	31.5	34.5	8.5	17	18	8	9.5	41.5	6	36	6
Goniopholididae	32.5	31.5	34.5	35.5	32.5	44.5	17	45	16	48	36	13.5
Crocodylomorpha	32.5	31.5	34.5	35.5	32.5	44.5	28.5	45	41.5	48	36	50
Ankylosauridae	32.5	31.5	34.5	35.5	49	44.5	47.5	45	41.5	48	36	33
Nodosauridae	32.5	31.5	34.5	35.5	49	44.5	47.5	45	41.5	48	36	35

Hadrosauridae	32.5	31.5	4	1	32.5	13	2	5	4	5	10	4
Neoceratopsia	32.5	31.5	34.5	35.5	49	44.5	34	45	41.5	48	36	38.5
Ceratopsidae	32.5	31.5	34.5	3	23	9.5	47.5	11	11	10	36	31.5
Pachycephalosauridae	32.5	31.5	34.5	35.5	49	26.5	47.5	26.5	41.5	48	36	25.5
Tyrannosauridae	32.5	31.5	34.5	35.5	32.5	26.5	19.5	17	41.5	17.5	36	12
cf. *R. gilmorei*	3.5	31.5	34.5	35.5	13	44.5	28.5	45	41.5	21	36	19
cf. *R. isosceles*	32.5	31.5	34.5	35.5	49	44.5	15	17	41.5	17.5	36	18
Dromaeosaurinae	32.5	31.5	34.5	35.5	49	44.5	24	45	41.5	21	36	24
Saurornitholestinae	32.5	31.5	34.5	8.5	23	44.5	26.5	45	41.5	15	5	16.5
Dromaeosauridae	32.5	31.5	34.5	35.5	49	44.5	34	45	41.5	48	36	50
cf. *P. lacustris*	32.5	31.5	34.5	35.5	49	44.5	30	26.5	41.5	29.5	36	35
cf. Aves	3.5	31.5	34.5	35.5	32.5	26.5	47.5	17	19	48	36	50
indet. theropod	32.5	31.5	34.5	35.5	49	44.5	47.5	45	22	29.5	36	50
Metatheria	32.5	2	34.5	35.5	13	21	26.5	20.5	41.5	48	10	21.5
Multituberculata	32.5	31.5	34.5	35.5	23	44.5	13	26.5	41.5	48	36	16.5

Table 5-3. The rank and relative abundances of the additively consistent taxa in samples from MR-12, MR-6, and MR-9. RA, relative abundance.

MR-12			MR-6			MR-9		
Rank	Taxon	RA	Rank	Taxon	RA	Rank	Taxon	RA
1	*Myledaphus*	0.308	1	*Lepisosteus*	0.254	1	*Lepisosteus*	0.284
2	*Lepisosteus*	0.160	2	*Myledaphus*	0.235	2	*Myledaphus*	0.127
3	indet. teleost	0.088	3	Solemydidae	0.097	3	Anura	0.088
4	Lepisosteidae	0.076	4	*Gilchristosuchus*	0.082	4	Hadrosauridae	0.074
5	Anura	0.051	5	Hadrosauridae	0.063	5.5	*Adocus*	0.049
6	Caudata	0.033	6	Lepisosteidae	0.050	5.5	lizard ossicles	0.049
						7	Lepisosteidae	0.044

Table 5-4. The ranks and possible ranges of true assemblage relative abundances of the most common taxa in sites MR-12, MS, CBS, MR-6, MR-9, MR-20, and 3WC.

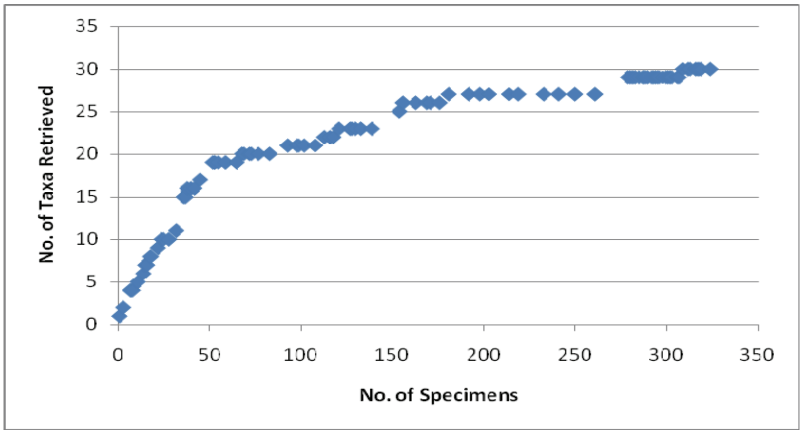
MR-12			MS			CBS		
Rank	Taxon	Range	Rank	Taxon	Range	Rank	Taxon	Range
1	*Myledaphus*	0.264–0.352	1	*Lepisosteus*	0.347–0.377	1	*Myledaphus*	0.173–0.267
2	*Lepisosteus*	0.116–0.204	2.5	Hadrosauridae	0.177–0.207	3.5	*Lepisosteus*	0.061–0.155
4	indet. teleost	0.044–0.132	2.5	*Gilchristosuchus*	0.128–0.158	3.5	Anura	0.048–0.142
4	Lepisosteidae	0.032–0.120	4	*Myledaphus*	0.049–0.079	3.5	*Gilchristosuchus*	0.045–0.139
4	Anura	0.007–0.095	7	Vidalamiinae	0.017–0.047	3.5	indet. teleost	0.034–0.128
			7	Lepisosteidae	0.008–0.038	3.5	*Albanerpeton*	0.028–0.122
			7	indet. teleost	0.008–0.038	3.5	Caudata	0.004–0.098
			7	Eusuchia	0.004–0.034			
			7	Baenidae	0.001–0.031			

MR-6			MR-9			MR-20			3WC		
Rank	Taxon	Range	Rank	Taxon	Range	Rank	Taxon	Range	Rank	Taxon	Range
1.5	*Lepisosteus*	0.219–0.289	1	*Lepisosteus*	0.224–0.334	1.5	*Lepisosteus*	0.256–0.328	1	*Lepisosteus*	0.291–0.323
1.5	*Myledaphus*	0.200–0.270	3	*Myledaphus*	0.070–0.180	1.5	Lepisosteidae	0.236–0.308	2.5	*Myledaphus*	0.149–0.181
4.5	Solemydidae	0.062–0.132	3	Anura	0.032–0.142	4	*Myledaphus*	0.066–0.138	2.5	*Gilchristosuchus*	0.120–0.152
4.5	*Gilchristosuchus*	0.047–0.117	3	Hadrosauridae	0.017–0.127	4	*Gilchristosuchus*	0.028–0.100	4	Hadrosauridae	0.082–0.114
4.5	Hadrosauridae	0.028–0.098				4	Hadrosauridae	0.016–0.088	5	Solemydidae	0.052–0.084
4.5	Lepisosteidae	0.015–0.085							7	Eusuchia	0.028–0.060
									7	Lepisosteidae	0.012–0.044
									7	Caudata	0.003–0.035

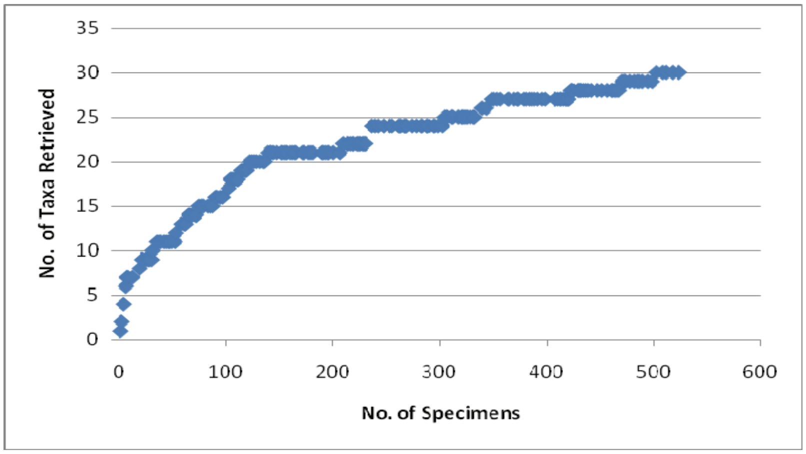
Table 5-5. The rank, relative abundance, and possible range of true assemblage relative abundances of the most common taxa in combined stratigraphic Level II (MR-12, MS, CBS), and Level III (MR-6, MR-9, MR-20, and 3WC).

Level II				Level III			
Rank	Taxon	RA	Range	Rank	Taxon	RA	Range
1	*Lepisosteus*	0.320	0.306–0.334	1	*Lepisosteus*	0.295	0.282–0.308
2	Hadrosauridae	0.159	0.145–0.173	2	*Myledaphus*	0.164	0.151–0.177
3	*Gilchristosuchus*	0.126	0.112–0.140	3	*Gilchristosuchus*	0.113	0.100–0.126
4	*Myledaphus*	0.101	0.087–0.115	4	Hadrosauridae	0.085	0.072–0.098
7	indet. teleost	0.034	0.020–0.048	5.5	Lepisosteidae	0.064	0.051–0.077
7	Lepisoteidae	0.028	0.014–0.042	5.5	Solemydidae	0.061	0.048–0.074
7	Vidalamiinae	0.026	0.012–0.040	7	Eusuchia	0.036	0.023–0.049
7	Anura	0.026	0.012–0.040	9.5	Caudata	0.019	0.006–0.032
7	Eusuchia	0.017	0.003–0.031	9.5	Anura	0.018	0.005–0.031
				9.5	indet. lizard	0.017	0.004–0.030
				9.5	indet. teleost	0.016	0.003–0.029

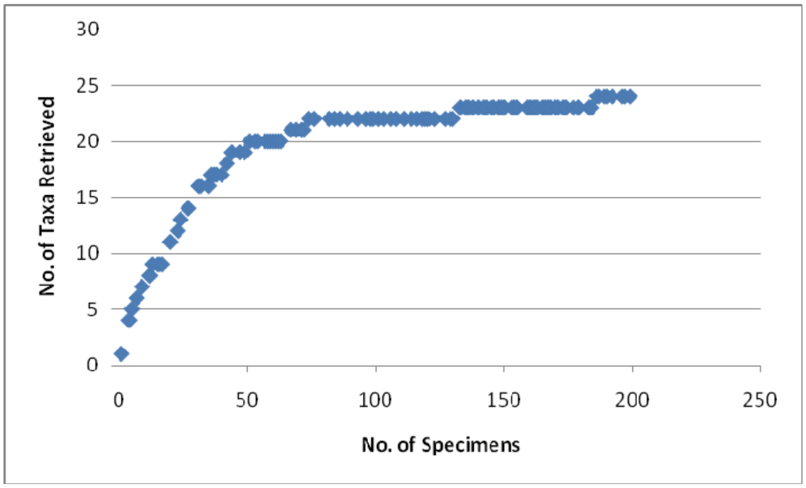
Fig. 5-1. The taxon richness of three sites counted using a method similar to Jamniczky et al. (2003). A) MR-12, B) MR-6, C) MR-9.



A



B



C

Fig. 5-2. R-mode hierarchical cluster analysis with average linkage. A) coastal taxa, B) possible transitional taxa, and C) possible inland taxa.

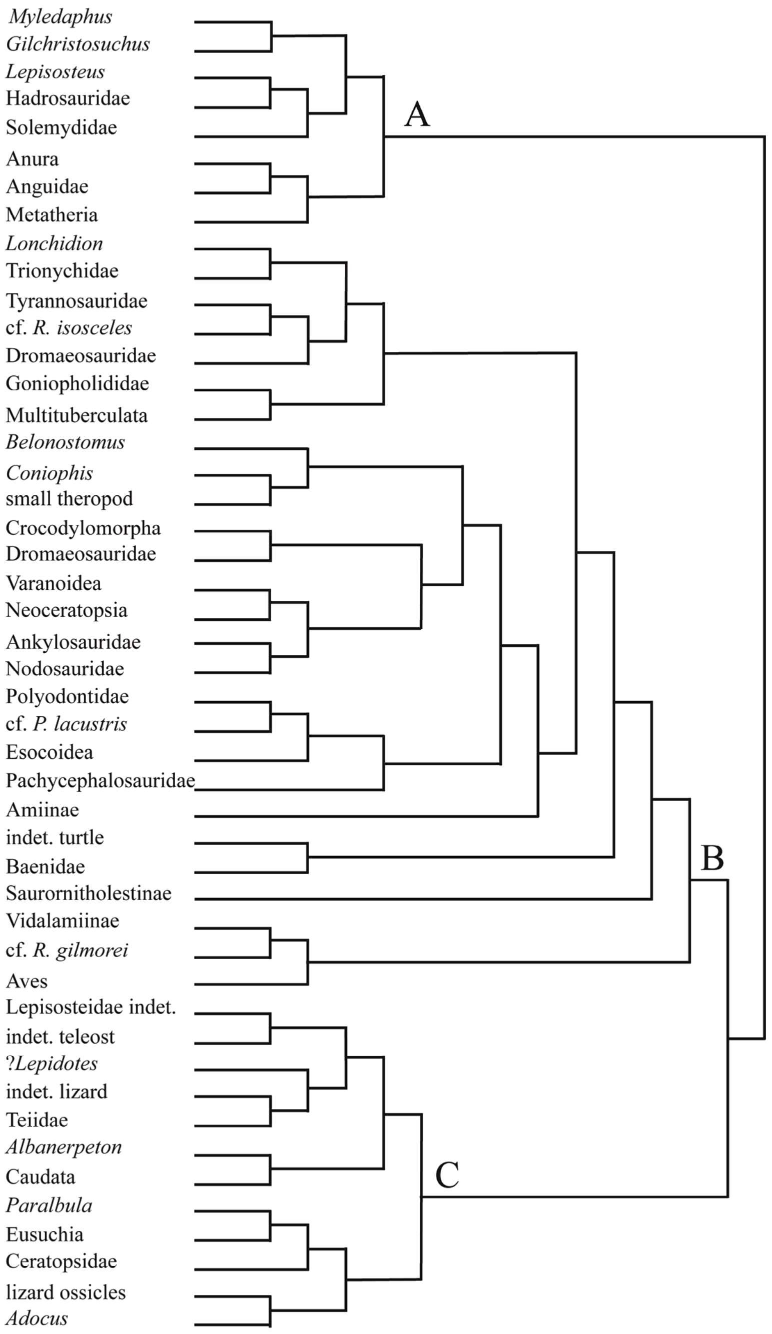
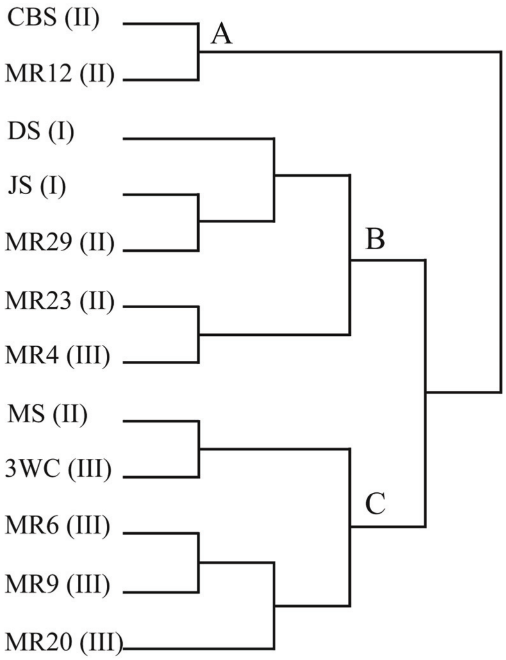


Fig. 5-3. Q-mode hierarchical cluster analysis with average linkage. A) well-sampled coastal sites, B) poorly-sampled sites, and C) well-sampled inland and coastal sites. Roman numeral refers to stratigraphic level.



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Chapter 6 — Distribution patterns of vertebrate taxa in western North America in the Santonian: a case study of the Milk River and Straight Cliffs formations

Introduction

Palaeobiogeographical zonation of western North America is a potentially useful tool in evaluating climatic change, rates of evolution, and modes of dispersal. Late Cretaceous vertebrates were first demonstrated to show provinciality by Lehman (1987, 1997, 2001). Numerous subsequent studies have proposed arguments in support of (Brinkman 1990, 2003; Brinkman et al. 1998, 2004; Sankey 2006; Larson et al. in press) and against such provinciality (Sullivan and Lucas 2003; Vavrek and Larsson 2010) in terms of latitudinal zonation and environmental zonation. Demonstrating such patterns can be difficult, but it is possible when two criteria are met: the likely equivalency of age of the beds in question, and there is a real or hypothetical (temperature- or environmental-dependent) barrier between assemblages. In western North America, such differences are often found in the well-exposed and well-sampled Campanian and Maastrichtian beds of the Western Interior Basin (Lehman 2001), whereas only large-scale (Baszio 1997; Brinkman 2003) or preliminary attention (often by way of faunal lists; Kirkland et al. 1999; Eaton et al. 1999) has been given to similar patterns in older units.

The late Santonian Deadhorse Coulee Member of the Milk River Formation (Alberta, Canada) preserves the oldest well-sampled non-marine vertebrate assemblage in Canada (Chapter 2). The Santonian John Henry Member of the Straight Cliffs Formation (Utah, USA) is time equivalent to the Milk River Formation and preserves a similar vertebrate assemblage (Eaton 2006) in a diverse array of palaeoenvironments. Assemblages from this time provide excellent information on vertebrate distribution patterns immediately prior to the better-known Campanian assemblages of the Western Interior. The Santonian is also ideal for testing hypotheses of the effects of temperature on vertebrate provinciality, because this time represents a global thermal high relative to the Campanian (Wolfe and Upchurch 1987), providing testable predictions of assemblage distributions by comparing Santonian to Campanian assemblages.

Brinkman (1990) and Brinkman et al. (2004) showed with vertebrate microfossil assemblages that distinct palaeocommunities with inferred environmental provinciality could be identified via quantitative methods. This sort of analysis is ideally suited to vertebrate microfossil assemblages because of the relatively easy collection of statistically significant sample sizes, and the recovery of rare but potentially informative taxa. Baszio (1997) discussed latitudinal zonation as a control on changes in the relative abundances of dinosaur teeth through time in the Western Interior. Moore et al. (2007) were able to calculate, based on sample size, the confidence with which relative abundances of a sample could be so similar as to be indistinguishable. Using these quantitative methods, analyses of Santonian non-marine assemblages were assessed for palaeocommunity structure. These structures were compared to those of the Campanian as an independent test of vertebrate provinciality.

Material and Methods

Specimens were collected from the Deadhorse Coulee Member from a number of different localities, with material accessioned at the UALVP and TMP. Although at least four separate stratigraphic levels with abundant fossil vertebrates have been identified (Chapter 2), vertebrate microfossils have only been processed in enough abundance from sites at two stratigraphic levels (Level II and Level III). Material collected previously that was used for this study was wet-screen washed by hand with largest screen openings measuring 1.2 mm (18x16 openings/linear inch) and 0.85 mm (20 openings/linear inch). Material collected in this study was wet-screen washed in an automated agitation system with the smallest screen size with openings measuring 0.85 mm (20 openings/linear inch).

The material collected from the John Henry Member came from two localities. One locality, UMNH VP Loc. 99 (Eaton 2006), was deposited in a marine-influenced coastal unit in the early-to-middle Santonian. UMNH VP Loc. 424 was deposited in a fully non-marine variegated unit in the late Santonian. These sites were considered time equivalent to each other as well as the Deadhorse Coulee Member of the Milk River Formation. They represent, at most, a 2.3 million year difference (Gradstein et al. 2004), a possible timeframe similar to other palaeocommunity studies (Brinkman 1990; Brinkman et al. 2004). Any differences in terms of relative abundances of higher taxonomic groups between these localities are considered to be more likely attributable to latitudinal or environmental variation than changes through time. Matrix was wet-screened, with the smallest screen opening measuring 0.28 mm (30 openings/linear inch). Vertebrate material was identified to taxonomic levels comparable to the Deadhorse Coulee Member assemblages (Chapter 5) and counted (Table 6-1).

To evaluate differences between the coastal and inland assemblages in the John Henry localities, the range of possible abundances for each taxon in one site was compared to the range of abundances in the other site (Moore et al. 2007). Ranges of abundances were calculated with a 75% confidence interval. This method is able to evaluate changes in absolute abundance of taxa among common elements in assemblages (Chapter 5). Uncommon taxa do not have abundances appreciably dissimilar to zero. Ranges of abundances that overlap less than half of either abundance were interpreted as taxon preference for either a coastal or an inland environment.

As a test of this method, a Spearman's rho analysis was conducted with JMP Version 5 (2002) on the ranks of relative abundances of the taxa at the two Utah sites and the two Alberta levels compared to their estimated distances from the palaeoshoreline. The Alberta localities are thought to be intermediate in distance from the shoreline between those of the coastal and inland Utah sites. Significance was set at 95%, although p-values of 80% or more were noted.

Because of the low number of localities that could be placed in any particular group, the Spearman's rho was a more applicable analysis than a Kruskal-Wallis analysis (Brinkman et al. 2004).

To compare the assemblages and evaluate the existence of northern and southern taxa, a similar analysis was performed. The assemblages from the two Utah sites and the Level II and III Alberta sites were combined into two assemblages. The ranges of relative abundance were again calculated with a 75% confidence interval for each taxon (Moore et al. 2007).

Results

The comparison between coastal and inland Utah localities showed differences between nine taxa (Table 6-2). Four taxa were found to be more common in the coastal site: *Rhinobatos*, *Lepisosteus*, Vidalamiinae, and Multituberculata. The five taxa that were more common in the inland site were *Albanerpeton*, Caudata, cf. *Gilchristosuchus palatinus*, basal Theria, and Metatheria.

Only some (Vidalamiinae, Caudata, Varanoidea, and Metatheria) of these taxonomic cohort trends were significantly supported in the Spearman's rho analysis (Table 6-3). Vidalamiines were shown to have a significant abundance increase in coastal environments, and caudatans, varanoids, and metatherians increased in abundance in inland environments. However, due to the small number of sites in the analysis, many taxa showed a trend toward having different relative abundances without being significantly different. The only taxa trending towards greater dominance in coastal setting are *Lepisosteus* (p=0.23) and *Paralbula* (p=0.20). *Albanerpeton* (p=0.20), *Adocus* (p=0.20), indeterminate turtle (p=0.20), Teiidae (p=0.20), Anguidae (p=0.20), *Coniophis* (p=0.26), cf. *Gilchristosuchus palatinus* (p=0.05), Eusuchia (p=0.05), Ankylosauridae (p=0.26), Nodosauridae (p=0.26), Pachycephalosauridae (p=0.26), Dromaeosaurinae (p=0.20), and indeterminate small theropod (p=0.26) all showed non-significant trends of abundance increase in inland environments. Sampling more localities may provide the greater sample size necessary to confirm this. All other p-values were 0.60 or higher. No basal therian teeth were identified from the Deadhorse Coulee samples, so the comparison of this group of mammals with this analysis may not be justified.

The calculated range abundances revealed several taxa that may belong to either a northern or southern cohort of vertebrates (Table 6-4). The northern palaeocommunity consists of *Myledaphus*, Lepisosteidae, Solemydidae, and Hadrosauridae. The southern palaeocommunity consists of Vidalamiinae, *Denazinemys* sp., Goniopholididae, and possibly Multituberculata.

Discussion

Many taxa in this study showed similar patterns in terms of environmental preferences to those in the Deadhorse Coulee Member alone (Chapter 5). These analyses support the indentification of Vidalamiinae, and probably *Lepisosteus*, as coastal taxa. In order of support, Caudata and possibly Varanoidea, *Albanerpeton*, cf. *Gilchristosuchus palatinus*, *Adocus*, Teiidae, *Coniophis*, indeterminate turtle, Eusuchia, Ankylosauridae, Nodosauridae, Pachycephalosauridae, Dromaeosaurinae, and an indeterminate small theropod are supported as preferring inland environments.

A coastal-to-marine distribution has been proposed for *Rhinobatos*, *Lepisosteus*, *Paralbula*, and Vidalamiinae (Brinkman et al. 2004; Grande and Bemis 1998). The support from this analysis for these findings is expected and validates the utility of the method. Similarly, Caudata, *Albanerpeton*, and pachycephalosaurids have previously been shown to demonstrate inland affinities (Brinkman 1990; Brinkman et al. 2004), a justifiable trend given extant amphibian physiology and habitat preferences. It is surprising, however, that neither the current analysis, nor that of the Deadhorse Coulee Member (Chapter 5), noted anurans in this same palaeocommunity assemblage. This is especially surprising given the results of Brinkman (1990) and Brinkman et al. (2004), which show anurans clustering with the other amphibians. Examination of the Santonian data suggests that a similar inland abundance distribution exists for anurans, as well as a northern distribution, although neither the inland nor northern distributions are significantly supported. Teiids, varanoids, and cf. *Gilchristosuchus palatinus*, although not previously noted for coastal or inland affinities (Brinkman et al. 2004; Wu and Brinkman 1993), may be other components of this inland palaeocommunities. However, more work needs to be done concerning the abundance of individual teiid species, as the trend observed in this study may be an over-generalization. The recovery of indeterminate turtle, *Coniophis*, Ankylosauridae, Nodosauridae, Dromaeosaurinae, and indeterminate small theropod as inland taxa is not significantly supported, and the only occurrences of these taxa in the data used in the current study are often only a few specimens from Level III of the Deadhorse Coulee Member. Whether or not these taxa actually belong to an inland palaeocommunity is yet to be demonstrated.

The recovery of anguids and metatherians as inland taxa contrasts with the results of the analysis within the Deadhorse Coulee Member (Chapter 5), which suggested that these taxa had a preference for coastal habitats. In the case of the anguids, this reinforces the uncertainty of both analyses and provides no conclusive support for either interpretation. In the case of metatherians, the current study provides strong support for inland preferences. Indeed, the results of the R-mode cluster analysis of the Deadhorse Coulee Member (Chapter 5) grouped metatherians with anguids, as well as anurans, none of which have been previously identified as being coastal in distribution (Brinkman et al. 2004). Like the teiids, the pattern seen in the metatherians (as well as the other mammal groups) would benefit from a species-specific study of rank abundances.

Both the current study and that for the Deadhorse Coulee Member (Chapter 5) support the inclusion of Eusuchia and *Adocus* in an inland community. These results contrast with the results of Brinkman et al. (2004), who regarded these taxa (with Eusuchia being equivalent to *Leidyosuchus* and alligatorines in that study) as coastal in terms of abundance distributions. Although the non-significant nature of this trend in the current study would not be worthy of note in isolation, this observation does agree with similar results from the Deadhorse Coulee Member (Chapter 5). Alligatorines and *Adocus* are inferred to be coastal in distribution only in the southern Foremost-Oldman assemblages (Brinkman et al. 2004) and not in the more northern Oldman-Dinosaur Park assemblages (Brinkman 1990). The Foremost-Oldman assemblages represent a time interval that may still have been experiencing a decline in mean annual temperature after the Santonian thermal maximum (Wolfe and Upchurch 1987). This may have caused a decrease in the abundance of these taxa in this unit due to temperature rather than a palaeoenvironmental shift to more inland environments. Another possibility for this discrepancy may be due to fact that the species represented in the current study are not likely the same species as those in Campanian beds (Brinkman 2003; Ryan and Evans 2005; Chapter 3; Chapter 7) and may belong to different palaeocommunities than their later counterparts. Closer examination of palaeocommunities involving these taxa from these and other localities may help elucidate these patterns.

Myledaphus is known to have a northern distribution in the Campanian (Lehman 1997). Champsosaurs are rare in the Deadhorse Coulee Member and their remains have not been identified from vertebrate microfossil localities. This group also belongs to a northern palaeocommunity (Lehman 1997; Tarduno et al. 1998; Larson et al. in press). Recovering the Solemydidae as a northern taxon was unexpected because European solemydid taxa have been postulated to have distributions controlled by equable temperatures (Lapparent de Broin and Murelaga 1999). However, the abundance distribution of this taxon agrees with the known geographic distribution of North American solemydids, which in the Late Cretaceous range from Utah (Eaton et al. 1999) to northern British Columbia (Rylaarsdam et al. 2006). Campanian records of the taxon, though, are from a restricted band of southern localities (Brinkman et al. 2004; Eaton et al. 1999; Demar and Breithaupt 2008; Sullivan and Lucas 2003; Sankey 2006). The change in distribution of this taxon may be due to a change in the global temperature gradient (Amiot 2004) in the Campanian after a thermal high. During this change, it is likely that, as mean global temperature decreases, the mean temperature at the equator remains roughly the same, but mean temperature near the poles drastically declines. Although not statistically significant, the absence of Polyodontidae from the Utah localities, particularly the inland locality is interpreted as a real absence. Given their likely immigration path from Asia sometime prior to the latest Santonian (Chapter 3; Grande et al. 2002), a northern distribution of this taxon would expected. Hadrosauridae has not previously been identified as a northern taxon, but Lehman (1997) did show such a trend in lambeosaurine hadrosaurs.

Denazinemys sp. and Goniopholididae are more characteristic of southern palaeocommunities (Lehman 1997; Sullivan and Lucas 2003). Although not previously noted for vertebrate microfossil localities, the distribution of Vidalamiinae is consistent with the biogeography of other members of the subfamily (Grande and Bemis 1998). *Lonchidion*, a marine-freshwater shark, also shows a trend for increased abundance in the southern Campanian localities

(Lehman 1997). This may not be the case in the Santonian, during which time it is absent from the John Henry Member localities. *Coniophis* may have a southern distribution (Lehman 1997) and, indeed, is completely absent in Alberta during the Campanian (Caldwell 2005). *Coniophis* is not present in the John Henry Member, but it is rare in all localities where is does occur (Lehman 1997; Demar and Breithaupt 2008), making up, at most, 2% of the vertebrate assemblage (Demar and Breithaupt 2008). It is possible that the rarity of *Coniophis* in these southern assemblages is due to a real rarity of preservation pontential of the taxon. The southern preference of the taxa in this palaeocommunity is indicated by the lack of all of these taxa from the Campanian deposits of Alberta (and of *Denazinemys* sp. from the Santonian of Alberta). As well, similar taxa appear in southern Alberta during the next global thermal maximum near the end of the Maastrichtian (Estes 1964; Baszio 1997). As hypothesized, changes in abundance of these taxa at the various localities occurred in a predictable fashion between the late Santonian and middle Campanian. As the global mean temperature dropped, taxa in the southern (warmer) palaeocommunity became rare or absent in more northerly localities (Alberta and Montana), whereas the taxa in the northern (colder) palaeocommunity became more abundant in more southern localities. The results of this study concerning the major mammalian groups may not be supported by analyses of distribution abundances of lower-level taxa, as species diversity in these groups are high (Chapter 3). If these results are correct, they demonstrate mammal provinciality in the Cretaceous of the Western Interior Basin.

Conclusions

This study provides strong quantitative support for the provinciality of non-marine and freshwater vertebrate taxa in the Late Cretaceous of North America. By analyzing the relatively poorly-known Santonian localities of Alberta and Utah that were deposited during a global thermal high relative to Campanian time, comparisons can be made to Campanian assemblages to validate hypothesized northern and southern palaeocommunities. As well, coastal and inland palaeocommunities can be compared to younger localities to document similarities and differences as these communities change through time.

During the Santonian, the following taxa belong to a coastal palaeocommunity: *Rhinobatos*, *Lepisosteus*, Vidalamiinae, and possibly Multituberculata. Taxa likely belonging to an inland palaeocommunity are Caudata, *Albanerpeton*, cf. *Gilchristosuchus palatinus*, Metatheria, basal Theria, Teiidae, *Adocus*, and Eusuchia. Anura is not demonstrably inland in its distribution in the Santonian, in contrast with its distribution in Campanian beds (Brinkman et al. 2004), although this result may be confounded with a possible northern distribution of this taxon. This is the first whole fauna study to find trends of distribution in the major mammalian groups (Brinkman 1990; Brinkman et al. 2004).

Latitudinal provincialism that is believed to correlate with temperature trends is also evident. Taxa such as *Myledaphus*, Lepisosteidae, Solemydidae, and Hadrosauridae characterize a northern palaeocommunity illustrated by the DCM.

This contrasts with a palaeocommunity of southern vertebrate taxa in the John Henry Member that includes Vidalamiinae, *Denazinemys* sp., Goniopholididae, and possibly Multituberculata. These northern and southern palaeocommunities are mostly consistent through time, with many taxa fitting these distribution patterns during Santonian and Campanian times. The distributions of these temperature controlled palaeocommunities explain many of the differences (both in changes of abundance and non-overlap of taxa) that have been documented between northern and southern assemblages (Lehman 1997; Brinkman 2004; Sullivan and Lucas 2003; Eaton et al. 1999; Sankey 2006).

Analyses of rank abundance (Brinkman 1990) and non-overlapping possible ranges of true relative abundance (Moore et al. 2007) provide independent and often supporting results for trends seen in the data. The use of multiple tests provides validation that the patterns observed in this study are real. Using these methods (even on a relatively small dataset), predictable taxon distribution patterns emerge that support many aspects of previously suggested non-marine vertebrate provincialism. These methods may provide a useful tool in further evaluating these trends in the future.

Table 6-1. Absolute abundances of all taxa at sites UMNH VP Loc. 99 and UMNH VP Loc. 424.

Taxon	UMNH VP 99	UMNH VP 424
Myledaphus	3	
Rhinobatos	44	1
Belonostomus	12	1
?*Lepidotes*	26	5
Lepisosteus	418	3
Vidalamiinae indet.	268	
Paralbula	5	
Esocoidea	1	
indet. teleost	28	36
Albanerpeton	3	72
Caudata	7	259
Anura	2	17
indet. turtle	1	1
Adocus	6	20
Solemydidae	12	1
Baenidae	2	
cf. *Denazinemys*		33
Trionychidae	2	7
indet. lizard	3	
Teiidae	2	14
Cordylidae		5

Varanoidea		1
Anguidae		22
cf. *Gilchristosuchus*	71	242
Eusuchia	16	41
Goniopholididae	32	18
Ornithopoda	1	
Iguanodontia	2	
Hadrosauridae	31	25
Leptoceratopsidae	2	
Ceratopsidae	30	10
Pachycephalosauridae		1
cf. *Richardoestesia gilmorei*	5	11
cf. *Richardoestesia isosceles*	2	5
Dromaeosaurinae	1	3
Saurornitholestinae	1	1
cf. *Paronychodon lacustris*	4	2
Microraptorinae	6	25
indet. small theropod		2
Alticonodon		2
Multituberculata	93	44
indet. Theria	30	80
Metatheria	3	47
"thumb" beast	9	4
indet. Mammalia	12	32

Table 6-2. The rank, relative abundances, and possible range of true assemblage relative abundances of the most common taxa in sites UMNH VP Loc. 99 and UMNH VP Loc. 424. RA, relative abundance.

UMNH VP 99				UMNH VP 424			
Rank	Taxon	RA	Range	Rank	Taxon	RA	Range
1	*Lepisosteus*	0.315	0.292−0.339	1	Caudata	0.237	0.213−0.261
2	Vidalamiinae	0.224	0.201−0.247	2	*Gilchristosuchus*	0.221	0.197−0.246
3.5	Multituberculata	0.078	0.055−0.101	3.5	indet. Theria	0.073	0.049−0.097
3.5	*Gilchristosuchus*	0.059	0.036−0.082	3.5	*Albanerpeton*	0.066	0.042−0.090
6.5	Goniopholididae	0.027	0.004−0.050	7.5	Metatheria	0.043	0.019−0.067
6.5	Hadrosauridae	0.026	0.003−0.049	7.5	Multituberculata	0.040	0.016−0.064
6.5	Ceratopsidae	0.025	0.002−0.048	7.5	Eusuchia	0.038	0.013−0.062
6.5	indet. Theria	0.025	0.002−0.048	7.5	indet. teleost	0.033	0.009−0.057
				7.5	*Denazinemys*	0.030	0.006−0.054
				7.5	indet. Mammalia	0.029	0.005−0.053

Table 6-3. Rank abundances of all taxa at UMNH VP Loc. 99 and UMNH VP Loc. 424 and combined Deadhorse Coulee Member Level II and Level III localities with results of the Spearman's rho analysis. Ties are averaged.

Taxon	UMNH VP 99	UMNH VP 424	MR Level II	MR Level III	ρ	Prob>ρ
Myledaphus	26.5	48	4	2	0.2	0.80
Lonchidion	50	48	17	43	-0.2	0.80
Rhinobatos	5	33	50	54	0.4	0.60
Belonostomus	15	33	50	47	0.2	0.80
?*Lepidotes*	12	22	24	26.5	0.4	0.60
Lepisosteus	1	25.5	1	1	0.7746	0.23
Lepisosteidae	50	48	6	5	-0.4	0.60
Polyodontidae	50	48	50	39	-0.7379	0.26
Amiinae	50	48	31.5	39	-0.2	0.80
Vidalamiinae	2	48	7	43	1	0.00
Paralbula	22	48	36	24	0.8	0.20
Esocoidea	38	48	50	34.5	0	1.00
indet. teleost	11	8	5	10	-0.4	0.60
Albanerpeton	26.5	4	11	12	-0.8	0.20
Caudata	18	1	13	8	-1	0.00
Anura	32	16	8	9	-0.2	0.80
indet. turtle	38	33	50	36.5	-0.8	0.20
Adocus	19.5	14	14.5	11	-0.8	0.20
Solemydidae	15	33	16	6	0.4	0.60
Baenidae	32	48	10	21	0.4	0.60

Denazinemys	50	9	50	54	-0.3162	0.68
Trionychidae	32	20	12	30	-0.4	0.60
indet. lizard	26.5	48	22.5	18	0.2	0.80
Teiidae	32	17	20.5	15.5	-0.8	0.20
Cordylidae	50	22	50	54	-0.3162	0.68
Varanoidea	50	33	36	34.5	-1	0.00
Auguidae	50	13	19	23	-0.8	0.20
lizard ossicles	50	48	27.5	13	-0.4	0.60
Coniophis	50	48	50	43	-0.7379	0.26
indet. Crocodylomorpha	50	48	33	54	0	1.00
Gilchristosuchus	4	2	3	3	-0.9487	0.05
Eusuchia	13	7	9	7	-0.9487	0.05
Goniopholididae	7	15	20.5	18	0.2	0.80
Ankylosauridae	50	48	50	39	-0.7379	0.26
Nodosauridae	50	48	50	43	-0.7379	0.26
Ornithopoda	38	48	50	54	0.4	0.60
Iguanodontia	32	48	50	54	0.4	0.60
Hadrosauridae	8	11.5	2	4	0.4	0.60
Leptoceratopsidae	32	37	50	47	0.2	0.80
Ceratopsidae	9.5	19	26	15.5	0.4	0.60
Pachycephalosauridae	50	33	50	29	-0.7379	0.26
cf. *R. gilmorei*	22	18	27.5	25	-0.4	0.60
cf. *R. isosceles*	32	22	18	18	-0.3162	0.68
Tyrannosauridae	50	48	22.5	14	-0.2	0.80
Dromaeosauridae	50	48	39	32.5	-0.4	0.60

Dromaeosaurinae	38	25.5	29.5	31	-0.8	0.20
Saurornitholestinae	38	33	29.5	43	0	1.00
cf. *P. lacustris*	24	28	34	28	0.3162	0.68
Microraptorinae	19.5	11.5	50	54	-0.2	0.80
cf. Aves	50	48	36	36.5	-0.2	0.80
indet. small theropod	50	28	50	22	-0.7379	0.26
Alticonodon	50	28	50	54	-0.3162	0.68
Multituberculata	3	6	14.5	54	0.4	0.60
indet. Theria	9.5	3	50	54	-0.2	0.80
Metatheria	26.5	5	25	20	-1	0.00
"thumb" beast	17	24	39	54	0.4	0.60
indet. Mammalia	15	10	31.5	26.5	-0.4	0.60

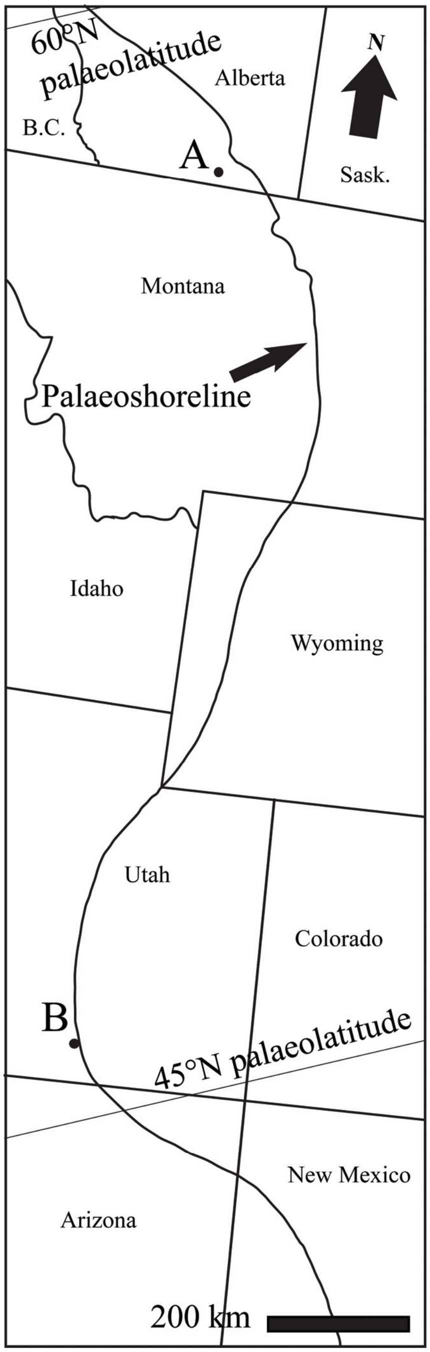
Table 6-4. The relative abundance, and possible range of true assemblage relative abundances similarities of the taxa in northern and southern localities. RA, relative abundance.

	John Henry Member		Deadhorse Coulee Member	
Taxon	RA	Range	RA	Range
Myledaphus	0.001	0−0.018	0.135	0.125−0.144
Rhinobatos	0.012	0.003−0.036	0.000	0−0.009
Lonchidion	0.000	0−0.017	0.004	0−0.014
Polyodontidae	0.000	0−0.017	0.000	0−0.010
Belonostomus	0.006	0−0.022	0.000	0−0.010
?*Lepidotes*	0.014	0−0.030	0.003	0−0.013
Lepisosteus	0.166	0.150−0.183	0.308	0.299−0.317
Lepisosteidae	0.000	0−0.017	0.047	0.038−0.057
Amiinae	0.000	0−0.017	0.001	0−0.011
Vidalamiinae	0.117	0.100−0.134	0.013	0.003−0.022
Paralbula	0.002	0−0.019	0.002	0−0.012
Esocoidea	0.000	0−0.017	0.001	0−0.010
indet. teleost	0.028	0.011−0.045	0.030	0.020−0.039
Albanerpeton	0.033	0.016−0.049	0.010	0.001−0.020
Caudata	0.116	0.100−0.133	0.015	0.005−0.024
Anura	0.008	0−0.025	0.022	0.012−0.031
indet. turtle	0.001	0−0.018	0.001	0−0.010
Adocus	0.011	0−0.028	0.011	0.002−0.021
Solemydidae	0.006	0−0.022	0.036	0.027−0.046

Baenidae	0.001	0−0.018	0.009	0−0.019
Denazinemys	0.014	0−0.031	0.000	0−0.009
Trionychidae	0.004	0−0.021	0.006	0−0.016
indet. lizard	0.001	0−0.018	0.006	0−0.015
Teiidae	0.007	0−0.024	0.007	0−0.016
Cordylidae	0.002	0−0.019	0.000	0−0.009
Varanoidea	0.000	0−0.017	0.001	0−0.010
Auguidae	0.010	0−0.026	0.006	0−0.015
lizard ossicles	0.000	0−0.017	0.005	0−0.015
Coniophis	0.000	0−0.0.017	0.003	0−0.013
indet. Crocodylomorpha	0.000	0−0.017	0.001	0−0.010
cf. *Gilchristosuchus*	0.137	0.120−0.153	0.120	0.110−0.129
Eusuchia	0.025	0.008−0.042	0.027	0.018−0.037
Goniopholididae	0.022	0.005−0.039	0.006	0−0.016
Ankylosauridae	0.000	0−0.017	0.000	0−0.010
Nodosauridae	0.000	0−0.017	0.000	0−0.010
Ornithopoda	0.000	0−0.017	0.000	0−0.009
Iguanodontia	0.001	0−0.018	0.000	0−0.009
Hadrosauridae	0.024	0.008−0.041	0.121	0.111−0.130
Leptoceratopsidae	0.001	0−0.018	0.000	0−0.010
Ceratopsidae	0.017	0.001−0.034	0.005	0−0.015
Pachycephalosauridae	0.000	0−0.017	0.001	0−0.011
Tyrannosauridae	0.000	0−0.017	0.007	0−0.016
cf. *R.gilmorei*	0.007	0−0.024	0.003	0−0.012
cf. *R. isosceles*	0.003	0−0.020	0.007	0−0.016

Dromaeosauridae	0.000	0−0.017	0.000	0−0.010
Dromaeosaurinae	0.002	0−0.018	0.003	0−0.012
Saurornitholestinae	0.001	0−0.018	0.004	0−0.013
cf. *P. lacustris*	0.003	0−0.019	0.001	0−0.010
Microraptorinae	0.014	0−0.030	0.000	0−0.009
cf. Aves	0.000	0−0.017	0.001	0−0.011
indet. small theropod	0.001	0−0.018	0.000	0−0.010
Alticonodon	0.001	0−0.018	0.000	0−0.009
Multituberculata	0.060	0.043−0.077	0.007	0−0.017
indet. Theria	0.048	0.031−0.065	0.000	0−0.009
Metatheria	0.022	0.005−0.039	0.003	0−0.013
"thumb" beast	0.006	0−0.022	0.000	0−0.010
indet. Mammalia	0.019	0.003−0.036	0.002	0−0.011

Fig. 6-1. Palaeogeography of localities during the late Santonian superimposed on modern political boundaries. A) Deadhorse Coulee Member localities, B) John Henry Member localities. Figure modified from Landman and Cobban (2007), Payenberg (2002), and Brinkman (2003).



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Chapter 7 — Multivariate analyses of small theropod teeth and implications for paleoecological turnovers through time

Introduction

Small theropods have often been identified based on isolated, shed tooth crowns from vertebrate microfossil bonebeds. Currie et al. (1990) looked specifically at theropod teeth from the Dinosaur Park Formation and made use of associated skeletal remains to confidently identify specimens. Based on these identifications, though, many subsequent workers (Baszio 1997; Sankey 2001; Fanti and Miyashita 2009) have identified shed theropod teeth to species without similar comparison to skeletal material within the formation of interest, often because such comparative material does not exist. Study of more abundant dinosaurs has shown faunal turnovers between and even within formations (Currie 2003; Ryan and Evans 2005), making the identification of a single species existing for several million years and in non-equivalent formations unlikely.

Canonical variate analysis has been used with moderate success in numerically identifying shed theropod teeth (Smith et al. 2005; Larson 2008). Here, a similar method, pairwise discriminant function analysis (DFA), is used to compare morphotypes of small theropods from various North American formations to determine whether they are quantitatively distinct. Although Buckley et al. (in press) showed that significant differences between juvenile and adult tyrannosaurs could be observed, such significant differences due to ontogeny were not noted for the small theropod *Coelophysis bauri* (Buckley 2008). Such a difference is here interpreted as the discrimination of different tooth morphs through an ontogenetic series involving a greater than tenfold increase.

Materials and methods

Measurements of over 1000 teeth from ten Late Cretaceous formations were collected (Appendix 4). Measurements were taken from Sankey et al. (2002, 2005), Sankey (2008), Smith et al. (2005), and Larson (2008). Unpublished data from Farlow et al. (1991) and Longrich (2008), as well as original measurements by the author were also used. Specimens from which original data were gathered are curated at the TMP. Principal measurements included fore-aft basal length (FABL), crown height (CH), basal width (BW), and posterior denticle density (PDD) (see Larson 2008 for usage) or their closest approximation if different measurements were employed in the gathered data. Anterior denticle density (ADD), because it was measured infrequently and was often absent, was used only when the difference between the sample sizes of the two morphotypes would otherwise violate the assumptions of the DFA. In some instances, fewer variables were analyzed due to lack of published measurements.

Specimens were a priori separated into several categories based on two parameters: morphotype and formation. Each category, consisting of at least five specimens having four or five measurements, was compared to every other category in a pairwise fashion using DFA in the statistical program JMP (2002). Hit ratios (the percentage of correctly identified specimens in the analysis) are tabulated in Table 7-1. Although Hammer and Harper (2006) considered a 90% hit ratio the minimum for differentiating morphotypes, a cut off of 85% was used in this analysis. This, as can be observed in Table 7-1, more consistently reflects the pattern seen in data in discriminating between different morphotypes. As well, multivariate analysis of variance analyses (MANOVA) were performed to determine the significance of the comparisons. Categories with fewer than five specimens were observed to be less reliable in determining significance, and were not included. Even with sample sizes between five and ten specimens, inconsistencies between DFA and MANOVA results were noted, probably due to the small samples not displaying the range of variation likely present in the morphotype. In addition, comparisons between type and referred isolated material from the same formation were used to test this method.

Results

The analyses show that many of the previously identified morphotypes, when separated by formation are distinct from each other (Table 7-1). As well, when these morphotypes are from roughly equivalent formations, there is no significant difference between them. Similar morphotypes from the Oldman, Dinosaur Park, and Judith River formations, the Lance and Hell Creek formations, and the Milk River and John Henry Member of the Straight Cliffs formations are indistinguishable from each other. Analyses conducted with only three variables often had decreased hit ratios; however, there seems to be no difference between analyses with four or five variables, and large differences in quantity between morphotypes seemed to have little effect. As morphotypes of cf. *Paronychodon lacustris* from all formations lack denticles, only three (sometimes only two) variables could be analyzed for those specimens. As such, there were frequent problems discerning the specimens. As well, samples with only three to ten specimens seemed to inflate the p-values of the MANOVA, increasing the amount of Type I error. Such was the case for many cf. *Richardestesia* taxa.

When the teeth of type material were compared to referred specimens from the same formation, *Atrociraptor marshalli* and *Saurornitholestes langstoni* teeth were indistinguishable from their referred teeth, while *Dromaeosaurus albertensis* had p-value=0.0037. The type and known referred material of other species are insufficient for the analyses.

Recognized morphotypes

Subfamily Saurornitholestinae

The Milk River Formation saurornitholestine was regarded as significantly different from all other theropod tooth categories in the MANOVA and all but one of the comparable-sized categories in the DFA. The DFA did not discriminate between this category and the Milk River cf. *R. gilmorei*. This similarity has been noted in the past (Baszio 1997), but with the significantly different means seen in the MANOVA and differing denticle morphology, this likely represents an overlap in tooth size in two distinct taxa. The similarity in the DFA to the Aguja saurornitholestine is likely a factor of disparate sample size, resulting in a hit ratio that is close to, but not over, the cut off of 85%.

Teeth from the type specimen of *Bambiraptor feinbergorum* were distinct from all other categories in both the DFA and MANOVA analyses.

The type specimen teeth of *Saurornitholestes langstoni* were indistinguishable in both the DFA and MANOVA from other cf. *Saurornitholestes* teeth from the Dinosaur Park Formation. The Dinosaur Park category was also indistinguishable from both the Oldman and Lance categories in the DFA, although the MANOVA regarded the Lance category as significantly different. As well, the Hell Creek saurornitholestine, although only analyzed with three variables, matches the Lance in both of the analyses. Although possibly different taxa, specimens from these Campanian and Maastrichtian localities are at this time indistinguishable both qualitatively and quantitatively. Lance and Hell Creek specimens are here regarded as cf. *Saurornitholestes* sp.. The Lance category is also similar to the Horseshoe Canyon dromaeosaurine in the DFA, although this is not supported by the MANOVA or the denticle morphology.

Measurements from the type teeth of *Atrociraptor marshalli* were compared to referred teeth from the same formation (the Horseshoe Canyon Formation). These teeth were indistinguishable in both the MANOVA and DFA analyses, with results of p=0.4454 and 72%, respectively. This species ranges from the lower to the upper Horseshoe Canyon Formation (Larson et al., in press). The only quantitatively similar category to *A. marshalli* was the Milk River dromaeosaurid. These categories were identical in both the MANOVA and DFA analysis. Although they cannot be distinguished quantitatively, the small sample size and large stratigraphic separation make the referral of these two categories to the same taxon questionable. However, in lack of any evidence for separation, these Milk River teeth can be regarded as cf. *Atrociraptor* sp.

The Aguja saurornitholestine was not found to be distinct from the Milk River dromaeosaurine, or the John Henry and Horseshoe Canyon *Richardoestesia* cf. *R. gilmorei* in the DFA, although the Milk River dromaeosaurine was significantly different in the MANOVA. The DFA, in fact, differentiated categories from the Milk River dromaeosaurine often just over 80% of the time. It is possible that this poor resolution is due to sampling of the category not encompassing the complete range of variation for the taxon. The similarity of the Aguja saurornitholestine to the two cf. *Richardoestesia* categories cannot be explained as easily, and may indicate the presence of previously undocumented cf. *Richardoestesia* cf. *R. gilmorei* from this formation. Alternatively, the small sample size for this category may not illustrate the full variation present from whole animals, and may seem similar to other categories with better known dentitions.

Subfamily Dromaeosaurinae

Dromaeosaurus albertensis type material was shown in the DFA to be identical to those of referred material from the Dinosaur Park Formation with a hit ratio of 78%. However, the MANOVA analysis resulted in a p=0.0004, a significant difference in multivariate means. This indicates that the type material does not adequately represent the variability present in the species as seen in the isolated teeth. In the DFA, these teeth are also shown to be identical to those from the Oldman and Horseshoe Canyon formations. However, in the MANOVA, only the Oldman category is supported, and both analyses indicate a significant difference between the Oldman and Horseshoe Canyon categories. These results support the referral of the Oldman category to *D. albertensis*, but not the referral of the Horseshoe Canyon category. This corroborates the occurrence of the twisted anterior carina morphological characteristic of the species to the exclusion of all other taxa.

The Horseshoe Canyon Formation category represents a distinct morphotype in all comparisons, except as previously mentioned and in the case of the Milk River dromaeosaurid. This referral would not be supported by the denticle morphology, and, as previously mentioned, this category may be referable to *Atrociraptor*.

Teeth referred to *Zapsalis abradens* from the Dinosaur Park Formation correspond closely to the measurements of the type specimen in the Judith River Formation described by Cope (1876b). This name, in the current study, was regarded as valid as the distinct morphology and absence in the type specimen of

D. albertensis support this morphotype as a distinct species. These teeth correspond to those referred to as *Dromaeosaurus* Type A by Sankey et al. (2002). These specimens are characterized by dromaeosaurine-like denticles and pronounced longitudinal ridges. *Z. abradens* was dissimilar to all of the other categories in both the DFA and MANOVA analyses.

The teeth of the Milk River cf. *Zapsalis* sp. (which possess ridges like those of *Z. abradens*) were not distinct from those of the Milk River dromaeosaurine (which lack ridges) in the DFA. However, they were significantly different in the MANOVA, indicating that these categories belong to the same taxon and represent variation along the tooth row. This finding illustrates the need to exercise caution when identifying morphotypes as distinct taxa, as qualitative characteristics like ridges can give misleading identifications. The Milk River cf. *Zapsalis* sp. was differentiated from every other category in both analyses. A morphotype referable to *Zapsalis* also occurs in the Lance and Hell Creek formations, although the available sample size was not great enough to provide reliable results in the analyses.

Family Troodontidae

Teeth referred to *Troodon formosus* from the type formation (the Judith River Formation) were indistinguishable from troodontid teeth from the Dinosaur Park Formation in both the DFA and MANOVA. They were not similar to any other category of teeth.

Troodontid teeth from the Horseshoe Canyon Formation were also not distinct from the Dinosaur Park Formation teeth in the DFA. However, they were distinct in the MANOVA, and the hit ratio of 83% in the DFA makes this similarity suspect. No such similarity was seen in the analyses with the Judith River *T. formosus*. Given these results, these teeth are regarded as distinct morphotypes, although Currie (1987) found no basis for separating the fragmentary specimens found in the Dinosaur Park and Horseshoe Canyon formations as distinct species.

Pectinodon bakkeri was described on the basis of dental material from the Lance Formation (Carpenter 1982). It was found to be a valid taxon by Longrich (2008) based on qualitative characters. Both analyses show discrimination of *P. bakkeri* teeth to the exclusion of every other category except those of cf. *Pectinodon* from the Hell Creek Formation, indicating that these categories are the same morphotype. Teeth referable to *Pectinodon* have also been documented from the Dinosaur Park Formation, although the abundance of these teeth is not large enough to include in the analyses.

The tooth taxon *Paronychodon lacustris*, originally described from the Judith River Formation (Cope 1876a), as currently diagnosed (Currie et al. 1990), does not possess denticles. As such, only three commonly used measurements (FABL, BW, and CH) were available for this study, which was insufficient to adequately differentiate these teeth from other small theropod teeth. In the available data, these teeth are present in the Milk River, Straight Cliffs, Oldman, Dinosaur Park, Aguja, Lance, and Hell Creek Formations. These teeth have been tentatively hypothesized as belonging to a troodontid based on enamel microstructure (Hwang 2005; Larson 2008), and lacking any better-supported hypothesis, that classification is retained here.

Family incertae sedis: the *Richardoestesia* complex

Teeth referred to the genus *Richardoestesia* present a taxonomic problem in the fossil record of North America. This problem is partly due to questionable referrals of morphotypes to *Richardoestesia gilmorei* and the diagnosis of *R. isosceles* (Sankey 2001). Another problem is the large degree of similarity, both qualitatively and quantitatively, in all of the teeth referred to these taxa, despite great disparity of ages and locations. These issues caused unexpected and often conflicting results in the DFA and MANOVA analyses of the current study (Table 7-1). However, given the results of both of the analyses, a tentative identification of different morphotypes can be reached.

Richardoestesia gilmorei, the type of which, because of its possession of only germ teeth, does not facilitate comparison with measurements of shed teeth, closely matches the measurements of the Oldman cf. *R. gilmorei*. However, both of these categories closely match the Oldman and Dinosaur Park *R. isosceles*. This indicates that teeth from these formations that were identified as *R. isosceles* have been misidentified. The Horseshoe Canyon cf. *R. gilmorei* may also be referable to this morphotype, but sample size for this category has caused it to appear similar to many other categories in the MANOVA.

Richardoestesia isosceles, the type of which is a partial tooth from the Aguja Formation of Texas, appears to be distinct from all of the other *Richardoestesia* categories except for the Oldman and Dinosaur Park *R. isosceles*. Given that these two categories may be referable to *R. gilmorei*, this supports the possibility that *R. isosceles* is a subjective junior synonym of *R. gilmorei*. However, *R. isosceles* teeth sensu stricto do appear distinct from *R. gilmorei* teeth.

The Milk River Formation and John Henry Member of the Straight Cliffs Formation, which are considered to be stratigraphic equivalents (Eaton 2006), also appear to have indistinguishable *Richardoestesia* morphotypes. Both formations include a shorter *Richardoestesia* sp. cf. *R. gilmorei* and a taller *Richardoestesia* sp. cf. *R. isosceles*. Both of these morphotypes are consistently different from each other. A similar pattern can be seen in the Lance and Hell Creek formations, in which two readily identifiable morphotypes can be seen in both formations: a shorter one referable to *Richardoestesia* sp. cf. *R. gilmorei* and a taller one referable to *Richardoestesia* sp. cf. *R. isosceles*. These two morphs are different from the qualitatively similar morphotypes seen in the Milk River and Straight Cliffs formations. Each of the Lance and Hell Creek morphs are also indistinguishable when comparing similar morphs from the two formations in which they occur.

Interpretations and conclusions

Using the results of the pairwise DFA, stratigraphic ranges of morphotypes can be tabulated (Fig. 7-1). Each distinguishable morphotype found in the analyses likely represents a distinct taxon (Hammer and Harper, 2006; Buckley, 2008), bringing the minimum of numerically supported small theropod taxa in this study to 19. That the type and referred material (as well as referred material from time-equivalent formations) were consistently indistinguishable provides great support for the usefulness of this methodology. In situ dental material in closely related taxa seemed to greatly improve the robustness of the analyses, as illustrated by the well-resolved dromaeosaurids and poorly-resolved *Richardoestesia* taxa. Small sample sizes for some morphotypes makes interpretation difficult. Therefore, the Horseshoe Canyon cf. *R. gilmorei*, the Lance *Zapsalis* sp., and all of the cf. *P. lacustris* were left out of Fig. 7-1.

The conclusion that Oldman and Dinosaur Park *R. gilmorei* and *R. isosceles* are indistinguishable indicates that in these formations, specimens identified as *R. isosceles* may have been misidentified. This implies that *R. isosceles* may not be present in these formations at all.

These results show that identification of small theropod teeth is possible, even when comparable skeletal material is lacking. The method employed was consistent in all of the formations tested, and may be useful in other areas of the world for different time periods, particularly those with poor skeletal representation of specimens. Resolution was especially high between teeth from taxa from different families, so comparisons of any theropod species should be possible. It is useful to keep in mind, however, that these methods are dependent on having sufficiently large sample sizes, and are not useful for diagnosing new species. Furthermore, these results indicate that small theropod diversity in the Late Cretaceous of western North America is much greater than has been fully appreciated, and illustrate turnovers in the fauna roughly equivalent to other dinosaurian lineages. For the first time, shed theropod teeth can be used to better understand theropod diversity changes through the fossil record and how this relates to faunal turnover.

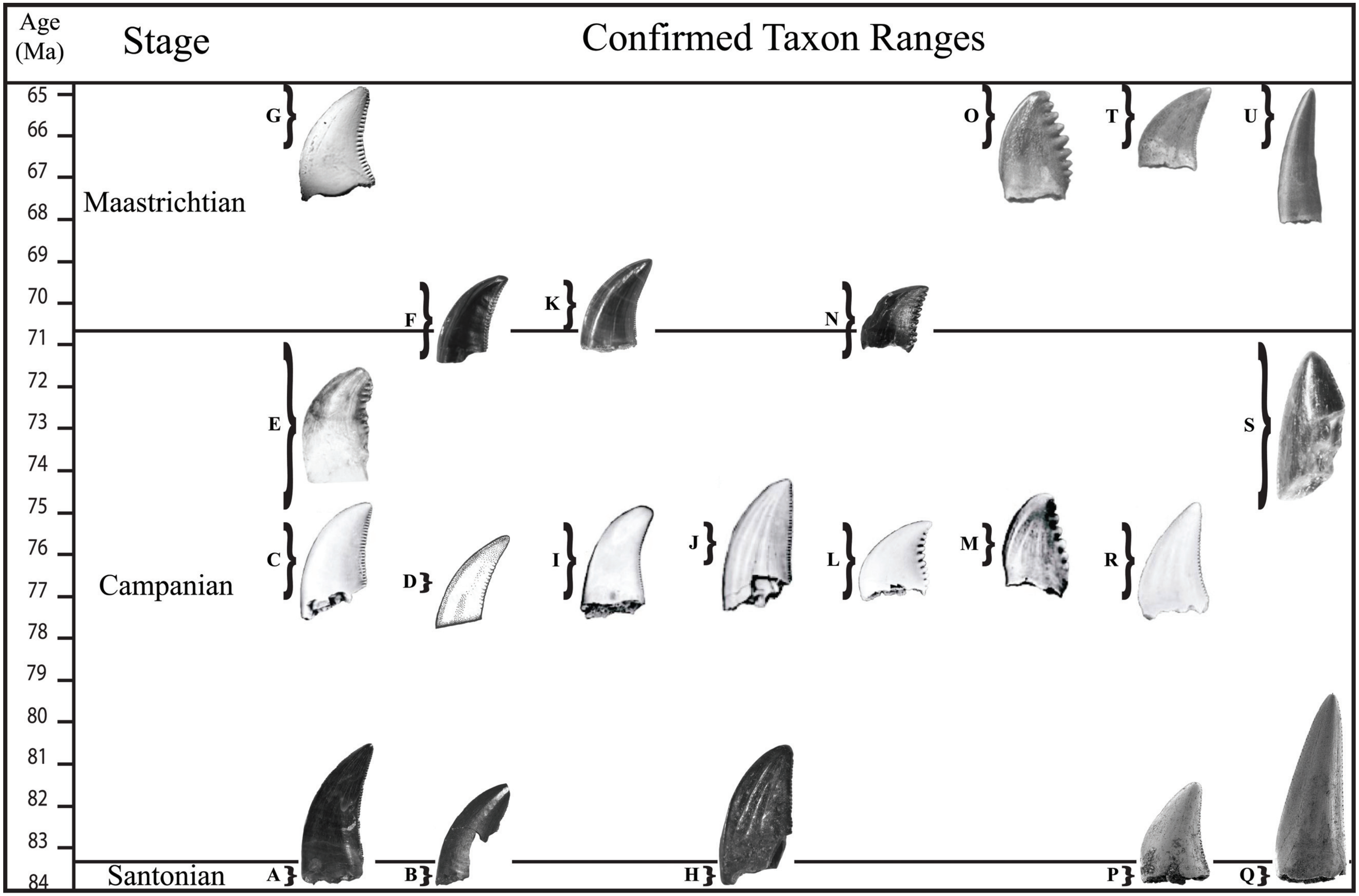
Table 7-1. Hit ratios for each pairwise Discriminant Function Analysis (DFA) of theropod tooth morphotypes showing the percentage of correctly identified elements. *, analysed with only three variables.

†	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z	AA	AB	AC	AD	AE	AF	AG	AH	AI
A	X	93	91	87	96	82	94	77*	92	100	99	99	96	100	98	100	100	100	100	100	100	82	93	90	96	93	87	79*	98	100	100	99	98	100	99
B		X	87	90	100	100	97	91*	85	100	96	100	95	100	100	100	100	100	100	100	100	92	100	93	96	100	100	90*	99	100	100	96	100	100	96
C			X	71	100	93	83	80*	84	92	97	93	90	98	100	100	100	100	100	98	96	96	93	92	97	88	91	90*	99	100	100	94	100	100	97
D				X	87*	93	79	71*	86	91	93	96*	95	93	91	99	90	100	100	97	97	96	93	93	92	94	88	84*	99	100	100	97	100	98	98
E					X	94	97	84*	88	100	85	94	95	100	69	100	100	100	100	100	100	100	100	100	100	100	100	93*	99	100	100	96	100	100	100
F						X	100	79*	82	100	99	100	100	100	94	100	100	100	100	100	100	78	82	100	92	77	91	74*	95	100	89	96	100	97	100
G							X	70*	75	91	89	81	95	100	91	100	100	100	100	100	100	99	100	100	98	100	95	78*	99	100	100	93	100	100	100
H								X	76*	88*	87*	91*	91*	93*	96*	100*	100*	100*	100*	100*	100*	88*	87*	83*	85*	78*	77*	67*	94*	100*	96*	75*	98*	95*	92*
I									X	90	90	88	80	98	84	100	100	100	100	100	100	96	100	100	100	100	92	76*	99	100	100	97	100	100	100
J										X	67	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100*	99	100	100	95	100	100	100
K											X	78	95	94	95	100	100	100	100	100	100	100	100	99	100	99	99	92*	99	100	100	99	100	100	100
L												X	95	94	82	100	100	100	100	100	100	100	100	100	100	100	96	95*	99	100	100	100	100	100	100
M													X	100	100	100	100	100	100	100	100	96	100	100	100	100	100	95*	99	100	100	96	100	100	100
N														X	94	100	100	100	100	100	100	100	100	100	100	100	100	100*	100	100	100	100	100	100	100
O															X	100	100	100	100	100	100	100	100	100	100	100	100	100*	99	100	100	100	100	100	100
P																X	76	83	100	100	93	100	100	100	100	100	100	100*	100	100	100	100	100	100	100
Q																	X	100	100	100	100	100	100	100	100	100	100	100*	100	100	100	100	100	100	100

	R	S	T	U	V	W	X	Y	Z	AA	AB	AC	AD	AE	AF	AG	AH	AI
R	X	100	100	94	100	100	100	100	100	100	100*	100	100	100	100	100	100	100
S		X	81	100	100	100	100	100	100	100	100*	100	100	100	100	100	100	100
T			X	54	100	100	100	100	100	100	100*	100	100	100	100	100	100	100
U				X	100	100	100	100	100	100	100*	100	100	100	100	100	100	100
V					X	59	75	88	90	88	87*	90	96	94	90	89	95	93
W						X	100	79	83	95	89*	90	100	88	96	100	91	96
X							X	85	87	100	86*	81	100	92	85	100	96	77
Y								X	80	83	92*	73	100	68	66	86	82	79
Z									X	86	87*	95	100	77	95	100	86	82
AA										X	72*	89	94	87	90	100	89	94
AB											X	93*	100*	100*	83*	100*	95*	93*
AC												X	80	74	67	74	65	63
AD													X	92	90	100	89	95
AE														X	60	93	82	89
AF															X	76	85	82
AG																X	97	100
AH																	X	62
AI																		X

†A) Milk River Saurornitholestinae, B) *Bambiraptor feinbergorum*, C) Oldman Saurornitholestinae, D) *Saurornitholestes langstoni*, E) *Atrociraptor marshalli*, F) Aguja Saurornitholestinae, G) Lance Saurornitholestinae, H) Hell Creek Saurornitholestinae, I) Milk River Dromaeosaurinae, J) Oldman Dromaeosaurinae, K) *Dromaeosaurus albertensis*, L) Horseshoe Canyon Dromaeosaurinae, M) Milk River *Zapsalis* sp., N) *Zapsalis abradens*, O) Milk River Dromaeosauridae, P) Dinosaur Park *Troodon*, Q) *Troodon formosus*, R) Horseshoe Canyon *Troodon*, S) Dinosaur Park *Pectinodon*, T) *Pectinodon bakkeri*, U) Hell Creek *Pectinodon*, V) Milk River cf. *R. gilmorei*, W) John Henry cf. *R. gilmorei*, X) Oldman cf. *R. gilmorei*, Y) *Richardoestesia gilmorei*, Z) Horseshoe Canyon cf. *R. gilmorei*, AA) Lance cf. *R. gilmorei*, AB) Hell Creek cf. *R. gilmorei*, AC) Milk River cf. *R. isosceles*, AD) John Henry *R. isosceles*, AE) Oldman cf. *R. isosceles*, AF) Dinosaur Park cf. *R. isosceles*, AG) *Richardoestesia isosceles*, AH) Lance cf. *R. isosceles*, AI) Hell Creek cf. *R. isosceles*.

Figure 7-1. Summary chart of confirmed morphotypes showing their relative stratigraphic ages as observed in this study. A) Milk River Saurornitholestinae, B) cf. *Atrociraptor* sp., C) *Saurornitholestes langstoni*, D) *Bambiraptor feinbergorum*, E) Aguja Saurornitholestinae, F) *Atrociraptor marshalli*, G) cf. *Saurornithololestes* sp., H) cf. *Zapsalis* sp., I) *Dromaeosaurus albertensis*, J) *Zapsalis abradens*, K) Horseshoe Canyon Dromaeosaurinae, L) *Troodon formosus*, M) cf. *Pectinodon* sp., N) *Troodon* sp., O) *Pectinodon bakkeri*, P) Aquilan cf. *Richardoestesia gilmorei*, Q) Aquilan cf. *Richardoestesia isosceles*, R) *Richardoestesia gilmorei*, S) *Richardoestesia isosceles*, T) Lancian cf. *Richardoestesia gilmorei*, and U) Lancian cf. *Richardoestesia isosceles*.


Age (Ma)
Stage
Confirmed Taxon Ranges
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
Maastrichtian
Campanian
Santonian
G
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Chapter 8 — General discussion and concluding remarks

This study presents new information on the fossil vertebrate assemblage of the Santonian DCM in southern Alberta. These strata, consisting of non-marine siltstones and sandstones with laterally discontinuous lignitic beds, preserve the earliest relatively substantial non-marine vertebrate fauna in western Canada and are of interest because they predate the well-studied Campanian assemblages of Alberta.

The stratigraphic placement of old vertebrate quarries, the creation of detailed stratigraphic sections, and accurate elevation data obtained via the use of differential GPS have allowed documentation of the geographic and temporal distribution of vertebrate fossils and their depositional environments. Vertebrate fossils occur throughout the lower 28 m of the DCM, but are primarily recovered from localities clustered around three stratigraphic levels. Two of these fossil-rich levels appear to have accumulated in floodplain deposits, while the third (and highest) level occurs in channel sandstones and contains fossils that were likely reworked and deposited as a channel lag. The fossils collected from these localities, both in the future and from previous studies, can now be interpreted in light of this contextual evidence of preservation, such as known stratigraphic distributions of described species. As well, the mapping of these localities allows for further collection work to be directed towards these locations and stratigraphic levels (for greatest chance of well-preserved material), or in exploratory prospecting for potentially important localities outside of these known areas.

The known fauna of the DCM, when diagnosable to species, indicates a unique fauna characteristic of the Aquilan North American Land Mammal "Age" (Lillegraven and McKenna 1986). Other taxa, when known from relatively complete material, are also recognized as distinct species, such as the new species of *Neurankylus*, *N. lithographicus* (Chapter 4) and a new pachycephalosaurid dinosaur (Chapter 3). It is suspected that continued collection from the DCM will yield many more new species that lived during this time interval. Higher level taxonomy, as well, indicates a unique fauna with members of more commonly found older groups (ie. triconodontids, goniopholidids) mixed with typical terminal Cretaceous members (ie. baenids, ceratopsids, "alphadontids"), creating a distinct "transitional" fauna.

The progradational shoreline at the time of deposition (Meyer 1998; Payenberg et al. 2002) allows for the preservation of sites with subtle changes in abundances to a more inland assemblage, although all known localities are certainly coastal and preserve essentially identical assemblages in terms of represented taxa. The fact that all localities examined occur roughly 40 km from the palaeoshoreline can be attributed to two probable causes: 1) the coincidental postdepositional structure of the beds eroding overlying sediment parallel to the palaeoshoreline, and 2) the proximity of sites in terms of absolute time of deposition. Further exploratory studies may alleviate both of these factors. Indeed, vertebrate fossils from stratigraphically lower localities have been collected but await processing and description.

Comparisons to the temporally similar Utah assemblages have demonstrated provinciality in the Santonian of western North American, as has been suggested for Campanian localities (Lehman 1997; Brinkman et al. 2004). Coastal, inland, northern, and southern palaeocommunities are all supported with taxa specific to each. This comparison also provides evidence for the timing of a dispersal event from Asia, sometime prior to the latest Santonian.

Comparisons to younger assemblages provide support of temperature-dependent taxon distributions with abundances that represent those of northern/southern palaeocommunities matching those of mean global temperature (Wolfe and Upchurch 1987). Although higher taxonomic groups exhibit these predictable abundance changes with respect to changing palaeoenvironmental shifts to different community provinces, morphometric evidence (discriminant function analysis of quantitative characters) supports the separation of these lineages on a finer taxonomic scale, consistent with the duration of other communities between turnover events (Ryan and Evans 2005).

Together, the documentation, description, and analyses of the current study are valuable tools for evaluating numerous aspects of the vertebrate fauna of the DCM of the Milk River Formation and will be useful for future explorations of the unit. Vertebrate microfossil bonebed material is especially useful for relative abundance analyses because the localities usually preserve a high diversity of taxa represented by diagnostic (if fragmentary) elements. As well, large samples can be taken to acquire the minimum number of elements with statistically viable sample sizes with relatively little effort compared to macrovertebrate assemblages. Due to the large sample sizes possible, multivariate methodologies like discriminant function analysis become useful tools in establishing different morphologies and the expected range in variation of fossil organisms and one day may establish patterns of evolution in these organisms through time.

Conversely, vertebrate microfossil material is, in general, disarticulated, and this causes problems in the description of new species and referral of differing elements to actual species. It is possible that this problem may be remedied by comparisons of relative abundance (Brinkman and Neuman 2002), and certainly, future articulated specimens not yet discovered and described will help the situation, but for now most such associations remain impossible, leaving taxa as indeterminable higher taxonomic units.

Descriptions of whole assemblages are necessary for our understanding of palaeoecologies and how and why these assemblages change through time. Linking faunal trends with shifts in palaeoenvironments is certain to become a popular line of investigation. Further research into poorly-described or unknown assemblages has the potential to increase our knowledge of these past ecosystems and integrate them into a whole-world picture of changing landscapes through time.

The future of vertebrate microfossil studies, with proper validation techniques verifying results, will be able to illustrate patterns of vertebrate relative abundances and use that data to establish actual faunal trends. These faunal trends are useful in determining ecosystem response to environmental change, extinction of species, or species migration. Using a combination of systematic palaeontology, geology, experimental validation, and statistics, vertebrate microfossil studies will increasing be able to reveal more about the past ecosystems. To research global analyses of assemblages, well-sampled data from a large array of represented times and localities must be available, and it is hoped that further studies, when possible, are conducted on other poorly-understood assemblages.

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Appendix 1

Modifications to character matrix of Lyson, T.R., and Joyce, W.G. 2009. A revision of *Plesiobaena* (Testudines: Baenidae) and an assessment of baenid ecology across the K/T boundary. Journal of Paleontology 83: 833–853.

Taxa added:

Dinochelys whitei, *Dorsetochelys delairi*, *'Dorsetochelys' buzzops*, *Uluops uluops*, *Arundelemys dardeni*, *Thescelus insiliens*, *Neurankylus baueri*, *Neurankylus* ROM864, Ojo Alamo *Neurankylus*, *Neurankylus lithographicus*, *Neurankylus wyomingensis*, Lance *Neurankylus*

Characters modified:

Character 36: rescored for *N. eximius*

Character 38: changed and combined with Character 57

Character 39: scored for P. brinkman

Character 50: rescored for consistency

Character 53: scored for P. brinkman

Character 57: deleted – combined with 38

Character 60: deleted – too variable to be reliable

Character 71. Temporal emargination: 0) does not expose otic cap-sule; 1) stapedial foramen exposed in dorsal view; 2) anterior to an-terior margin of otic capsule.

Character 72. Contribution of supraoccipital to stapedial foramen: 0) enters stapedial foramen; 1) excluded from stapedial foramen.

Character 73. Anterior nuchal projection: 0) absent; 1) present.

Character 74. Skull ornamentation: 0) pustolose (*Glyptops*-like); 1) rugose.

Character 75. Foramen posterius canalis caroticum internus position: 0) in posterior half; 1) in anterior half of pterygoid-basisphenoid su-ture.

Character 76. Ventral angle between pterygoid occipital process and transverse process of pterygoid: 0) less than 90 degrees; 1) more than 90 degrees or equal.

Character 77. Narrowest part of ventral pterygoid: 0) even or post-erior to anteriormost portion of ventral exposure of basisphenoid; 1) anterior to basisphenoid.

Character 78. Opisthotic in posterior view: 0) width less than 1.5 times height; 1) width greater than 1.5 times height.

Character 79. External ventrolateral quadrate-quadratojugal suture: 0) shorter; 1) roughly equal in height or taller than tympanic recess.

Character 80. Foramen nervi hypoglossi directed: 0) posterolaterally not visible from posterior view; 1) posteriorly visible from posterior view.

Character 81. Exoccipital processes of basioccipital: 0) thinner; 1) roughly same thickness as height of condyle.

Character 82. Anterior border of frontals: 0) extends anterior to pre-frontals; 1) does not extend past prefrontals.

Character 83. Anterior border of frontals: 0) pointed anteromedially; 1) straight.

Character 84. Shell ornamentation: 0) rugose (*Glyptops*-like); 1) faintly ridged.

Character 85. Dorsal medial keel on posterior vertebrals: 0) absent; 1) present.

Character 86. Dorsolateral gutters on carapace: 0) absent; 1) present.

Character 87. Cervical scute: 0) small and rectangular long edge on carapace margin; 1) small and rectangular short edge on margin; 2) not as above.

Character 88. Anterior edge of nuchal: 0) slightly recessed; 1) anterior or even with first marginals.

Character 89. Nuchal lateral margins: 0) tapers anteriorly; 1) parallel; 2) widens anteriorly.

Character 90. Second and third vertebrals: 0) do not narrow anteriorly; 1) narrow anteriorly.

Character 91. Fifth vertebral: 0) wide anterolateral sulci not present on second suprapygal (same width as fourth vertebral); 1) narrow sulci present on second suprapygal (narrower than fourth vertebral).

Character 92. Fourth marginal resembling asymmetrical trapezoid: 0) no; 1) yes, widest part posterior.

Character 93. Early fusion of first suprapygal to eighth neural: 0) absent; 1) present.

Character 94. Posterior neurals: 0) hexagonal; 1) square.

Character 95. First-second costal suture: 0) slightly posteriorly inclined or perpendicular to long axis; 1) slightly anteriorly inclined; 2) greatly anteriorly inclined.

Character 96. Greatest plastron length: 0) less; 1) equal or greater than greatest carapace width.

Character 97. Carapace width to carapace length: 0) around 0.8; 1) around 0.85.

Character 98. Plastron length to carapace length: 0) less than or equal 0.8; 1) greater than 0.8.

Character 99. Anterior lobe length to posterior lobe length: 0) 0.82 or less; 1) greater than 0.84.

Character 100. Gular shape: 0) rectangular with large gular humeral sulcus; 1) heart-shaped with little or no gular-humeral sulcus; 2) semicircular no humeral contact.

Character 101. Gulars: 0) do not overlap entoplastron; 1) overlap en-toplastron.

Character 102. Gular-extragular sulci: 0) straight, 1) bent.

Character 103. Inframarginals: 0) narrower; 1) roughly equal to; 2) wider than ventral exposure of marginals.

Character 104. Size: 0) large (carapace width 300 mm or greater, skull condyle-premaxilla length greater than 60 mm; *Neurankylus*-sized); 1) small (carapace width less than 300 mm, skull condyle-premaxilla length 60 mm or less; *Plesiobaena*-sized).

Appendix 2

Specimens examined for phylogenetic analysis, asterisk indicates specimens examined from published material only.

Neurankylus eximius: CMN 1504*, AMNH 6098, ROM 854, ROM 1943, TMP 1989.036.0112, TMP 1999.055.0134, TMP 2003.012.0171, UALVP 30824.

Neurankylus lithographicus: TMP 2007.035.0045, TMP 1991.113.0001, TMP 1994.377.0001, TMP 1998.102.0014, TMP 2007.036.0001.

Neurankylus baueri: USNM 8344*, USNM 8531*, PMU.R24*, PMU.R25*, PMU.R27*.

Neurankylus wyomingensis: USNM 7581*.

other *Neurankylus* specimens: ROM 864, PMU.R26*, PMU.R28*, YPM 8239.

Appendix 3

Character-taxon matrix of baenid turtles used for parsimony and Bayesian analyses. *, previous character removed for parsimony analysis.

[1] *Pleurosternon bullockii* 0010000000 0000000000 000?0?0000
00?0?00000 00*00000*000 0000000000 0000001000 000-00?0*??
0011021000 0011?0?101 0?0

[2] *Glyptops plicatulus* 0110010000 0000000000 000?0?0000
00?0000100 00*00000*000 0000000000 0000000000 ?00-0000*00
0000000000 0001011101 000

[3] *Dinochelys whitei* ??1000???? ?000000?0? 0????????? ?????00000
00*00000*000 ?10101000? ???0???0?? ?00?????*?? 0010000001 0001101100
0-1

[4] *Dorsetochelys delairi* 001000?001 0000000100 0000?10200
2????10100 10*00000*00? ????0?0000 0?00012010 ?00110?0*??
0001000000 0001?1???? ??0

[5] *"Dorsetochelys" buzzops* 110001?0?0 0000000000 00?1?10111 1?00??????
??*?????*??? ????????00 0?00002010 ??0?0010*11 ??0??????? ??????????

??1

[6] *Uluops uluops* 110000?0?0 0000000000 0011?1021? 1?????????
??*?????*??? ????????00 0?00002010 ??0110?0*?? ?????????? ??????????
??1

[7] *Arundelemys dardeni* 000000?000 000011001- 100?000210 21????????
??*?????*??? ????????00 0000102012 1?11001?*11 00???????? ??????????
??1

[8] *Trinitichelys hiatti* 0000001000 0001000100 10001002??
21??????00 ?0*0000?*000 110?000000 0000001001 00100010*?1
1100001?1? 00?1???01 001

[9] *Neurankylus eximius* 10???0???? ??00100??? ?101???211 21???00100
00*00000*010 120(01)0100?? ??0?100?11 10111010*11 1011111210
0101101111 110

[10] *Neurankylus baueri* ?????????? ?????????? ?????????? ?????10100
00*00000*000 ?2000000?? ?????????? ?0??????*?? ??11111011
1(01)10010(01)01 010

[11] *Neurankylus* ROM864 ?????????? ?????????? ?????????? ??????0100 00*00000*0?0 ?1000100?? ?????????? ?0??????*?? ??10111?10 1??1010?01 100

[12] *Neurankylus* Ojo Alamo ?????????? ?????????? ?????????? ?????10100 00*00000*000 ?2000000?? ?????????? ?0??????*?? ??11111010 111?????11 110

[13] *Neurankylus lithographicus* 0????????? ?????????? ?????0021? 21??????00 00*0000?*0?0 ?0000?00?? ??0??????? 1011100?*00 ??1?1?1?10 1??200010? 010

[14] *Neurankylus wyomingensis* ?????????? ?????????? ?????????? ?????0010? 0?*?0??0*0?? ???0?0???? ?????????? ????????*?? ??001???10 ?????????? ?10

[15] *Neurankylus* Lance ?????????? ?????????? ?????????? ?????10000 0?*00000*0?? ???01100?? ?????????? ????????*?? ??10101?10 ????0000?? ?10

[17] *Thescelus insiliens* 100??0??0? 0000021100 100??0121? 20???00100 00*10000*001 1211010100 000000?001 001101?0*?? 0110000000

0??1111121 120

[19] *Plesiobaena antiqua* 1000001011 01(02)1101010 1000110111
1001011210 10*00000*011 121(01)010100 0010001002 011010?0*??
0110001100 0(01)11111020 121

[20] *Peckemys brinkman* 1000001011 0??1111110 1000100211
100111?200 10*10000*001 121?0?0000 0012001001 00110110*11
??10001?00 0???1??0-- -21

[21] *Cedrobaena putorius* 1000011111 1??1111100 111011(01)211
1001?????? ??*?????*??? ???????00 0000010101 0?1111?0*?? ??????????
?????????? ??1

[22] *Boremys pulchra* 111000?10? 0101101?00 1000?00211
1010031201 10*1(01)011*101 1110111100 0000001002 001110?1*??
0110001001 0011011120 021

[23] *Boremys grandis* ?????????? ?????????? ?????????? ?????31201
10*10110*100 11101111?? ?????????? ?0??????*?? ??10011200 ???1111121
120

[24] *Eubaena cephalica* 1110102100 0101121000 1000300211
10???????? ??*?????*??? ????????00 0001101001 0?1110?0*?? 00????????
?????????? ??1

[25] *Palatobaena cohen* 2000012111 1122011110 1000210211
10011?1210 ?0*00000*011 1211110111 1111111102 01111010*11
1110001000 0??01??1-- -21

[26] *Palatobaena bairdi* 2000012111 1122111210 1110210211
10011????? ??*?????*??? ????????11 1101112100 ??111010*11 11????????
?????????? ??1

[27] *Palatobaena gaffneyi* 2000112111 1122111110 1110210111
10???????? ??*?????*??? ????????11 110111210? 1?111010*11 01????????
?????????? ??1

[28] *Stygiochelys estesi* 1101001110 1112101100 1001001111
11???????? ??*1111?*0?0 ?21?1?0100 0001001002 0?101010*11 01????????
?????????? ??1

[29] *Baena arenosa* 1101001110 01?2101201 0111000211
1121021200 11*11010*000 1211110100 0000000010 ?11110?0*??

0110021100 0110101021 121

[30] *Chisternon undatum* 1101001110 0112101201 0011001111
1120021201 10*11110*001 1211110100 0000101011 001100?0*??
011002110? 0?00011121 010

[31] *Gammerabaena sonsalla*?000011110 111102101? ??1??10211 10????????
??*?????*??? ?????0??00 00?11??10? ????????*?? ?????????? ?????????? ???

[32] *Goleremys mckennai* 1000001100 0102101210 10??100211 10????????
??*?????*??? ????????01 00000??00? ????????*?? ?????????? ?????????? ???

Appendix 4

Measurements for small theropod teeth with source data reference. FABL, fore-aft basal length; CH, crown height; BW, basal width; and PDD, posterior denticle density.

Specimen number	ID (this study)	FABL	CH	BW	ADD	PDD	Source
John Henry Member of Straight Cliffs Formation (85.8-?84 Ma)							
UMNH 424-14398	Dromaeosaurinae	3.97	4.44	2.15	35.0	25.5	this study
Milk River Formation (~83.5 Ma)							
UALVP48422	Dromaeosaurinae	4.32	5.23	2.40	30.0	25.0	Larson (2008)
UALVP48424	Dromaeosaurinae	5.48	11.55	3.40		20.5	Larson (2008)
UALVP49568	Dromaeosaurinae	2.16	4.90	1.52		22.0	Larson (2008)
UALVP49569	Dromaeosaurinae	4.32	7.06	1.88	47.0	23.0	Larson (2008)
UALVP47995	Dromaeosaurinae	4.15	4.73	1.88		25.0	Larson (2008)
UALVP47996	Dromaeosaurinae	3.74	4.07	1.52	37.5	22.5	Larson (2008)
UALVP48062	Dromaeosaurinae	4.90	7.39	1.96	35.0	25.0	Larson (2008)
UALVP48069	Dromaeosaurinae	3.32	6.64	1.62		25.0	Larson (2008)
UALVP48071	Dromaeosaurinae	3.74	5.06	1.56	32.5	22.5	Larson (2008)
UALVP48420	Dromaeosaurinae	6.30	9.10	2.80	25.0	20.0	Larson (2008)
UALVP48426	Dromaeosaurinae	5.31	5.64	2.44	35.0	21.5	Larson (2008)
UALVP48439	Dromaeosaurinae	8.58	15.93	5.06	25.0	20.0	Larson (2008)
UALVP48472	Dromaeosaurinae	4.32	4.90	2.36	27.5	23.0	Larson (2008)
UALVP49570	Dromaeosaurinae	3.49	4.73	1.60	37.0	22.5	Larson (2008)
UALVP49571	Dromaeosaurinae	4.73	8.05	3.00		25.0	Larson (2008)
UALVP49572	Dromaeosaurinae	2.30	3.40	1.20	40.0	25.0	Larson (2008)
UALVP49573	Dromaeosaurinae	7.53	8.23	4.23	21.5	19.0	Larson (2008)
UALVP49574	Dromaeosaurinae	8.75	11.38	6.56		23.0	Larson (2008)
UALVP49575	Dromaeosaurinae	3.07	5.31	1.70		25.5	Larson (2008)
UALVP49576	Dromaeosaurinae	3.40	6.97	1.78	35.0	25.0	Larson (2008)

CMNFV uncat	Dromaeosaurinae	5.60	9.50	3.00	25.0	18.5	Larson (2008)
UALVP48028	Dromaeosaurinae	2.66	4.98	2.32		23.0	Larson (2008)
UALVP49594	Dromaeosaurinae	2.66	3.82	2.20		20.5	Larson (2008)
UALVP49595	Dromaeosaurinae	2.74	5.73	2.00	30.0	21.3	Larson (2008)
Foremost Formation (79.5-77 Ma)							
TMP88.86.30	Dromaeosaurinae	2.90	7.30	2.00		20.0	Sankey et al. (2002)
Oldman Formation (77-76 Ma)							
TMP99.55.328	Dromaeosaurinae	3.90	8.50	2.30		20.0	Sankey et al. (2002)
TMP89.77.6	Dromaeosaurinae	4.50	11.50	2.90		16.3	Sankey et al. (2002)
TMP89.77.6	Dromaeosaurinae	4.70	11.00	2.80		17.5	Sankey et al. (2002)
TMP92.77.2	Dromaeosaurinae	5.90	10.50	3.90		20.0	Sankey et al. (2002)
TMP85.68.32	Dromaeosaurinae	5.30	14.50	4.20		17.5	Sankey et al. (2002)
TMP87.153.56	Dromaeosaurinae	5.70	9.50	3.90		17.5	Sankey et al. (2002)
Dinosaur Park Formation (76-75 Ma)							
TMP85.36.332	Dromaeosaurinae	3.60	6.40	2.30		25.0	Sankey et al. (2002)
TMP95.143.45	Dromaeosaurinae	4.10	9.00	2.80		20.0	Sankey et al. (2002)
TMP80.8.298	Dromaeosaurinae	4.30	9.80	2.70		15.0	Sankey et al. (2002)
TMP80.8.308	Dromaeosaurinae	4.90	8.50	2.70		17.5	Sankey et al. (2002)
TMP81.16.281	Dromaeosaurinae	5.00	10.00	3.20		15.0	Sankey et al. (2002)
TMP95.406.4	Dromaeosaurinae	5.00	11.40	3.50		17.5	Sankey et al. (2002)
TMP86.130.218	Dromaeosaurinae	5.10	10.80	3.10		16.3	Sankey et al. (2002)
TMP86.130.211	Dromaeosaurinae	5.20	9.50	3.10	15.2	15.0	Sankey et al. (2002) and Longrich (2008)
TMP81.26.175	Dromaeosaurinae	5.40	11.00	3.20	19.8	17.5	Sankey et al. (2002) and Longrich (2008)
TMP98.93.172	Dromaeosaurinae	5.40	10.50	2.90		17.5	Sankey et al. (2002)
TMP81.14.60	Dromaeosaurinae	5.50	11.50	3.70		17.5	Sankey et al. (2002)
TMP95.171.40	Dromaeosaurinae	5.50	12.30	3.70		20.0	Sankey et al. (2002)
TMP95.171.40	Dromaeosaurinae	6.20	14.00	3.50		20.0	Sankey et al. (2002)
TMP66.25.16	Dromaeosaurinae	5.70	14.00	3.30	18.6	16.3	Sankey et al. (2002) and Longrich (2008)
TMP79.8.732	Dromaeosaurinae	6.10	13.00	3.90		17.5	Sankey et al. (2002)

TMP80.16.2094	Dromaeosaurinae	7.10	13.50	4.00		17.5	Sankey et al. (2002)
TMP81.27.66	Dromaeosaurinae	7.00	13.50	4.50		15.0	Sankey et al. (2002)
TMP82.18.137	Dromaeosaurinae	6.40	11.00	4.00		16.3	Sankey et al. (2002)
TMP83.67.38	Dromaeosaurinae	7.80	13.20	4.10		15.0	Sankey et al. (2002)
TMP84.67.115	Dromaeosaurinae	6.00	12.00	3.20	17.4	17.5	Sankey et al. (2002) and Longrich (2008)
TMP84.89.48	Dromaeosaurinae	6.00	14.50	3.50		22.5	Sankey et al. (2002)
TMP86.18.99	Dromaeosaurinae	6.00	13.50	3.70		16.3	Sankey et al. (2002)
TMP86.76.11	Dromaeosaurinae	7.90	17.20	5.10		17.5	Sankey et al. (2002)
TMP89.155.2	Dromaeosaurinae	7.90	14.50	4.00		16.3	Sankey et al. (2002)
TMP89.36.354	Dromaeosaurinae	6.10	13.00	3.70		15.0	Sankey et al. (2002)
TMP93.36.460	Dromaeosaurinae	5.40	16.50	4.00		15.0	Sankey et al. (2002)
TMP93.36.462	Dromaeosaurinae	6.50	13.50	3.70		17.5	Sankey et al. (2002)
TMP93.36.472	Dromaeosaurinae	6.50	13.00	4.00		18.8	Sankey et al. (2002)
TMP94.12.241	Dromaeosaurinae	7.20	15.50	3.90		18.8	Sankey et al. (2002)
TMP94.12.247	Dromaeosaurinae	7.10	15.50	4.30		15.0	Sankey et al. (2002)
TMP94.12.652	Dromaeosaurinae	6.40	12.50	4.30		18.8	Sankey et al. (2002)
TMP94.172.39	Dromaeosaurinae	5.60	12.00	3.90		15.0	Sankey et al. (2002)
TMP95.127.26-a	Dromaeosaurinae	6.30	10.50	3.60		15.0	Sankey et al. (2002)
TMP95.137.1	Dromaeosaurinae	6.10	10.50	3.30		25.0	Sankey et al. (2002)
TMP96.12.362	Dromaeosaurinae	6.30	13.50	3.90		16.3	Sankey et al. (2002)
TMP95.151.10	Dromaeosaurinae	6.80	13.00	3.30		18.8	Sankey et al. (2002)
TMP79.14.1000	Dromaeosaurinae	4.20	8.80	2.70		15.0	Sankey et al. (2002)
TMP79.15.2	Dromaeosaurinae	5.50	13.00	3.90		15.0	Sankey et al. (2002)
TMP81.16.161	Dromaeosaurinae	4.00	10.50	3.00		15.0	Sankey et al. (2002)
TMP81.22.93	Dromaeosaurinae	3.50	7.80	2.70		17.5	Sankey et al. (2002)
TMP84.89.47	Dromaeosaurinae	5.00	11.00	4.10		16.3	Sankey et al. (2002)
TMP85.36.336	Dromaeosaurinae	4.90	11.00	3.50		20.0	Sankey et al. (2002)
TMP85.52.10	Dromaeosaurinae	3.80	6.50	2.00		22.5	Sankey et al. (2002)
TMP85.59.81	Dromaeosaurinae	5.50	12.00	3.40		16.3	Sankey et al. (2002)
TMP85.68.47	Dromaeosaurinae	4.90	9.80	2.50		16.3	Sankey et al. (2002)

TMP86.54.67	Dromaeosaurinae	3.80	8.00	2.80		17.5	Sankey et al. (2002)
TMP88.50.127	Dromaeosaurinae	4.10	10.00	2.50		17.5	Sankey et al. (2002)
TMP90.145.1	Dromaeosaurinae	5.80	10.70	3.90		15.0	Sankey et al. (2002)
TMP94.12.266	Dromaeosaurinae	3.80	9.20	2.90		15.0	Sankey et al. (2002)
TMP95.134.5	Dromaeosaurinae	5.10	11.00	4.20		17.5	Sankey et al. (2002)
TMP95.151.8	Dromaeosaurinae	4.30	10.50	3.10		17.5	Sankey et al. (2002)
TMP95.181.9	Dromaeosaurinae	3.00	7.30	2.10		20.0	Sankey et al. (2002)
p812648	Dromaeosaurinae	6.20	11.00		17.0	18.0	Farlow et al. (1991)
p80897	Dromaeosaurinae	7.00	1.00		15.0	14.0	Farlow et al. (1991)
p836738	Dromaeosaurinae	7.80	12.00	4.20	17.0	15.0	Farlow et al. (1991)
nmceuncat	Dromaeosaurinae	7.10	11.00		16.0	15.0	Farlow et al. (1991)
nmceuncat	Dromaeosaurinae	6.00	12.00		16.0	15.0	Farlow et al. (1991)
p8218137	Dromaeosaurinae	6.20	9.00		16.0	16.0	Farlow et al. (1991)
p8220388	Dromaeosaurinae	7.90	19.00		18.0	16.0	Farlow et al. (1991)
p849912	Dromaeosaurinae	7.40	14.00		20.0	17.0	Farlow et al. (1991)
TMP80.8.214	Dromaeosaurinae	5.04	9.04	3.12		25.1	Longrich (2008)
TMP85.66.56	Dromaeosaurinae	5.16	10.96	2.96	14.2	15.2	Longrich (2008)
TMP2001.12.179	Dromaeosaurinae	5.04	10.31		12.8	14.2	Longrich (2008)
TMP2001.12.181	Dromaeosaurinae	7.30	12.52	4.53	15.2	14.7	Longrich (2008)
AMNH5356	*Dromaeosaurus albertensis*	7.21	12.86	4.06	13.8	17.0	Smith et al. (2005)
AMNH5356	*Dromaeosaurus albertensis*	6.84	11.58	3.70	15.0	15.0	Smith et al. (2005)
AMNH5356	*Dromaeosaurus albertensis*	7.64	12.38	4.02	15.8	17.5	Smith et al. (2005)
AMNH5356	*Dromaeosaurus albertensis*	6.28	10.68	3.13	8.8	15.0	Smith et al. (2005)
AMNH5356	*Dromaeosaurus albertensis*	6.69	10.98	3.32	15.0	16.3	Smith et al. (2005)
AMNH5356	*Dromaeosaurus albertensis*	5.70	9.70	3.11	17.5	22.5	Smith et al. (2005)
AMNH5356	*Dromaeosaurus albertensis*	5.46	9.40	4.03	15.0	25.0	Smith et al. (2005)
AMNH5356	*Dromaeosaurus albertensis*	6.09	11.55	3.81	13.8	15.0	Smith et al. (2005)
AMNH5356	*Dromaeosaurus albertensis*	6.47	11.22	3.91	15.0	17.5	Smith et al. (2005)
AMNH5356	*Dromaeosaurus albertensis*	6.56	11.27	3.89	15.0	17.5	Smith et al. (2005)
AMNH5356	*Dromaeosaurus albertensis*	5.56	8.52	3.27	17.0	17.5	Smith et al. (2005)

Judith River Group (Formation) (79.5-75 Ma)							
Bobs site	Dromaeosaurinae	6.00	13.00	4.60		15.0	Sankey et al. (2002)
Cretaceous (Belly River-St Mary River) (79.5-67 Ma)							
TMP82.11.2	Dromaeosaurinae	6.20	11.50	3.20		15.0	Sankey et al. (2002)
Aguja Middle Campanian (~79 Ma)							
LSUMG726:6218	Dromaeosaurinae	8.30	15.00	5.80		25.0	Sankey et al. (2005)
LSUMG834:8211	Dromaeosaurinae	7.00	10.00	3.50		17.5	Sankey et al. (2005)
Aguja Upper Campanian (?76-71? Ma)							
LSUMG741:6023	Dromaeosaurinae	2.00	3.00	1.20		22.5	Sankey et al. (2005)
LSUMG113:1375	Dromaeosaurinae	3.60	5.50	3.20		32.5	Sankey et al. (2005)
Horseshoe Canyon Formation (68-72 Ma)							
TMP03.45.60	Dromaeosaurinae	5.43	9.63	2.49	20.0	20.0	this study
TMP1998.63.71	Dromaeosaurinae	4.57	6.56	1.99	21.5	21.5	this study
TMP98.64.17	Dromaeosaurinae	5.95	9.63	3.15	25.0	16.5	this study
TMP99.50.116	Dromaeosaurinae	7.70	11.73	4.03	20.0	17.5	this study
TMP00.45.40	Dromaeosaurinae	6.56	9.98	2.82	22.5	19.0	this study
TMP00.45.102	Dromaeosaurinae	6.48	9.63	2.91		20.0	this study
TMP00.45.82	Dromaeosaurinae	6.13	11.03	3.40	19.0	16.0	this study
TMP01.45.83	Dromaeosaurinae	7.88	16.63	4.73	20.0	15.0	this study
TMP02.45.50	Dromaeosaurinae	6.65	11.20	3.32	21.5	18.0	this study
TMP98.63.32	Dromaeosaurinae	7.44	11.76	4.06	20.5	15.5	this study
Lance Formation (65.5-66.5 Ma)							
UCMP186891	Dromaeosaurinae	7.00	17.00			22.5	Sankey (2008)
DSCN 1690	Dromaeosaurinae	6.81	13.89	2.72	27.2	20.8	Longrich (2008)
DSCN 1498	Dromaeosaurinae	2.88	6.48			24.8	Longrich (2008)
AMNH A	Dromaeosaurinae	5.07	7.24	2.32		22.5	Longrich (2008)
AMNH (M?)	Dromaeosaurinae	5.72	8.70	2.57		21.4	Longrich (2008)
AMNH (5412?)	Dromaeosaurinae	5.62	11.18	2.68		23.4	Longrich (2008)
L	Dromaeosaurinae	5.77	10.15	2.60		20.3	Longrich (2008)
R	Dromaeosaurinae	6.32	9.28	2.74	25.1	19.1	Longrich (2008)

N	Dromaeosaurinae	5.40	9.41	2.81		19.8	Longrich (2008)
K	Dromaeosaurinae	5.60	8.55	2.42	29.9	22.5	Longrich (2008)
Q	Dromaeosaurinae	5.60	7.80	2.89		19.8	Longrich (2008)
AMNH27099: 5457	Dromaeosaurinae	6.70	8.48	2.83	28.7	21.4	Longrich (2008)
AMNH27099: 5457	Dromaeosaurinae	5.80	10.34	3.10		19.2	Longrich (2008)
AMNH27099 5462	Dromaeosaurinae	6.13	9.70	2.54	25.5	21.7	Longrich (2008)
AMNH27099 5462	Dromaeosaurinae	5.50	8.35	2.34	44.1	25.0	Longrich (2008)
AMNH27099 5464	Dromaeosaurinae	7.12	10.80	3.50	29.1	17.6	Longrich (2008)
AMNH5475	Dromaeosaurinae	5.70	8.49	2.22		22.7	Longrich (2008)
	Dromaeosaurinae	5.49	7.36	2.60	38.7	20.0	Longrich (2008)
5AMNH477L	Dromaeosaurinae	4.73	6.83	1.89	36.9	25.8	Longrich (2008)
AMNH5477R	Dromaeosaurinae	4.78	7.02	2.04	33.3	20.8	Longrich (2008)
AMNH5695	Dromaeosaurinae	5.52	10.60	3.02		22.7	Longrich (2008)
AMNH(M) 5690	Dromaeosaurinae	6.25	13.16	3.63		18.2	Longrich (2008)
AMNH5688	Dromaeosaurinae	3.48	6.87	2.17		22.9	Longrich (2008)
cent	Dromaeosaurinae	4.08	7.99	1.56		25.0	Longrich (2008)
AMNH5682	Dromaeosaurinae	4.05	7.69	2.55		21.6	Longrich (2008)
AMNH5697	Dromaeosaurinae	4.48	10.73	3.08		23.8	Longrich (2008)
AMNH5703	Dromaeosaurinae	3.14	7.73	2.01		25.5	Longrich (2008)
AMNH5671.2	Dromaeosaurinae	4.99	8.85	2.19		22.4	Longrich (2008)
AMNH5545.1	Dromaeosaurinae	4.42	7.80			23.6	Longrich (2008)
AMNH5671.1	Dromaeosaurinae	4.84	6.45	2.07		24.8	Longrich (2008)
Upper Hell Creek Formation (65.5-66.75 Ma)							
UCMP124987	Theropoda	6.00	15.00			20.0	Sankey (2008)
UCMP120339	Theropoda	9.00	17.00			20.0	Sankey (2008)
UCMP186957	Dromaeosauridae	4.50	7.00			22.4	Sankey (2008)
UCMP120305	Megalosauridae	9.00	17.00			17.5	Sankey (2008)
UCMP186960	Dromaeosauridae	5.00	10.00			22.5	Sankey (2008)
UCMP187037	cf. *Dromaeosaurus*	3.60	10.00			22.5	Sankey (2008)
UCMP187039	Dromaeosauridae	4.50	9.00			25.0	Sankey (2008)

UCMP186967	Dromaeosauridae	7.00	13.00			20.0	Sankey (2008)
UCMP186968	Dromaeosauridae	6.00	10.00			17.5	Sankey (2008)
UCMP186972	Dromaeosauridae	6.00	10.00			20.0	Sankey (2008)
UCMP186970	Dromaeosauridae	7.00	13.00			20.0	Sankey (2008)
UCMP186973	Dromaeosauridae	2.80	7.00			25.0	Sankey (2008)
UCMP186971	Dromaeosauridae	7.00	13.00			20.0	Sankey (2008)
Milk River Formation (~83.5 Ma)							
UALVP48431	cf. *Zapsalis*	2.44	4.73	2.04		20.0	Larson (2008)
UALVP48468	cf. *Zapsalis*	3.32	5.31	1.80	35.0	22.5	Larson (2008)
UALVP49582	cf. *Zapsalis*	4.07	7.06	1.64		21.5	Larson (2008)
UALVP49583	cf. *Zapsalis*	4.90	8.22	2.40		20.5	Larson (2008)
UALVP49584	cf. *Zapsalis*	2.91	5.64	2.16		20.5	Larson (2008)
UALVP49585	cf. *Zapsalis*	2.74	5.31	2.28		23.5	Larson (2008)
UALVP49586	cf. *Zapsalis*	2.08	4.81	1.96		24.3	Larson (2008)
UALVP49587	cf. *Zapsalis*	2.24	4.98	1.74		26.0	Larson (2008)
UALVP49588	cf. *Zapsalis*	2.82	5.81	2.16		21.5	Larson (2008)
UALVP49589	cf. *Zapsalis*	2.99	5.23	2.28		24.0	Larson (2008)
UALVP49590	cf. *Zapsalis*	2.32	4.23	1.58		24.5	Larson (2008)
Dinosaur Park Formation (76-75 Ma)							
TMP84.163.80	cf. *Zapsalis abradens*	6.10	10.00	2.40		16.3	Sankey et al. (2002)
TMP80.16.833	cf. *Zapsalis abradens*	6.30	11.00	3.20		17.5	Sankey et al. (2002)
TMP82.19.458	cf. *Zapsalis abradens*	5.70	12.50	2.50		17.5	Sankey et al. (2002)
TMP82.19.458	cf. *Zapsalis abradens*	5.80	13.00	2.50		17.5	Sankey et al. (2002)
TMP82.19.7	cf. *Zapsalis abradens*	7.20	15.00	3.20		15.0	Sankey et al. (2002)
TMP85.58.65	cf. *Zapsalis abradens*	5.40	10.50	2.50		17.5	Sankey et al. (2002)
TMP85.6.2	cf. *Zapsalis abradens*	6.50	13.00	3.00		16.3	Sankey et al. (2002)
TMP86.77.112	cf. *Zapsalis abradens*	7.90	14.00	3.10		16.3	Sankey et al. (2002)
TMP87.36.5	cf. *Zapsalis abradens*	6.60	15.50	3.00		16.3	Sankey et al. (2002)
TMP89.36.312	cf. *Zapsalis abradens*	6.40	11.50	3.10		16.3	Sankey et al. (2002)
TMP94.12.268	cf. *Zapsalis abradens*	5.80	11.00	2.50		18.8	Sankey et al. (2002)

TMP97.133.2	cf. *Zapsalis abradens*	6.30	12.00	3.40		17.5	Sankey et al. (2002)
Judith River Group (Formation) (79.5-75 Ma)							
TMP79.15.3	cf. *Zapsalis abradens*	6.30	15.50	3.00		15.0	Sankey et al. (2002)
TMP84.91.40	cf. *Zapsalis abradens*	6.00	12.50	3.00		16.3	Sankey et al. (2002)
TMP84.91.40	cf. *Zapsalis abradens*	6.40	12.00	3.00		15.0	Sankey et al. (2002)
TMP85.6.131	cf. *Zapsalis abradens*	6.30	11.20	2.40		17.5	Sankey et al. (2002)
TMP85.6.133	cf. *Zapsalis abradens*	6.40	11.70	3.00		16.3	Sankey et al. (2002)
TMP86.36.425	cf. *Zapsalis abradens*	7.00	12.00	3.00		15.0	Sankey et al. (2002)
TMP87.50.8	cf. *Zapsalis abradens*	6.80	13.70	3.30		15.0	Sankey et al. (2002)
TMP89.50.202	cf. *Zapsalis abradens*	5.30	9.30	2.10		16.3	Sankey et al. (2002)
TMP90.50.208	cf. *Zapsalis abradens*	5.80	11.50	2.60		17.5	Sankey et al. (2002)
TMP90.53.21	cf. *Zapsalis abradens*	5.00	11.00	2.30		17.5	Sankey et al. (2002)
TMP91.50.60	cf. *Zapsalis abradens*	6.40	14.00	2.50		15.0	Sankey et al. (2002)
Lance Formation (65.5-66.5 Ma)							
UCMP187125	cf. *Zapsalis*	4.00	7.00			20.0	Sankey (2008)
UCMP187129	cf. *Zapsalis*	4.00	9.00			22.5	Sankey (2008)
UCMP187124	cf. *Zapsalis*	6.00	12.00			20.0	Sankey (2008)
UCMP187105	cf. *Zapsalis*	5.00	8.00			25.0	Sankey (2008)
UCMP187143	cf. *Zapsalis*	3.60	8.00			25.0	Sankey (2008)
UCMP187139	cf. *Zapsalis*	3.20	7.00			27.5	Sankey (2008)
Milk River Formation (~83.5 Ma)							
UALVP47980	Saurornitholestinae	4.15	5.06	1.64	35.0	23.8	Larson (2008)
UALVP47981	Saurornitholestinae	4.23	5.98	1.72	65.0	30.0	Larson (2008)
UALVP47983	Saurornitholestinae	4.57	6.56	1.83	50.0	25.0	Larson (2008)
UALVP47987	Saurornitholestinae	2.08	2.32	1.00	45.0	30.0	Larson (2008)
UALVP48029	Saurornitholestinae	3.74	5.89	1.72	40.0	25.0	Larson (2008)
UALVP48030	Saurornitholestinae	4.15	6.39	1.76	35.0	20.0	Larson (2008)
UALVP48031	Saurornitholestinae	1.84	2.20	0.84	55.0	30.0	Larson (2008)
UALVP48037	Saurornitholestinae	3.49	5.48	1.76	47.5	30.0	Larson (2008)
UALVP48044	Saurornitholestinae	2.49	4.81	1.28	45.0	25.0	Larson (2008)

UALVP48046	Saurornitholestinae	3.15	5.40	1.44	35.0	28.8	Larson (2008)
UALVP48047	Saurornitholestinae	2.64	3.40	1.16	40.0	25.0	Larson (2008)
UALVP48053	Saurornitholestinae	3.40	4.98	1.48	40.0	25.0	Larson (2008)
UALVP48054	Saurornitholestinae	2.74	4.40	1.10	41.0	31.5	Larson (2008)
UALVP48059	Saurornitholestinae	2.40	3.40	1.26	42.5	26.3	Larson (2008)
UALVP48061	Saurornitholestinae	4.32	6.47	1.66	31.5	22.5	Larson (2008)
UALVP48063	Saurornitholestinae	3.15	3.98	1.30	47.5	27.5	Larson (2008)
UALVP48064	Saurornitholestinae	4.07	7.22	1.62	32.5	25.0	Larson (2008)
UALVP48065	Saurornitholestinae	3.57	4.48	1.52	40.0	25.0	Larson (2008)
UALVP48066	Saurornitholestinae	4.40	6.89	1.68	55.0	27.5	Larson (2008)
UALVP48067	Saurornitholestinae	3.90	5.48	1.76	50.0	25.0	Larson (2008)
UALVP48068	Saurornitholestinae	4.23	4.48	1.88	40.0	21.5	Larson (2008)
UALVP48070	Saurornitholestinae	2.72	3.72	1.10	43.0	26.3	Larson (2008)
UALVP48073	Saurornitholestinae	2.74	5.06	1.12	50.0	32.5	Larson (2008)
UALVP48074	Saurornitholestinae	2.91	4.90	1.12	40.0	28.8	Larson (2008)
UALVP48075	Saurornitholestinae	3.08	3.24	1.24	38.0	23.0	Larson (2008)
UALVP48076	Saurornitholestinae	2.44	3.60	1.12	45.0	32.5	Larson (2008)
UALVP48077	Saurornitholestinae	3.12	3.76	1.18	45.0	30.0	Larson (2008)
UALVP48078	Saurornitholestinae	2.80	3.12	1.32	50.0	27.5	Larson (2008)
UALVP48080	Saurornitholestinae	2.40	2.68	1.18		28.5	Larson (2008)
UALVP48082	Saurornitholestinae	3.07	5.15	1.56	50.0	26.3	Larson (2008)
UALVP48095	Saurornitholestinae	2.84	3.32	1.42	33.0	25.0	Larson (2008)
UALVP48118	Saurornitholestinae	4.81	7.47	1.82	35.0	25.0	Larson (2008)
UALVP48126	Saurornitholestinae	3.57	6.06	1.86		27.5	Larson (2008)
UALVP48127	Saurornitholestinae	3.90	5.81	1.68		23.8	Larson (2008)
UALVP48128	Saurornitholestinae	3.24	4.15	1.24	45.0	25.0	Larson (2008)
UALVP48129	Saurornitholestinae	2.40	3.40	1.02	42.5	28.0	Larson (2008)
UALVP48135	Saurornitholestinae	1.76	2.00	0.84	55.0	30.0	Larson (2008)
UALVP48137	Saurornitholestinae	2.36	3.16	1.06		35.0	Larson (2008)
UALVP48221	Saurornitholestinae	2.08	2.52	0.88	50.0	40.0	Larson (2008)

UALVP48223	Saurornitholestinae	2.00	2.72	0.86	40.0	40.0	Larson (2008)
UALVP48249	Saurornitholestinae	1.64	2.28	0.80	50.0	40.0	Larson (2008)
UALVP48466	Saurornitholestinae	3.98	6.64	2.12	26.0	21.5	Larson (2008)
UALVP48478	Saurornitholestinae	2.28	2.64	1.16	34.0	22.5	Larson (2008)
UALVP50475	Saurornitholestinae	2.36	2.52	1.10	40.0	28.5	Larson (2008)
UALVP50476	Saurornitholestinae	2.66	4.15	1.12	41.0	31.0	Larson (2008)
UALVP50477	Saurornitholestinae	2.16	3.57	1.14		31.0	Larson (2008)
UALVP50478	Saurornitholestinae	2.91	3.82	1.32		28.0	Larson (2008)
UALVP50479	Saurornitholestinae	2.57	3.82	1.20	45.0	36.0	Larson (2008)
UALVP50480	Saurornitholestinae	2.16	4.23	1.02		33.0	Larson (2008)
UALVP50481	Saurornitholestinae	3.74	5.56	1.52	41.0	27.5	Larson (2008)
UALVP50482	Saurornitholestinae	3.07	5.06	1.44	45.0	30.0	Larson (2008)
UALVP50483	Saurornitholestinae	4.15	7.30	1.76	32.5	24.0	Larson (2008)
UALVP50484	Saurornitholestinae	2.83	3.40	1.12	45.0	31.0	Larson (2008)
UALVP50485	Saurornitholestinae	3.11	4.48	1.32	33.0	25.5	Larson (2008)
UALVP50486	Saurornitholestinae	2.91	3.90	1.36	35.0	25.0	Larson (2008)
UALVP50487	Saurornitholestinae	2.24	2.49	0.96	50.0	32.5	Larson (2008)
UALVP50488	Saurornitholestinae	2.57	4.07	1.30	44.0	29.5	Larson (2008)
UALVP50489	Saurornitholestinae	3.07	4.73	1.42	44.0	26.0	Larson (2008)
UALVP50490	Saurornitholestinae	4.32	5.81	1.90	32.5	22.0	Larson (2008)
UALVP50491	Saurornitholestinae	3.24	5.06	1.28	51.5	27.0	Larson (2008)
UALVP50492	Saurornitholestinae	3.40	4.90	1.58	40.0	26.5	Larson (2008)
UALVP50493	Saurornitholestinae	2.49	4.77	1.26		30.0	Larson (2008)
UALVP50494	Saurornitholestinae	2.91	5.23	1.46	57.5	29.5	Larson (2008)
UALVP50495	Saurornitholestinae	2.74	4.57	1.26	53.0	26.5	Larson (2008)
UALVP50496	Saurornitholestinae	4.32	6.47	1.44	40.5	27.0	Larson (2008)
UALVP50497	Saurornitholestinae	3.74	5.23	1.76	40.0	27.0	Larson (2008)
UALVP50498	Saurornitholestinae	2.91	3.40	1.24	42.5	25.5	Larson (2008)
UALVP50499	Saurornitholestinae	4.15	6.31	1.80	37.0	24.5	Larson (2008)
UALVP50500	Saurornitholestinae	3.57	6.23	1.60	53.0	23.5	Larson (2008)

UALVP50501	Saurornitholestinae	2.32	3.49	1.16	45.0	30.0	Larson (2008)
UALVP50502	Saurornitholestinae	2.36	2.76	0.94	48.5	29.0	Larson (2008)
UALVP50503	Saurornitholestinae	3.90	7.22	1.60		26.0	Larson (2008)
UALVP50504	Saurornitholestinae	3.40	4.98	1.40	46.0	29.5	Larson (2008)
UALVP50505	Saurornitholestinae	4.57	6.64	1.92	40.0	22.5	Larson (2008)
UALVP50506	Saurornitholestinae	4.23	7.55	1.64	38.5	27.5	Larson (2008)
UALVP50507	Saurornitholestinae	4.40	6.14	1.92	31.5	25.0	Larson (2008)
UALVP50508	Saurornitholestinae	2.28	2.76	1.08	35.0	24.0	Larson (2008)
UALVP50509	Saurornitholestinae	2.57	4.65	1.48		31.5	Larson (2008)
UALVP50510	Saurornitholestinae	2.16	3.57	1.26		28.5	Larson (2008)
UALVP50511	Saurornitholestinae	2.49	5.06	1.28	35.7	26.0	Larson (2008)
UALVP50512	Saurornitholestinae	2.16	3.86	1.26		27.5	Larson (2008)
UALVP50513	Saurornitholestinae	2.82	3.61	1.24	41.0	31.5	Larson (2008)
UALVP50514	Saurornitholestinae	2.91	4.07	1.26	55.0	27.5	Larson (2008)
UALVP50515	Saurornitholestinae	3.49	5.19	1.46	41.0	26.0	Larson (2008)
UALVP50516	Saurornitholestinae	2.40	2.88	0.90	40.0	39.0	Larson (2008)
UALVP50517	Saurornitholestinae	2.52	2.88	1.00		33.0	Larson (2008)
UALVP50518	Saurornitholestinae	2.60	2.94	1.04	42.5	31.0	Larson (2008)
UALVP50519	Saurornitholestinae	1.96	2.48	0.80	58.0	28.5	Larson (2008)
UALVP50520	Saurornitholestinae	3.57	5.48	1.38	44.0	27.5	Larson (2008)
UALVP50521	Saurornitholestinae	3.07	4.23	1.24	39.5	27.0	Larson (2008)
UALVP50522	Saurornitholestinae	3.98	5.23	1.62	45.0	23.5	Larson (2008)
UALVP50523	Saurornitholestinae	4.48	7.06	1.70	41.0	26.0	Larson (2008)
UALVP50524	Saurornitholestinae	3.90	6.39	1.80	38.5	24.0	Larson (2008)
UALVP50525	Saurornitholestinae	3.07	5.31	1.52		25.5	Larson (2008)
UALVP50526	Saurornitholestinae	2.74	4.07	1.10	55.0	30.5	Larson (2008)
UALVP50527	Saurornitholestinae	2.32	3.82	0.94	50.0	33.5	Larson (2008)
UALVP50528	Saurornitholestinae	3.49	5.98	1.74		28.0	Larson (2008)
UALVP50529	Saurornitholestinae	4.19	6.81	1.82	35.0	22.5	Larson (2008)
UALVP50530	Saurornitholestinae	3.90	6.14	1.62	40.5	26.5	Larson (2008)

UALVP50531	Saurornitholestinae	4.15	8.38	1.80	34.0	25.5	Larson (2008)
UALVP50532	Saurornitholestinae	4.57	6.31	1.76	33.5	22.5	Larson (2008)
UALVP50533	Saurornitholestinae	3.98	6.72	1.66		24.5	Larson (2008)
UALVP50534	Saurornitholestinae	3.98	6.72	1.66	38.0	25.0	Larson (2008)
UALVP50535	Saurornitholestinae	4.07	6.14	1.70	32.5	25.0	Larson (2008)
UALVP50536	Saurornitholestinae	3.65	5.56	1.52	38.5	25.0	Larson (2008)
UALVP50537	Saurornitholestinae	2.49	2.66	1.36		29.0	Larson (2008)
UALVP50538	Saurornitholestinae	3.74	6.56	1.32		27.5	Larson (2008)
UALVP50539	Saurornitholestinae	3.32	5.64	1.38		28.5	Larson (2008)
UALVP50540	Saurornitholestinae	2.91	5.48	1.26		27.5	Larson (2008)
UALVP50541	Saurornitholestinae	3.82	5.06	1.74	36.0	21.5	Larson (2008)
UALVP50542	Saurornitholestinae	2.57	3.28	1.08	44.0	30.5	Larson (2008)
UALVP50543	Saurornitholestinae	2.16	3.24	0.98	48.5	27.0	Larson (2008)
UALVP50544	Saurornitholestinae	2.82	3.32	1.30	40.0	27.5	Larson (2008)
UALVP50545	Saurornitholestinae	2.41	3.61	0.98	46.5	30.5	Larson (2008)
UALVP50546	Saurornitholestinae	1.91	3.65	1.02		40.0	Larson (2008)
UALVP50547	Saurornitholestinae	2.41	2.49	1.16	41.0	29.5	Larson (2008)
UALVP50548	Saurornitholestinae	2.45	2.66	1.16		37.5	Larson (2008)
UALVP50549	Saurornitholestinae	4.07	5.31	1.60		23.5	Larson (2008)
UALVP50550	Saurornitholestinae	3.98	6.56	1.82	36.3	23.8	Larson (2008)
UALVP50551	Saurornitholestinae	3.15	4.07	1.16	45.0	27.5	Larson (2008)
UALVP50552	Saurornitholestinae	2.32	3.24	1.04	47.5	30.7	Larson (2008)
UALVP50553	Saurornitholestinae	2.57	3.82	1.06	46.0	33.8	Larson (2008)
UALVP50554	Saurornitholestinae	3.15	4.15	1.40	43.8	28.8	Larson (2008)
UALVP50555	Saurornitholestinae	2.49	4.15	1.06	45.0	30.0	Larson (2008)
UALVP50556	Saurornitholestinae	4.90	7.30	1.64	45.0	27.5	Larson (2008)
UALVP50557	Saurornitholestinae	2.74	3.74	1.06	57.5	31.0	Larson (2008)
UALVP50558	Saurornitholestinae	3.57	5.81	1.46		27.5	Larson (2008)
UALVP50559	Saurornitholestinae	3.90	6.23	1.76	50.0	23.8	Larson (2008)
UALVP50560	Saurornitholestinae	3.65	6.23	1.52	42.5	27.5	Larson (2008)

UALVP50561	Saurornitholestinae	3.57	5.23	1.66		26.5	Larson (2008)
UALVP50562	Saurornitholestinae	3.65	4.57	1.64	47.5	25.5	Larson (2008)
UALVP50563	Saurornitholestinae	3.07	5.48	1.52		28.0	Larson (2008)
UALVP50564	Saurornitholestinae	3.57	4.81	1.38	37.5	21.5	Larson (2008)
UALVP50565	Saurornitholestinae	4.15	5.64	1.74	40.0	25.0	Larson (2008)
UALVP50566	Saurornitholestinae	3.40	5.48	1.64		26.0	Larson (2008)
UALVP50567	Saurornitholestinae	3.98	5.48	1.68	38.5	26.5	Larson (2008)
UALVP50568	Saurornitholestinae	3.98	6.89	1.88	50.0	28.0	Larson (2008)
UALVP50569	Saurornitholestinae	3.57	6.47	1.52		24.0	Larson (2008)
UALVP50570	Saurornitholestinae	3.07	3.40	1.36	45.0	25.0	Larson (2008)
UALVP50571	Saurornitholestinae	3.30	5.20	1.20	55.0	27.5	Larson (2008)
UALVP50572	Saurornitholestinae	2.80	4.70	1.10	42.5	30.0	Larson (2008)
UALVP50573	Saurornitholestinae	3.70	4.50	1.50	37.5	25.0	Larson (2008)
UALVP50574	Saurornitholestinae	3.50	4.10	1.60	40.0	25.0	Larson (2008)
UALVP50575	Saurornitholestinae	3.30	4.30	1.40	32.5	22.5	Larson (2008)
UALVP50576	Saurornitholestinae	2.00	2.10	1.10		35.0	Larson (2008)
UALVP50577	Saurornitholestinae	2.20	2.84	1.02	40.0	35.0	Larson (2008)
UALVP50578	Saurornitholestinae	3.70	6.80	1.50	45.0	30.0	Larson (2008)
UALVP50579	Saurornitholestinae	2.10	3.40	1.10	50.0	35.0	Larson (2008)
UALVP50580	Saurornitholestinae	2.64	3.48	1.00		37.5	Larson (2008)
UALVP50581	Saurornitholestinae	3.74	5.94	1.42	47.5	30.0	Larson (2008)
UALVP50582	Saurornitholestinae	3.07	4.73	1.08		28.0	Larson (2008)
UALVP50583	Saurornitholestinae	2.57	3.15	1.16	75.0	30.0	Larson (2008)
UALVP50584	Saurornitholestinae	3.82	6.14	1.48	31.0	24.5	Larson (2008)
UALVP50585	Saurornitholestinae	3.15	5.73	1.56		27.5	Larson (2008)
UALVP50586	Saurornitholestinae	1.64	1.88	0.72	50.0	35.0	Larson (2008)
UALVP50587	Saurornitholestinae	2.16	3.82	1.44		30.5	Larson (2008)
UALVP50588	Saurornitholestinae	2.44	3.28	1.12	38.5	30.5	Larson (2008)
UALVP50589	Saurornitholestinae	4.40	6.39	2.04	26.0	22.5	Larson (2008)
UALVP50590	Saurornitholestinae	4.65	6.97	1.94	30.0	21.5	Larson (2008)

UALVP50591	Saurornitholestinae	3.74	4.69	1.56	35.0	25.0	Larson (2008)
UALVP50592	Saurornitholestinae	3.49	6.47	1.60		26.0	Larson (2008)
UALVP50593	Saurornitholestinae	3.40	6.31	1.72	39.0	25.0	Larson (2008)
UALVP50594	Saurornitholestinae	3.40	4.48	1.36	31.0	24.0	Larson (2008)
UALVP50595	Saurornitholestinae	2.32	2.74	1.04	43.5	23.0	Larson (2008)
UALVP50596	Saurornitholestinae	3.15	3.32	1.36	27.5	23.5	Larson (2008)
UALVP50597	Saurornitholestinae	2.32	2.66	1.18	54.0	23.5	Larson (2008)
UALVP50598	Saurornitholestinae	4.07	5.98	1.54	40.0	28.0	Larson (2008)
UALVP50599	Saurornitholestinae	3.20	4.32	1.30	38.5	28.0	Larson (2008)
UALVP50600	Saurornitholestinae	2.57	2.99	1.12	57.5	30.0	Larson (2008)
UALVP50601	Saurornitholestinae	2.32	3.07	1.02	55.0	30.0	Larson (2008)
UALVP50602	Saurornitholestinae	2.57	2.82	1.02	50.0	30.0	Larson (2008)
UALVP50603	Saurornitholestinae	1.91	2.57	0.90	62.0	30.0	Larson (2008)
UALVP50604	Saurornitholestinae	4.48	5.77	1.80	37.0	25.5	Larson (2008)
UALVP50605	Saurornitholestinae	2.57	3.69	1.28	40.0	30.0	Larson (2008)
UALVP50606	Saurornitholestinae	3.74	4.81	1.36		30.0	Larson (2008)
UALVP50607	Saurornitholestinae	2.99	3.90	1.26	45.0	25.5	Larson (2008)
UALVP50608	Saurornitholestinae	2.49	3.49	1.02	44.0	30.0	Larson (2008)
UALVP50609	Saurornitholestinae	1.74	3.32	0.92		35.5	Larson (2008)
UALVP50610	Saurornitholestinae	3.90	4.98	1.64	37.5	23.0	Larson (2008)
UALVP50611	Saurornitholestinae	4.07	8.13	1.72	31.0	24.0	Larson (2008)
UALVP50612	Saurornitholestinae	3.40	4.57	1.58	41.5	24.5	Larson (2008)
UALVP50613	Saurornitholestinae	3.15	3.49	1.40		25.0	Larson (2008)
UALVP50614	Saurornitholestinae	3.65	5.23	1.60	39.0	26.0	Larson (2008)
UALVP50615	Saurornitholestinae	4.48	5.89	1.82	40.0	24.5	Larson (2008)
CMNFV8725	Saurornitholestinae	5.20	7.10	2.30	28.0	23.0	Larson (2008)
UALVP48052	Saurornitholestinae	2.66	5.06	1.62	45.0	30.0	Larson (2008)
UALVP48081	Saurornitholestinae	2.99	5.23	1.50	35.0	26.3	Larson (2008)
UALVP50626	Saurornitholestinae	3.15	5.98	1.56	35.0	26.0	Larson (2008)
UALVP50627	Saurornitholestinae	2.41	4.07	1.48		25.0	Larson (2008)

UALVP50628	Saurornitholestinae	3.07	4.90	1.62	33.3	26.0	Larson (2008)
UALVP50629	Saurornitholestinae	3.07	5.56	1.78		25.5	Larson (2008)
Oldman Formation (77-76 Ma)							
TMP95.177.48c	Saurornitholestinae	2.10	3.40	0.90		35.0	Sankey et al. (2002)
TMP95.180.4	Saurornitholestinae	2.10	3.50	0.70		25.0	Sankey et al. (2002)
TMP95.92.27	Saurornitholestinae	2.80	6.50	1.40		22.5	Sankey et al. (2002)
TMP87.154.63	Saurornitholestinae	3.40	8.10	1.90		21.3	Sankey et al. (2002)
TMP87.154.64	Saurornitholestinae	4.20	8.50	2.00		22.5	Sankey et al. (2002)
TMP87.79.90	Saurornitholestinae	4.40	8.50	1.90		20.0	Sankey et al. (2002)
TMP95.177.48a	Saurornitholestinae	2.90	6.00	1.50		20.0	Sankey et al. (2002)
TMP95.177.48b	Saurornitholestinae	1.90	4.70	1.00		27.5	Sankey et al. (2002)
TMP95.92.16	Saurornitholestinae	5.00	12.50	2.20		20.0	Sankey et al. (2002)
TMP95.92.16	Saurornitholestinae	5.00	13.50	2.20		22.5	Sankey et al. (2002)
TMP87.153.55	Saurornitholestinae	6.00	12.00	2.90		20.0	Sankey et al. (2002)
TMP87.77.120	Saurornitholestinae	5.30	11.30	3.20		18.8	Sankey et al. (2002)
TMP95.92.54	Saurornitholestinae	6.90	13.00	3.10		20.0	Sankey et al. (2002)
TMP95.92.28	Saurornitholestinae	2.00	5.00	1.10		25.0	Sankey et al. (2002)
TMP87.62.87	Saurornitholestinae	4.40	10.30	2.30		20.0	Sankey et al. (2002)
TMP1988.121.39	Saurornitholestinae	5.10	9.00	2.30	30.0	20.0	Currie and Varricchio (2004)
TMP2003.12.83	Saurornitholestinae	4.96	7.89	2.48	31.0	26.3	Longrich (2008)
TMP2000.57.80	Saurornitholestinae	3.80	7.91	2.25		19.4	Longrich (2008)
TMP2002.79.4	Saurornitholestinae	5.08	9.00	2.14	29.9	19.5	Longrich (2008)
TMP2002.79.3	Saurornitholestinae	5.28	9.08	2.13	30.7	25.3	Longrich (2008)
Dinosaur Park Formation (76-75 Ma)							
TMP87.158.78	Saurornitholestinae	2.70	4.20	1.10		32.5	Sankey et al. (2002)
TMP87.19.68	Saurornitholestinae	2.00	4.60	1.00		30.0	Sankey et al. (2002)
TMP87.31.54	Saurornitholestinae	2.40	4.80	1.10		27.5	Sankey et al. (2002)
TMP87.4.47	Saurornitholestinae	2.20	4.10	0.70		35.0	Sankey et al. (2002)
TMP87.48.77	Saurornitholestinae	4.60	6.70	1.70		25.0	Sankey et al. (2002)
TMP95.127.25c	Saurornitholestinae	3.70	6.70	1.80		21.3	Sankey et al. (2002)

TMP95.147.26	Saurornitholestinae	1.90	2.80	0.70		32.5	Sankey et al. (2002)
TMP95.151.10	Saurornitholestinae	2.40	3.90	0.90		32.5	Sankey et al. (2002)
TMP95.181.11	Saurornitholestinae	1.90	5.00	1.00		25.0	Sankey et al. (2002)
TMP96.12.366	Saurornitholestinae	4.20	6.30	1.50		22.5	Sankey et al. (2002)
TMP87.158.80	Saurornitholestinae	3.90	9.00	1.90		21.3	Sankey et al. (2002)
TMP87.158.81	Saurornitholestinae	4.30	11.20	2.00		25.0	Sankey et al. (2002)
TMP87.33.55	Saurornitholestinae	4.00	9.90	2.10		20.0	Sankey et al. (2002)
TMP87.36.392	Saurornitholestinae	5.50	13.00	2.20		20.0	Sankey et al. (2002)
TMP87.51.23	Saurornitholestinae	3.80	8.20	1.40		25.0	Sankey et al. (2002)
TMP87.72.23	Saurornitholestinae	4.90	9.60	2.20		20.0	Sankey et al. (2002)
TMP87.72.26	Saurornitholestinae	5.00	13.00	2.30		20.0	Sankey et al. (2002)
TMP87.72.4	Saurornitholestinae	5.40	13.00	2.50		20.0	Sankey et al. (2002)
TMP95.12.109	Saurornitholestinae	5.90	13.00	2.80		18.8	Sankey et al. (2002)
TMP95.126.29	Saurornitholestinae	5.00	12.00	2.10		25.0	Sankey et al. (2002)
TMP95.127.25a	Saurornitholestinae	5.30	11.80	2.30		21.3	Sankey et al. (2002)
TMP95.127.25b	Saurornitholestinae	4.50	7.80	1.80		23.8	Sankey et al. (2002)
TMP95.127.25d	Saurornitholestinae	4.20	7.50	1.70		20.0	Sankey et al. (2002)
TMP95.129.2	Saurornitholestinae	4.90	9.60	2.20		20.0	Sankey et al. (2002)
TMP95.131.12	Saurornitholestinae	5.10	9.50	2.10		20.0	Sankey et al. (2002)
TMP95.137.2a	Saurornitholestinae	5.00	9.20	2.30		20.0	Sankey et al. (2002)
TMP95.137.2b	Saurornitholestinae	4.90	10.50	2.10		20.0	Sankey et al. (2002)
TMP95.179.3	Saurornitholestinae	4.70	10.40	2.20		21.3	Sankey et al. (2002)
TMP95.19.4	Saurornitholestinae	4.20	8.00	1.50		22.5	Sankey et al. (2002)
TMP95.2.18	Saurornitholestinae	4.20	10.50	2.50		18.8	Sankey et al. (2002)
TMP95.406.5	Saurornitholestinae	4.70	10.30	2.00		25.0	Sankey et al. (2002)
TMP96.12.361	Saurornitholestinae	5.90	13.00	2.70		20.0	Sankey et al. (2002)
TMP96.12.363	Saurornitholestinae	4.80	9.20	2.00		20.0	Sankey et al. (2002)
TMP96.12.38	Saurornitholestinae	5.10	11.70	2.10		25.0	Sankey et al. (2002)
TMP97.80.36	Saurornitholestinae	3.90	3.90	2.00		17.5	Sankey et al. (2002)
TMP87.36.11	Saurornitholestinae	4.50	9.50	2.40		20.0	Sankey et al. (2002)

TMP87.43.5	Saurornitholestinae	5.70	11.20	2.10		22.5	Sankey et al. (2002)
TMP87.46.53	Saurornitholestinae	4.80	9.40	2.20		20.0	Sankey et al. (2002)
TMP96.12.102	Saurornitholestinae	5.50	11.20	3.20		25.0	Sankey et al. (2002)
TMP96.12.104	Saurornitholestinae	5.60	10.80	2.60		20.0	Sankey et al. (2002)
TMP96.12.112	Saurornitholestinae	7.90	16.00	2.80		18.8	Sankey et al. (2002)
TMP96.12.115	Saurornitholestinae	5.50	14.00	2.70		21.3	Sankey et al. (2002)
TMP96.12.118?	Saurornitholestinae	5.10	9.00	2.20		27.5	Sankey et al. (2002)
TMP96.12.34	Saurornitholestinae	6.40	13.00	2.60		18.8	Sankey et al. (2002)
TMP96.12.360	Saurornitholestinae	5.00	9.00	1.90		21.3	Sankey et al. (2002)
TMP96.12.364	Saurornitholestinae	5.30	9.00	2.10		20.0	Sankey et al. (2002)
TMP95.182.21	Saurornitholestinae	3.50	7.60	1.70		20.0	Sankey et al. (2002)
TMP95.184.23	Saurornitholestinae	3.70	8.30	1.90		20.0	Sankey et al. (2002)
TMP95.21.5	Saurornitholestinae	4.70	9.20	2.40		18.8	Sankey et al. (2002)
TMP1974.10.1	*Saurornitholestes langstoni*	4.50	9.20	2.10	25.0	20.0	Currie and Varricchio (2004)
TMP1974.10.1	*Saurornitholestes langstoni*	3.90	8.90		35.0	25.0	Currie and Varricchio (2004)
Irvine Saurornitholestes 1	Saurornitholestinae	5.15	9.55		30.6	22.7	Longrich (2008)
Irvine Saurornitholestes 2	Saurornitholestinae	5.70	10.97			21.7	Longrich (2008)
Irvine Saurornitholestes 3	Saurornitholestinae	5.10	7.54		29.9	23.6	Longrich (2008)
TMP2005.49.96	Saurornitholestinae	4.69	8.01	2.28	34.3	17.9	Longrich (2008)
TMP2005.49.119	Saurornitholestinae	5.98	11.66	2.48	29.2	22.9	Longrich (2008)
TMP2005.49.120	Saurornitholestinae	5.77	11.25	2.49		27.7	Longrich (2008)
TMP2005.49.74	Saurornitholestinae	4.36	9.20	2.45		21.4	Longrich (2008)
TMP2005.49.23	Saurornitholestinae	4.89	8.74	2.45	27.5	19.1	Longrich (2008)
TMP2005.39.07	Saurornitholestinae	4.26	7.19	1.98	35.1	21.6	Longrich (2008)
TMP2005.39.01	Saurornitholestinae	5.26	10.78	2.37	25.9	18.9	Longrich (2008)
TMP2005.12.28	Saurornitholestinae	3.93	5.66	1.81		21.9	Longrich (2008)
TMP2005.09.47	Saurornitholestinae	5.24	10.80	2.77		20.2	Longrich (2008)
TMP2004.116.26	Saurornitholestinae	5.74	11.60	2.67		21.4	Longrich (2008)

TMP2004.103.17	Saurornitholestinae	3.67	4.42	1.61		18.4	Longrich (2008)
TMP2004.12.19	Saurornitholestinae	5.12	8.18	2.37	30.5	20.3	Longrich (2008)
TMP2003.12.132	Saurornitholestinae	5.42	9.21	2.37	30.9	21.0	Longrich (2008)
TMP2002.60.6	Saurornitholestinae	6.53	9.66	3.73	30.5	17.9	Longrich (2008)
TMP2001.12.183	Saurornitholestinae	4.70	7.67	2.17	42.1	21.7	Longrich (2008)
TMP2001.12.180	Saurornitholestinae	5.60	8.31	2.45	43.2	27.2	Longrich (2008)
TMP2002.60.8	Saurornitholestinae	5.62	10.04	2.37		20.2	Longrich (2008)
TMP2001.12.19	Saurornitholestinae	4.33	9.20		23.9	17.7	Longrich (2008)
TMP2000.12.111	Saurornitholestinae	5.77	11.03	2.41	34.4	22.5	Longrich (2008)
TMP2000.57.6	Saurornitholestinae	5.79	11.54	3.16		19.1	Longrich (2008)
TMP2000.12.116	Saurornitholestinae	4.66	10.10	2.57		24.0	Longrich (2008)
TMP2000.12.114	Saurornitholestinae	4.75	7.58	2.38	24.4	21.5	Longrich (2008)
TMP2005.12.??	Saurornitholestinae	7.50	12.85	3.68		24.5	Longrich (2008)
TMP2004.12.18	Saurornitholestinae	7.07	8.38	3.13		26.8	Longrich (2008)
TMP2003.12.189	Saurornitholestinae	5.34	10.10	2.82		19.4	Longrich (2008)
TMP83.36.236	Saurornitholestinae	3.82	7.52	1.75	41.7	30.5	Longrich (2008)
TMP1995.12.26	Saurornitholestinae	1.69	2.20	0.83	30.6	27.1	Longrich (2008)
Judith River Group (Formation) (79.5-75 Ma)							
TMP87.112.10	Saurornitholestinae	3.80	8.70	1.60		30.0	Sankey et al. (2002)
TMP87.112.21	Saurornitholestinae	6.30	5.60	1.40		23.8	Sankey et al. (2002)
TMP87.112.9	Saurornitholestinae	4.20	8.10	2.00		21.3	Sankey et al. (2002)
TMP87.112.28	Saurornitholestinae	5.50	11.50	2.20		21.3	Sankey et al. (2002)
TMP87.50.100	Saurornitholestinae	5.20	8.20	2.20		21.3	Sankey et al. (2002)
TMP87.36.184	Saurornitholestinae	3.50	7.50	1.90		21.3	Sankey et al. (2002)
TMP87.36.418	Saurornitholestinae	4.10	9.50	2.60		22.5	Sankey et al. (2002)
TMP87.36.70	Saurornitholestinae	4.10	9.50	2.40		20.0	Sankey et al. (2002)
TMP87.36.93	Saurornitholestinae	5.30	11.80	2.50		23.8	Sankey et al. (2002)
TMP95.12.31	Saurornitholestinae	5.00	10.50	2.40		20.0	Sankey et al. (2002)
TMP95.12.33	Saurornitholestinae	6.00	13.00	2.30		17.5	Sankey et al. (2002)
TMP95.12.38	Saurornitholestinae	5.70	11.00	2.20		18.8	Sankey et al. (2002)

TMP95.12.40	Saurornitholestinae	3.50	7.80	2.00		18.8	Sankey et al. (2002)
TMP95.12.42	Saurornitholestinae	2.90	7.00	1.70		22.5	Sankey et al. (2002)
TMP95.12.43	Saurornitholestinae	5.00	12.00	2.30		20.0	Sankey et al. (2002)
TMP95.12.74a	Saurornitholestinae	5.10	10.20	2.40		20.0	Sankey et al. (2002)
TMP95.12.74b	Saurornitholestinae	3.80	6.30	1.60		22.5	Sankey et al. (2002)
TMP95.12.74c	Saurornitholestinae	4.90	9.40	2.20		26.3	Sankey et al. (2002)
TMP95.124.4	Saurornitholestinae	3.30	6.20	1.50		21.3	Sankey et al. (2002)
TMP87.36.68	Saurornitholestinae	5.70	11.20	2.40		22.5	Sankey et al. (2002)
TMP87.50.38	Saurornitholestinae	6.30	14.20	2.40		20.0	Sankey et al. (2002)
p74105no1	Saurornitholestinae	4.00	9.00		35.0	21.0	Farlow et al. (1991)
p74105no2	Saurornitholestinae	4.10	8.00		36.0	20.0	Farlow et al. (1991)
p8016440	Saurornitholestinae	5.10	9.00	2.20	32.0	21.0	Farlow et al. (1991)
p848946	Saurornitholestinae	3.70	5.00		30.0	20.0	Farlow et al. (1991)
p8120259	Saurornitholestinae	2.10	3.00		no	30.0	Farlow et al. (1991)
p8216249	Saurornitholestinae	4.30	7.00		40.0	20.0	Farlow et al. (1991)
p84989	Saurornitholestinae	5.10	9.00		32.0	23.0	Farlow et al. (1991)
p8220173	Saurornitholestinae	3.10	5.00		45.0	25.0	Farlow et al. (1991)
p80161515	Saurornitholestinae	5.90	10.00		25.0	21.0	Farlow et al. (1991)
p808234	Saurornitholestinae	5.30	9.00		25.0	20.0	Farlow et al. (1991)
Two Medicine Formation, Montana (83-74 Ma, 76.7 for *B. feinbergi*)							
TMP87.83.1	Saurornitholestinae	6.50	12.50	3.20		15.0	Sankey et al. (2002)
KUVP129737	*Bambiraptor feinbergi*	2.37	5.33	1.41		25.0	Burnham et al. (2000)
KUVP129737	*Bambiraptor feinbergi*	2.34	5.01	1.41		20.0	Burnham et al. (2000)
KUVP129737	*Bambiraptor feinbergi*	2.08	4.82	1.40		30.0	Burnham et al. (2000)
KUVP129737	*Bambiraptor feinbergi*	2.37	4.91	1.61		30.0	Burnham et al. (2000)
KUVP129737	*Bambiraptor feinbergi*	2.47	5.58	1.24		24.0	Burnham et al. (2000)
KUVP129737	*Bambiraptor feinbergi*	2.61	5.99	1.41		25.0	Burnham et al. (2000)
KUVP129737	*Bambiraptor feinbergi*	2.35	5.86	1.20		24.2	Burnham et al. (2000)
KUVP129737	*Bambiraptor feinbergi*	2.54	4.62	0.99		32.5	Burnham et al. (2000)
KUVP129737	*Bambiraptor feinbergi*	3.22	5.66	1.37		23.7	Burnham et al. (2000)

KUVP129737	*Bambiraptor feinbergi*	2.15	4.03	1.57		25.0	Burnham et al. (2000)
Aguja Middle Campanian (~79 Ma)							
LSUMG726:5923	Saurornitholestinae	4.00	5.30	2.00		22.5	Sankey et al. (2005)
LSUMG746:6281	Saurornitholestinae	4.80	7.20	2.50		32.5	Sankey et al. (2005)
LSUMG140:6139	Saurornitholestinae	3.70	5.20	1.60		25.0	Sankey et al. (2005)
LSUMG489:5659	Saurornitholestinae	2.30	2.80	1.40		25.0	Sankey et al. (2005)
LSUMG491:5950	Saurornitholestinae	2.00	2.20	1.10		30.0	Sankey et al. (2005)
Horseshoe Canyon Formation Unit 1 (71-72 Ma)							
TMP1995.166.0001	*Atrociraptor marshalli*	5.00	10.00	3.50	13.5	11.5	Currie and Varricchio (2004)
TMP1995.166.0001	*Atrociraptor marshalli*	6.10	13.00		30.0	20.0	Currie and Varricchio (2004)
TMP1995.166.0001	*Atrociraptor marshalli*	6.60	15.30		25.0	20.0	Currie and Varricchio (2004)
TMP1995.166.0001	*Atrociraptor marshalli*	5.50	11.90		30.0	20.0	Currie and Varricchio (2004)
TMP1995.166.0001	*Atrociraptor marshalli*	5.60	7.80		35.0	20.0	Currie and Varricchio (2004)
TMP1995.166.0001	*Atrociraptor marshalli*	5.60	10.50		27.5	20.0	Currie and Varricchio (2004)
TMP1995.166.0001	*Atrociraptor marshalli*	4.40	7.00		40.0	22.5	Currie and Varricchio (2004)
TMP1995.166.0001	*Atrociraptor marshalli*	5.50	12.00	3.50	17.5	15.0	Currie and Varricchio (2004)
TMP1995.166.0001	*Atrociraptor marshalli*	3.20	5.70		30.0	25.0	Currie and Varricchio (2004)
TMP1995.166.0001	*Atrociraptor marshalli*	5.50	11.30		27.5	20.0	Currie and Varricchio (2004)
TMP1995.166.0001	*Atrociraptor marshalli*	5.20	7.50	2.80	25.0	20.0	Currie and Varricchio (2004)
TMP1995.166.0001	*Atrociraptor marshalli*	5.20	7.00	2.60	40.0	20.0	Currie and Varricchio (2004)
	cf. *Atrociraptor*	5.81	10.37		23.3	16.9	Longrich (2008)
TMP99.50.117	cf. *Atrociraptor*	4.07	6.39	1.99	28.5	17.5	this study
TMP00.45.35	cf. *Atrociraptor*	3.90	5.81	2.08	27.0	20.0	this study
TMP00.45.103	cf. *Atrociraptor*	4.90	10.15	2.41	22.5	15.5	this study

TMP03.45.52	cf. *Atrociraptor*	4.65	7.06	n/a	30.0	20.0	this study
TMP03.45.49	cf. *Atrociraptor*	4.23	6.56	2.16	23.0	20.0	this study
Aguja Upper Campanian (?76-71? Ma)							
LSUMG113:5109	Saurornitholestinae	2.80	4.00	1.20		30.0	Sankey et al. (2005)
LSUMG113:1309	Saurornitholestinae	1.80	2.20	0.80		35.0	Sankey et al. (2005)
LSUMG113:1307	Saurornitholestinae	4.00	6.20	1.80		45.0	Sankey et al. (2005)
LSUMG113:1308	Saurornitholestinae	4.00	5.50	1.90		25.0	Sankey et al. (2005)
Javelina Formation (~69 Ma)							
LSUMG229:5953	Saurornitholestinae	3.60	4.50	1.80		22.5	Sankey et al. (2005)
LSUMG229:3128	Saurornitholestinae	4.00	6.00	1.70		25.0	Sankey et al. (2005)
Scollard Formation (65.5-66.75 Ma)							
TMP1998.8.2	Saurornitholestinae	6.27	10.13	3.02	40.6	20.6	Longrich (2008)
Lance Formation (65.5-66.5 Ma)							
UCMP187070	Saurornitholestinae	2.50	5.00			30.0	Sankey (2008)
UCMP124401	Saurornitholestinae	4.50	8.00			25.0	Sankey (2008)
UCMP187079	Saurornitholestinae	2.20	4.00			30.0	Sankey (2008)
UCMP187054	Saurornitholestinae	3.00	4.50			35.0	Sankey (2008)
UCMP187027	Saurornitholestinae	4.00	7.00			30.0	Sankey (2008)
Upper Hell Creek Formation (65.5-66.75 Ma)							
UCMP134801	Saurornitholestinae	3.70	10.00			25.0	Sankey (2008)
UCMP187048	Saurornitholestinae	5.80	13.00			25.0	Sankey (2008)
UCMP187049	Saurornitholestinae	3.00	6.00			35.0	Sankey (2008)
UCMP186944	Saurornitholestinae	3.50	6.00			30.0	Sankey (2008)
UCMP187194	Saurornitholestinae	3.20	5.50			30.0	Sankey (2008)
UCMP186957	Saurornitholestinae	3.30	5.00			27.5	Sankey (2008)
UCMP186962	Saurornitholestinae	3.40	5.00			27.5	Sankey (2008)
UCMP187041	Saurornitholestinae	4.00	8.00			30.0	Sankey (2008)
UCMP187042	Saurornitholestinae	3.00	5.00			30.0	Sankey (2008)
UCMP187043	Saurornitholestinae	2.50	4.50			32.5	Sankey (2008)
UCMP187044	Saurornitholestinae	3.00	4.00			30.0	Sankey (2008)

UCMP187045	Saurornitholestinae	3.00	5.00			25.0	Sankey (2008)
UCMP187046	Saurornitholestinae	2.30	4.00			40.0	Sankey (2008)
UCMP187036	Saurornitholestinae	5.00	8.00			25.0	Sankey (2008)
UCMP187034	Saurornitholestinae	6.00	12.00			22.5	Sankey (2008)
UCMP187033	Saurornitholestinae	5.00	12.00			20.0	Sankey (2008)
UCMP187030	Saurornitholestinae	5.00	8.00			25.0	Sankey (2008)
UCMP187025	Saurornitholestinae	4.00	6.00			35.0	Sankey (2008)
UCMP187006	Saurornitholestinae	6.00	12.00			25.0	Sankey (2008)
UCMP187038	Saurornitholestinae	4.00	7.00			27.5	Sankey (2008)
UCMP187010	Saurornitholestinae	3.00	6.00			30.0	Sankey (2008)
UCMP187083	Saurornitholestinae	5.00	8.00			30.0	Sankey (2008)
UCMP174796	Saurornitholestinae	3.40	5.00			22.5	Sankey (2008)
UCMP187200	Saurornitholestinae	2.20	3.50			35.0	Sankey (2008)
UCMP187197	Saurornitholestinae	3.50	5.50			27.5	Sankey (2008)
UCMP187199	Saurornitholestinae	3.60	5.00			27.5	Sankey (2008)
UCMP187198	Saurornitholestinae	2.60	4.00			35.0	Sankey (2008)
UCMP186958	Saurornitholestinae	2.60	4.00			30.0	Sankey (2008)
UCMP186959	Saurornitholestinae	3.00	5.00			35.0	Sankey (2008)
UCMP186961	Saurornitholestinae	3.20	8.00			25.0	Sankey (2008)
UCMP79095	Saurornitholestinae	4.00	7.00			30.0	Sankey (2008)
Milk River Formation (~83.5 Ma)							
UALVP48460	Dromaeosauridae	5.43	8.58	3.08	35.0	20.0	Larson (2008)
UALVP48458	Dromaeosauridae	3.82	4.57	2.36	20.0	18.0	Larson (2008)
UALVP48480	Dromaeosauridae	2.04	2.12	1.06	15.0	20.0	Larson (2008)
UALVP48461	Dromaeosauridae	7.53	9.98	3.84	30.0	17.5	Larson (2008)
UALVP48462	Dromaeosauridae	8.75	17.33	4.07	17.5	15.0	Larson (2008)
UALVP50220	Dromaeosauridae	7.88	14.00	4.90	20.0	17.5	Larson (2008)
UALVP50221	Dromaeosauridae	3.82	4.15	1.86	44.0	20.0	Larson (2008)
UALVP50222	Dromaeosauridae	5.81	6.39	3.04	27.5	20.0	Larson (2008)
John Henry Member of Straight Cliffs Formation (85.8-?84 Ma)							

UMNH99-12805	cf. *Richardoestesia gilmorei*	2.68	3.30	1.36	none	41.0	this study
UMNH424-14238	cf. *Richardoestesia gilmorei*	2.31	2.79	1.15	47.5	41.0	this study
UMNH424-17370	cf. *Richardoestesia gilmorei*	3.49	4.42	1.62	none	35.0	this study
UMNH424-17382	cf. *Richardoestesia gilmorei*	3.32	5.58	1.80	none	32.0	this study
UMNH424-17220	cf. *Richardoestesia gilmorei*	1.82	2.21	0.71	none	38.5	this study
UMNH424-17220	cf. *Richardoestesia gilmorei*	2.05	2.38	0.75	46.0	38.0	this study
UMNH424-17220	cf. *Richardoestesia gilmorei*	3.62	5.78	1.42	31.0	33.5	this study
UMNH424-17220	cf. *Richardoestesia gilmorei*	3.68	6.63	2.00	none	33.0	this study
Milk River Formation (~83.5 Ma)							
UALVP47985	cf. *Richardoestesia gilmorei*	2.24	2.88	0.98	40.0	32.5	Larson (2008)
UALVP47986	cf. *Richardoestesia gilmorei*	2.52	4.15	1.30	35.0	30.0	Larson (2008)
UALVP47997	cf. *Richardoestesia gilmorei*	2.32	3.40	1.28		27.0	Larson (2008)
UALVP48038	cf. *Richardoestesia gilmorei*	4.15	5.81	1.64		32.5	Larson (2008)
UALVP48072	cf. *Richardoestesia gilmorei*	3.49	5.56	1.88		28.0	Larson (2008)
UALVP48112	cf. *Richardoestesia gilmorei*	3.65	5.40	1.20	54.0	28.5	Larson (2008)
UALVP48115	cf. *Richardoestesia gilmorei*	2.04	2.52	0.92	50.0	32.5	Larson (2008)
UALVP48142	cf. *Richardoestesia gilmorei*	1.88	3.04	0.95		45.0	Larson (2008)
UALVP48143	cf. *Richardoestesia gilmorei*	2.48	2.80	1.04		50.0	Larson (2008)
UALVP48158	cf. *Richardoestesia gilmorei*	1.88	2.12	0.88		35.0	Larson (2008)
UALVP48182	cf. *Richardoestesia gilmorei*	2.48	3.28	1.08	45.0	35.0	Larson (2008)
UALVP48183	cf. *Richardoestesia gilmorei*	1.60	2.96	0.98		45.0	Larson (2008)
UALVP48188	cf. *Richardoestesia gilmorei*	2.12	2.52	0.94		35.0	Larson (2008)
UALVP48195	cf. *Richardoestesia gilmorei*	1.92	2.92	1.00		55.0	Larson (2008)
UALVP48196	cf. *Richardoestesia gilmorei*	2.20	2.56	0.80		42.5	Larson (2008)
UALVP48212	cf. *Richardoestesia gilmorei*	2.82	5.06	1.48		40.0	Larson (2008)
UALVP48213	cf. *Richardoestesia gilmorei*	2.40	3.24	1.10		45.0	Larson (2008)
UALVP48214	cf. *Richardoestesia gilmorei*	2.12	3.20	1.08		32.5	Larson (2008)
UALVP48216	cf. *Richardoestesia gilmorei*	3.98	4.73	2.02		35.0	Larson (2008)
UALVP48224	cf. *Richardoestesia gilmorei*	1.32	1.76	0.62		45.0	Larson (2008)
UALVP48225	cf. *Richardoestesia gilmorei*	1.76	2.76	0.78		51.5	Larson (2008)

UALVP48247	cf. *Richardoestesia gilmorei*	3.07	4.57	1.54		31.3	Larson (2008)
UALVP48250	cf. *Richardoestesia gilmorei*	2.52	3.82	1.36		45.0	Larson (2008)
UALVP48251	cf. *Richardoestesia gilmorei*	2.48	3.40	1.20	41.5	35.0	Larson (2008)
UALVP48252	cf. *Richardoestesia gilmorei*	4.32	6.56	1.24	42.5	32.5	Larson (2008)
UALVP48253	cf. *Richardoestesia gilmorei*	1.80	2.88	0.82	50.0	35.0	Larson (2008)
UALVP48259	cf. *Richardoestesia gilmorei*	2.00	2.96	1.02		38.0	Larson (2008)
UALVP48266	cf. *Richardoestesia gilmorei*	2.36	3.16	1.06		32.5	Larson (2008)
UALVP48275	cf. *Richardoestesia gilmorei*	2.80	4.90	1.74		36.0	Larson (2008)
UALVP49806	cf. *Richardoestesia gilmorei*	2.08	2.68	1.16	52.5	45.0	Larson (2008)
UALVP49807	cf. *Richardoestesia gilmorei*	2.36	2.68	0.92	49.0	35.0	Larson (2008)
UALVP49808	cf. *Richardoestesia gilmorei*	2.44	2.80	0.94		33.0	Larson (2008)
UALVP49809	cf. *Richardoestesia gilmorei*	2.16	4.07	1.48		29.0	Larson (2008)
UALVP49810	cf. *Richardoestesia gilmorei*	3.15	4.32	1.84		37.5	Larson (2008)
UALVP49811	cf. *Richardoestesia gilmorei*	3.57	4.73	1.92	45.5	33.5	Larson (2008)
UALVP49812	cf. *Richardoestesia gilmorei*	2.82	4.73	1.20	45.0	32.0	Larson (2008)
UALVP49813	cf. *Richardoestesia gilmorei*	3.24	4.65	1.72		37.5	Larson (2008)
UALVP49814	cf. *Richardoestesia gilmorei*	2.57	3.82	1.22	40.0	33.5	Larson (2008)
UALVP49815	cf. *Richardoestesia gilmorei*	1.96	2.96	0.82		50.5	Larson (2008)
UALVP49816	cf. *Richardoestesia gilmorei*	3.32	6.39	1.88		38.8	Larson (2008)
UALVP49817	cf. *Richardoestesia gilmorei*	2.16	2.57	0.92	44.0	32.0	Larson (2008)
UALVP49818	cf. *Richardoestesia gilmorei*	3.65	7.30	1.78	41.0	31.0	Larson (2008)
UALVP49819	cf. *Richardoestesia gilmorei*	2.91	4.15	1.42	50.0	38.5	Larson (2008)
UALVP49820	cf. *Richardoestesia gilmorei*	3.15	5.56	1.84		36.0	Larson (2008)
UALVP49821	cf. *Richardoestesia gilmorei*	2.56	3.44	1.22		38.5	Larson (2008)
UALVP49822	cf. *Richardoestesia gilmorei*	2.16	3.52	0.90	50.0	32.5	Larson (2008)
UALVP49823	cf. *Richardoestesia gilmorei*	2.40	3.24	0.94	57.0	50.0	Larson (2008)
UALVP49824	cf. *Richardoestesia gilmorei*	1.92	3.04	0.81	60.0	47.0	Larson (2008)
UALVP49825	cf. *Richardoestesia gilmorei*	1.68	2.40	1.00		31.5	Larson (2008)
UALVP49826	cf. *Richardoestesia gilmorei*	2.91	4.07	1.24	45.0	34.5	Larson (2008)
UALVP49827	cf. *Richardoestesia gilmorei*	2.20	3.00	1.04		33.5	Larson (2008)

UALVP49828	cf. *Richardoestesia gilmorei*	2.08	2.68	0.96	39.0	31.5	Larson (2008)
UALVP49829	cf. *Richardoestesia gilmorei*	2.53	3.74	0.92		37.5	Larson (2008)
UALVP49830	cf. *Richardoestesia gilmorei*	2.74	4.32	1.22	51.0	37.5	Larson (2008)
UALVP49831	cf. *Richardoestesia gilmorei*	2.52	3.00	1.12		41.0	Larson (2008)
UALVP49832	cf. *Richardoestesia gilmorei*	2.16	3.98	1.04	52.0	33.5	Larson (2008)
UALVP49833	cf. *Richardoestesia gilmorei*	2.60	2.68	0.86	48.0	40.5	Larson (2008)
UALVP49834	cf. *Richardoestesia gilmorei*	1.83	3.49	0.90		33.5	Larson (2008)
UALVP49835	cf. *Richardoestesia gilmorei*	3.32	4.23	1.30	37.5	29.5	Larson (2008)
UALVP49836	cf. *Richardoestesia gilmorei*	3.57	6.31	1.84		28.5	Larson (2008)
UALVP49837	cf. *Richardoestesia gilmorei*	1.91	2.91	1.06	47.5	32.5	Larson (2008)
UALVP49838	cf. *Richardoestesia gilmorei*	4.07	6.56	2.28		31.5	Larson (2008)
UALVP49839	cf. *Richardoestesia gilmorei*	1.91	3.49	0.86	48.0	33.5	Larson (2008)
UALVP49840	cf. *Richardoestesia gilmorei*	2.24	3.98	1.20	40.0	27.5	Larson (2008)
UALVP49841	cf. *Richardoestesia gilmorei*	2.16	3.90	1.16		37.0	Larson (2008)
UALVP49842	cf. *Richardoestesia gilmorei*	3.15	3.90	1.48	32.5	33.0	Larson (2008)
UALVP49843	cf. *Richardoestesia gilmorei*	2.41	3.82	1.00	41.0	32.5	Larson (2008)
UALVP49844	cf. *Richardoestesia gilmorei*	2.57	3.28	1.06	35.0	30.0	Larson (2008)
UALVP49845	cf. *Richardoestesia gilmorei*	2.28	3.12	1.00	47.0	38.5	Larson (2008)
UALVP49846	cf. *Richardoestesia gilmorei*	2.08	2.64	0.90		46.0	Larson (2008)
UALVP49847	cf. *Richardoestesia gilmorei*	2.44	2.80	1.00	37.0	32.0	Larson (2008)
UALVP49848	cf. *Richardoestesia gilmorei*	2.44	3.04	1.14	38.0	31.5	Larson (2008)
UALVP49849	cf. *Richardoestesia gilmorei*	2.52	3.36	0.96	36.5	36.0	Larson (2008)
UALVP49850	cf. *Richardoestesia gilmorei*	2.16	3.00	0.86		40.0	Larson (2008)
UALVP49851	cf. *Richardoestesia gilmorei*	2.48	3.04	0.92		49.0	Larson (2008)
UALVP49852	cf. *Richardoestesia gilmorei*	2.04	2.90	0.70		45.0	Larson (2008)
UALVP49853	cf. *Richardoestesia gilmorei*	1.96	2.80	0.98		56.0	Larson (2008)
UALVP49854	cf. *Richardoestesia gilmorei*	2.60	2.88	1.06		45.0	Larson (2008)
UALVP49855	cf. *Richardoestesia gilmorei*	1.68	1.88	1.04		44.0	Larson (2008)
UALVP49856	cf. *Richardoestesia gilmorei*	1.76	2.08	0.98		41.5	Larson (2008)
UALVP49857	cf. *Richardoestesia gilmorei*	1.68	2.10	0.82		51.0	Larson (2008)

UALVP49858	cf. *Richardoestesia gilmorei*	2.41	3.98	1.26		27.5	Larson (2008)
UALVP49859	cf. *Richardoestesia gilmorei*	2.24	4.48	1.44		29.5	Larson (2008)
UALVP49860	cf. *Richardoestesia gilmorei*	2.82	3.53	1.16	40.5	30.0	Larson (2008)
UALVP49861	cf. *Richardoestesia gilmorei*	1.80	2.12	0.96		42.5	Larson (2008)
UALVP49862	cf. *Richardoestesia gilmorei*	2.00	2.12	0.78	60.0	45.0	Larson (2008)
UALVP49863	cf. *Richardoestesia gilmorei*	3.65	5.73	1.36		32.0	Larson (2008)
UALVP49864	cf. *Richardoestesia gilmorei*	2.32	2.76	1.20		43.5	Larson (2008)
UALVP49865	cf. *Richardoestesia gilmorei*	2.68	3.44	1.36	45.0	45.0	Larson (2008)
UALVP49866	cf. *Richardoestesia gilmorei*	2.24	3.15	0.96		39.0	Larson (2008)
UALVP49867	cf. *Richardoestesia gilmorei*	3.65	6.10	1.44	44.0	30.0	Larson (2008)
UALVP49868	cf. *Richardoestesia gilmorei*	3.40	4.48	1.60		40.5	Larson (2008)
UALVP49869	cf. *Richardoestesia gilmorei*	3.20	4.73	1.56		38.0	Larson (2008)
UALVP49870	cf. *Richardoestesia gilmorei*	3.07	4.19	1.50		36.5	Larson (2008)
UALVP49871	cf. *Richardoestesia gilmorei*	2.74	3.90	1.24		28.5	Larson (2008)
UALVP49872	cf. *Richardoestesia gilmorei*	2.82	3.90	1.28	37.5	31.0	Larson (2008)
UALVP49873	cf. *Richardoestesia gilmorei*	3.40	3.74	1.60		39.5	Larson (2008)
UALVP49874	cf. *Richardoestesia gilmorei*	3.15	3.65	1.18		35.5	Larson (2008)
UALVP49875	cf. *Richardoestesia gilmorei*	2.91	3.78	1.06	44.0	34.0	Larson (2008)
UALVP49876	cf. *Richardoestesia gilmorei*	2.41	2.99	1.08	36.0	35.5	Larson (2008)
UALVP49877	cf. *Richardoestesia gilmorei*	2.74	3.40	1.18		32.5	Larson (2008)
UALVP49878	cf. *Richardoestesia gilmorei*	2.41	2.95	0.88	54.0	34.0	Larson (2008)
UALVP49879	cf. *Richardoestesia gilmorei*	2.24	2.99	1.00	53.0	38.0	Larson (2008)
UALVP49880	cf. *Richardoestesia gilmorei*	2.20	2.48	1.00	40.0	39.5	Larson (2008)
UALVP49881	cf. *Richardoestesia gilmorei*	2.00	2.38	0.92		40.0	Larson (2008)
UALVP49882	cf. *Richardoestesia gilmorei*	1.92	2.44	0.80	42.0	43.5	Larson (2008)
UALVP49883	cf. *Richardoestesia gilmorei*	3.15	3.98	1.66		40.0	Larson (2008)
UALVP49884	cf. *Richardoestesia gilmorei*	1.88	2.32	0.84	43.5	41.0	Larson (2008)
UALVP49885	cf. *Richardoestesia gilmorei*	2.80	3.60	1.00	45.0	37.5	Larson (2008)
UALVP49886	cf. *Richardoestesia gilmorei*	1.90	2.10	1.10		40.0	Larson (2008)
UALVP49887	cf. *Richardoestesia gilmorei*	2.40	3.00	1.00		45.0	Larson (2008)

UALVP49888	cf. *Richardoestesia gilmorei*	2.40	4.20	1.40		47.5	Larson (2008)
UALVP49889	cf. *Richardoestesia gilmorei*	2.40	3.10	1.10	50.0	45.0	Larson (2008)
UALVP49890	cf. *Richardoestesia gilmorei*	2.40	3.30	1.10		50.0	Larson (2008)
UALVP49891	cf. *Richardoestesia gilmorei*	3.50	5.20	1.40	50.0	30.0	Larson (2008)
UALVP49892	cf. *Richardoestesia gilmorei*	2.24	3.49	0.96	40.0	32.5	Larson (2008)
UALVP49893	cf. *Richardoestesia gilmorei*	2.49	3.65	1.45		33.0	Larson (2008)
UALVP49894	cf. *Richardoestesia gilmorei*	3.74	4.98	2.20	40.0	31.3	Larson (2008)
UALVP49895	cf. *Richardoestesia gilmorei*	2.91	5.06	1.44		28.0	Larson (2008)
UALVP49896	cf. *Richardoestesia gilmorei*	2.66	3.90	1.10	50.0	33.0	Larson (2008)
UALVP49897	cf. *Richardoestesia gilmorei*	3.24	4.90	1.48		40.0	Larson (2008)
UALVP49898	cf. *Richardoestesia gilmorei*	3.40	4.48	1.52		34.0	Larson (2008)
UALVP49899	cf. *Richardoestesia gilmorei*	3.20	5.40	1.70		27.5	Larson (2008)
UALVP49900	cf. *Richardoestesia gilmorei*	3.15	4.69	1.56	60.0	42.5	Larson (2008)
UALVP49901	cf. *Richardoestesia gilmorei*	2.82	4.32	1.38		40.0	Larson (2008)
UALVP49902	cf. *Richardoestesia gilmorei*	2.86	4.98	1.46		35.0	Larson (2008)
UALVP49903	cf. *Richardoestesia gilmorei*	2.66	4.90	1.44		40.0	Larson (2008)
UALVP49904	cf. *Richardoestesia gilmorei*	3.65	4.07	1.70		40.0	Larson (2008)
UALVP49905	cf. *Richardoestesia gilmorei*	3.15	3.98	1.54		40.0	Larson (2008)
UALVP49906	cf. *Richardoestesia gilmorei*	2.99	4.48	1.52		36.5	Larson (2008)
UALVP49907	cf. *Richardoestesia gilmorei*	3.24	5.48	1.68		37.5	Larson (2008)
UALVP49908	cf. *Richardoestesia gilmorei*	2.74	3.24	1.26		43.0	Larson (2008)
UALVP49909	cf. *Richardoestesia gilmorei*	2.49	4.36	1.40		42.5	Larson (2008)
UALVP49910	cf. *Richardoestesia gilmorei*	2.91	4.90	1.76		37.5	Larson (2008)
UALVP49911	cf. *Richardoestesia gilmorei*	2.60	3.50	0.90	40.0	35.0	Larson (2008)
UALVP49912	cf. *Richardoestesia gilmorei*	2.49	3.65	1.18		38.8	Larson (2008)
UALVP49913	cf. *Richardoestesia gilmorei*	2.32	3.12	0.88		41.5	Larson (2008)
UALVP49914	cf. *Richardoestesia gilmorei*	2.08	2.70	0.96		40.0	Larson (2008)
UALVP49915	cf. *Richardoestesia gilmorei*	1.96	3.24	0.94		40.0	Larson (2008)
UALVP49916	cf. *Richardoestesia gilmorei*	2.91	4.81	2.20		34.0	Larson (2008)
UALVP49917	cf. *Richardoestesia gilmorei*	3.74	5.40	1.94	45.0	33.5	Larson (2008)

UALVP49918	cf. *Richardoestesia gilmorei*	3.82	4.98	1.76		32.5	Larson (2008)
UALVP49919	cf. *Richardoestesia gilmorei*	3.40	4.98	1.42	52.0	31.0	Larson (2008)
UALVP49920	cf. *Richardoestesia gilmorei*	2.99	4.73	1.58		36.0	Larson (2008)
UALVP49921	cf. *Richardoestesia gilmorei*	5.64	5.06	1.62		40.0	Larson (2008)
UALVP49922	cf. *Richardoestesia gilmorei*	2.95	4.32	1.46		36.5	Larson (2008)
UALVP49923	cf. *Richardoestesia gilmorei*	2.82	3.40	1.32		31.5	Larson (2008)
UALVP49924	cf. *Richardoestesia gilmorei*	3.15	4.07	1.34		36.0	Larson (2008)
UALVP49925	cf. *Richardoestesia gilmorei*	2.41	3.61	1.16	46.0	32.5	Larson (2008)
UALVP49926	cf. *Richardoestesia gilmorei*	2.76	3.40	1.14	45.0	36.0	Larson (2008)
UALVP49927	cf. *Richardoestesia gilmorei*	2.28	3.00	0.96	42.5	31.0	Larson (2008)
UALVP49928	cf. *Richardoestesia gilmorei*	2.82	3.15	1.06		34.0	Larson (2008)
UALVP49929	cf. *Richardoestesia gilmorei*	2.08	3.28	1.46		45.0	Larson (2008)
UALVP49930	cf. *Richardoestesia gilmorei*	2.52	3.12	0.97	41.5	35.5	Larson (2008)
UALVP49931	cf. *Richardoestesia gilmorei*	2.32	3.28	0.98		39.0	Larson (2008)
UALVP49932	cf. *Richardoestesia gilmorei*	2.00	2.68	0.96		36.5	Larson (2008)
UALVP49933	cf. *Richardoestesia gilmorei*	2.32	3.04	0.86		37.5	Larson (2008)
UALVP49934	cf. *Richardoestesia gilmorei*	2.40	2.80	0.81	32.0	34.0	Larson (2008)
UALVP49935	cf. *Richardoestesia gilmorei*	2.44	2.72	0.94		32.5	Larson (2008)
UALVP49936	cf. *Richardoestesia gilmorei*	2.00	2.80	0.84	50.0	37.0	Larson (2008)
UALVP49937	cf. *Richardoestesia gilmorei*	1.92	2.20	0.80	45.0	34.0	Larson (2008)
UALVP49938	cf. *Richardoestesia gilmorei*	1.84	2.86	0.70		32.5	Larson (2008)
UALVP49939	cf. *Richardoestesia gilmorei*	2.28	2.46	0.80	38.5	45.0	Larson (2008)
UALVP49940	cf. *Richardoestesia gilmorei*	2.00	2.28	0.94	44.0	37.0	Larson (2008)
UALVP49941	cf. *Richardoestesia gilmorei*	3.65	5.81	1.66	40.5	35.0	Larson (2008)
UALVP49942	cf. *Richardoestesia gilmorei*	2.82	4.32	1.56		40.0	Larson (2008)
UALVP49943	cf. *Richardoestesia gilmorei*	2.57	3.40	1.36		42.5	Larson (2008)
UALVP49944	cf. *Richardoestesia gilmorei*	1.88	2.16	0.90	54.0	40.0	Larson (2008)
UALVP49945	cf. *Richardoestesia gilmorei*	2.64	3.00	1.08		42.5	Larson (2008)
UALVP49946	cf. *Richardoestesia gilmorei*	1.36	2.00	0.72		73.0	Larson (2008)
UALVP49947	cf. *Richardoestesia gilmorei*	2.24	4.15	1.34		27.5	Larson (2008)

UALVP49948	cf. *Richardoestesia gilmorei*	2.24	3.90	1.56		27.5	Larson (2008)
UALVP49949	cf. *Richardoestesia gilmorei*	3.45	4.32	1.56		30.0	Larson (2008)
UALVP49950	cf. *Richardoestesia gilmorei*	2.74	3.82	1.12	36.5	29.0	Larson (2008)
UALVP49951	cf. *Richardoestesia gilmorei*	3.32	3.74	1.18		34.0	Larson (2008)
UALVP49952	cf. *Richardoestesia gilmorei*	3.15	3.74	1.16		35.0	Larson (2008)
UALVP49953	cf. *Richardoestesia gilmorei*	2.32	3.32	1.14		39.0	Larson (2008)
UALVP49954	cf. *Richardoestesia gilmorei*	3.82	5.69	1.34	51.0	30.5	Larson (2008)
UALVP49955	cf. *Richardoestesia gilmorei*	2.91	3.03	1.36		52.5	Larson (2008)
UALVP49956	cf. *Richardoestesia gilmorei*	2.49	4.48	1.26		28.0	Larson (2008)
UALVP49957	cf. *Richardoestesia gilmorei*	3.65	4.15	1.78	40.0	31.5	Larson (2008)
UALVP49958	cf. *Richardoestesia gilmorei*	1.99	2.99	0.92		41.5	Larson (2008)
UALVP49959	cf. *Richardoestesia gilmorei*	2.24	3.40	0.82		40.0	Larson (2008)
UALVP48114	cf. *Richardoestesia gilmorei*	2.40	5.06	1.22		29.0	Larson (2008)
UALVP48140	cf. *Richardoestesia gilmorei*	2.44	3.24	1.12		52.5	Larson (2008)
UALVP48156	cf. *Richardoestesia gilmorei*	2.56	2.88	1.00		35.0	Larson (2008)
UALVP48157	cf. *Richardoestesia gilmorei*	2.64	3.88	1.32		40.0	Larson (2008)
UALVP48159	cf. *Richardoestesia gilmorei*	2.40	3.60	1.20		40.0	Larson (2008)
UALVP48194	cf. *Richardoestesia gilmorei*	2.40	2.92	1.10		45.0	Larson (2008)
UALVP48208	cf. *Richardoestesia gilmorei*	4.07	10.50	2.68		30.0	Larson (2008)
UALVP48211	cf. *Richardoestesia gilmorei*	2.40	3.20	0.98		40.0	Larson (2008)
UALVP48215	cf. *Richardoestesia gilmorei*	4.48	5.89	2.24		35.0	Larson (2008)
UALVP48217	cf. *Richardoestesia gilmorei*	3.56	3.98	1.72		35.0	Larson (2008)
UALVP48219	cf. *Richardoestesia gilmorei*	3.40	3.65	1.74		35.0	Larson (2008)
UALVP48220	cf. *Richardoestesia gilmorei*	3.80	4.15	2.24	42.5	35.0	Larson (2008)
UALVP48276	cf. *Richardoestesia gilmorei*	2.44	2.76	1.12		40.0	Larson (2008)
UALVP50010	cf. *Richardoestesia gilmorei*	3.68	8.93	2.52		32.0	Larson (2008)
UALVP50011	cf. *Richardoestesia gilmorei*	2.91	4.57	1.48		55.0	Larson (2008)
UALVP50012	cf. *Richardoestesia gilmorei*	3.07	4.15	1.46		37.5	Larson (2008)
UALVP50013	cf. *Richardoestesia gilmorei*	3.03	6.89	1.42		31.5	Larson (2008)
UALVP50014	cf. *Richardoestesia gilmorei*	2.00	3.48	1.04		51.0	Larson (2008)

UALVP50015	cf. *Richardoestesia gilmorei*	1.48	3.12	0.96		51.0	Larson (2008)
UALVP50016	cf. *Richardoestesia gilmorei*	3.74	6.81	1.82		32.5	Larson (2008)
UALVP50017	cf. *Richardoestesia gilmorei*	2.32	4.65	1.36		29.0	Larson (2008)
UALVP50018	cf. *Richardoestesia gilmorei*	2.99	4.81	1.70		30.0	Larson (2008)
UALVP50019	cf. *Richardoestesia gilmorei*	1.60	2.60	0.84	53.0	51.5	Larson (2008)
UALVP50020	cf. *Richardoestesia gilmorei*	2.80	4.50	1.20		40.0	Larson (2008)
UALVP50021	cf. *Richardoestesia gilmorei*	2.20	4.00	1.60		40.0	Larson (2008)
UALVP50022	cf. *Richardoestesia gilmorei*	1.60	3.20	0.90		50.0	Larson (2008)
UALVP50023	cf. *Richardoestesia gilmorei*	2.49	4.48	1.46		29.5	Larson (2008)
UALVP50024	cf. *Richardoestesia gilmorei*	3.30	5.80	1.40		40.0	Larson (2008)
UALVP50025	cf. *Richardoestesia gilmorei*	1.64	2.68	0.90		40.0	Larson (2008)
UALVP50026	cf. *Richardoestesia gilmorei*	2.41	4.32	1.36		45.0	Larson (2008)
UALVP50027	cf. *Richardoestesia gilmorei*	2.24	5.23	1.26		40.0	Larson (2008)
UALVP48210	cf. *Richardoestesia gilmorei*	1.72	3.20	1.36		36.5	Larson (2008)
UALVP48265	cf. *Richardoestesia gilmorei*	2.40	3.72	1.84		50.0	Larson (2008)
UALVP48277	cf. *Richardoestesia gilmorei*	2.36	2.80	1.18		30.0	Larson (2008)
UALVP50040	cf. *Richardoestesia gilmorei*	2.20	5.10	1.70		55.0	Larson (2008)
UALVP50041	cf. *Richardoestesia gilmorei*	2.49	4.57	2.04	33.0	26.5	Larson (2008)
UALVP50042	cf. *Richardoestesia gilmorei*	3.15	5.15	1.56		27.0	Larson (2008)
UALVP50043	cf. *Richardoestesia gilmorei*	3.32	5.48	1.74	32.0	27.5	Larson (2008)
UALVP50044	cf. *Richardoestesia gilmorei*	2.99	5.15	2.32		37.5	Larson (2008)
UALVP50045	cf. *Richardoestesia gilmorei*	1.83	3.15	1.30		37.5	Larson (2008)
UALVP50046	cf. *Richardoestesia gilmorei*	3.15	5.23	1.92	47.0	35.0	Larson (2008)
UALVP50047	cf. *Richardoestesia gilmorei*	2.91	4.81	1.42		30.0	Larson (2008)
Oldman Formation (77-76 Ma)							
TMP86.171.61	cf. *Richardoestesia gilmorei*	1.90	3.40	0.90		40.0	Sankey et al. (2002)
TMP86.171.9	cf. *Richardoestesia gilmorei*	2.30	4.20	1.00		40.0	Sankey et al. (2002)
TMP87.80.35	cf. *Richardoestesia gilmorei*	3.90	7.50	3.00		30.0	Sankey et al. (2002)
TMP96.62.30b	cf. *Richardoestesia gilmorei*	1.80	3.10	0.70		35.0	Sankey et al. (2002)
Dinosaur Park Formation (76-75 Ma)							

TMP83.36.233	*Richardoestesia gilmorei*	4.70	12.30	2.30		26.3	Sankey et al. (2002)
TMP83.36.242	*Richardoestesia gilmorei*	3.70	8.30	1.60		35.0	Sankey et al. (2002)
TMP84.92.268	*Richardoestesia gilmorei*	3.50	5.50	1.50		35.0	Sankey et al. (2002)
TMP86.23.90	*Richardoestesia gilmorei*	4.00	10.00	1.70		35.0	Sankey et al. (2002)
TMP88.91.28	*Richardoestesia gilmorei*	2.90	5.30	1.00		35.0	Sankey et al. (2002)
TMP89.76.63	*Richardoestesia gilmorei*	2.80	5.20	0.90		35.0	Sankey et al. (2002)
TMP90.106.6	*Richardoestesia gilmorei*	1.70	4.00	0.70		47.5	Sankey et al. (2002)
TMP95.157.29	*Richardoestesia gilmorei*	1.40	2.80	0.70		55.0	Sankey et al. (2002)
TMP1982.24.78	*Richardoestesia gilmorei*	3.41	4.92	1.30	38.3	33.1	Longrich (2008)
TMP84.84.247	*Richardoestesia gilmorei*	3.14	6.13	1.50		35.2	Longrich (2008)
TMP1986.23.105	*Richardoestesia gilmorei*	2.21	4.80	1.16		46.3	Longrich (2008)
TMP87.99.48	*Richardoestesia gilmorei*	2.00	5.35	0.99		47.3	Longrich (2008)
TMP1987.114.5	*Richardoestesia gilmorei*	2.83	4.43	1.08		39.1	Longrich (2008)
TMP89.76.83	*Richardoestesia gilmorei*	2.87	3.35	1.21	43.9	36.5	Longrich (2008)
TMP86.171.9	*Richardoestesia gilmorei*	2.11	3.75	1.16		36.8	Longrich (2008)
Judith River Group (Formation) (79.5-75 Ma)							
TMP89.36.355	*Richardoestesia gilmorei*	3.80	10.00	2.00		35.0	Sankey et al. (2002)
p83452	*Richardoestesia gilmorei*	7.50	19.00		33.0	31.0	Farlow et al. (1991)
nmc343	*Richardoestesia gilmorei*	5.70	9.00		35.0	26.0	Farlow et al. (1991)
p80161230	*Richardoestesia gilmorei*	5.50	7.00			28.0	Farlow et al. (1991)
p83368	*Richardoestesia gilmorei*	5.80	12.00		30.0	26.0	Farlow et al. (1991)
hjohnson2	*Richardoestesia gilmorei*	4.80	6.00			28.0	Farlow et al. (1991)
p812257	*Richardoestesia gilmorei*	6.50	12.00		34.0	24.0	Farlow et al. (1991)
p808214	*Richardoestesia gilmorei*	5.20	9.00			26.0	Farlow et al. (1991)
hjohnson7	*Richardoestesia gilmorei*	6.50		1.00		25.0	Farlow et al. (1991)
nmcf1	*Richardoestesia gilmorei*	5.00	7.00		30.0	26.0	Farlow et al. (1991)
p83368no1	*Richardoestesia gilmorei*	3.90	7.00	1.70	50.0	32.5	Farlow et al. (1991)
Javelina Formation (~69 Ma)							
LSUMG235:1931	cf. *Saurornitholestes* B	3.00	3.50	1.30		35.0	Sankey et al. (2005)
Horseshoe Canyon Formation (68-72 Ma)							

	cf. *Richardoestesia gilmorei*	6.27	11.52		40.6	30.9	Longrich (2008)
TMP94.28.01	cf. *Richardoestesia gilmorei*	5.47	10.46		41.0	27.8	Longrich (2008)
TMP00.45.80	cf. *Richardoestesia gilmorei*	6.97	11.90	2.66	31.0	25.0	this study
TMP02.45.49	cf. *Richardoestesia gilmorei*	2.99	4.65	1.25	50.0	31.5	this study
TMP02.45.53	cf. *Richardoestesia gilmorei*	3.40	4.32	1.33	52.5	32.5	this study
TMP01.45.82	cf. *Richardoestesia isosceles*	3.85	8.93	2.24		37.5	this study
Lance Formation (65.5-66.5 Ma)							
IMG 1486	cf. *Richardoestesia gilmorei*	2.61	4.97		41.5	36.8	Longrich (2008)
IMG 1655	cf. *Richardoestesia gilmorei*	2.08	3.62		49.1	38.3	Longrich (2008)
IMG 1657	cf. *Richardoestesia gilmorei*	2.54	4.11		51.7	38.1	Longrich (2008)
IMG 1486	cf. *Richardoestesia gilmorei*	2.57	4.19		61.4	40.4	Longrich (2008)
AMNH5396.3	cf. *Richardoestesia gilmorei*	3.50	6.30	1.53	46.9	32.1	Longrich (2008)
AMNH5450	cf. *Richardoestesia gilmorei*	2.64	6.75	1.43	66.8	57.7	Longrich (2008)
AMNH5529.3	cf. *Richardoestesia gilmorei*	3.79	5.38	1.30	38.6	28.8	Longrich (2008)
AMNH5529.1	cf. *Richardoestesia gilmorei*	3.68	5.50	1.69	44.8	26.3	Longrich (2008)
	cf. *Richardoestesia gilmorei*	3.97	6.17	1.81	38.9	25.3	Longrich (2008)
AMNH5535.3	cf. *Richardoestesia gilmorei*	3.66	5.39	1.45	37.2	27.9	Longrich (2008)
AMNH5553.3	cf. *Richardoestesia gilmorei*	3.73	4.81	1.39	37.2	31.3	Longrich (2008)
AMNH5553.1	cf. *Richardoestesia gilmorei*	3.58	5.23	1.21	49.2	30.6	Longrich (2008)
AMNH5547	cf. *Richardoestesia gilmorei*	3.85	5.35	1.56		32.9	Longrich (2008)
AMNH5547.2	cf. *Richardoestesia gilmorei*	2.94	4.86	1.14		38.3	Longrich (2008)
AMNH5547.3	cf. *Richardoestesia gilmorei*	3.36	5.45	1.34		36.4	Longrich (2008)
AMNH5545	cf. *Richardoestesia gilmorei*	3.98	5.44			27.2	Longrich (2008)
AMNH5545.2	cf. *Richardoestesia gilmorei*	4.04	5.88			29.3	Longrich (2008)
DSCN 1694	cf. *Richardoestesia gilmorei*	3.88	8.40		52.7	33.3	Longrich (2008)
AMNH5749	cf. *Richardoestesia gilmorei*	3.61	6.37	1.55	46.0	31.3	Longrich (2008)
left	cf. *Richardoestesia gilmorei*	3.75	6.97	1.53	46.8	28.5	Longrich (2008)
AMNH5671.3	cf. *Richardoestesia gilmorei*	3.89	7.00	1.58		28.6	Longrich (2008)
AMNH1498(right)	cf. *Richardoestesia gilmorei*	3.59	5.96		46.9	30.4	Longrich (2008)
Upper Hell Creek Formation (65.5-66.75 Ma)							

UCMP128941	cf. *Richardoestesia gilmorei*	3.70	6.00			30.0	Sankey (2008)
UCMP120338	cf. *Richardoestesia gilmorei*	5.50	7.50			25.0	Sankey (2008)
UCMP119921	cf. *Richardoestesia gilmorei*	3.70	5.70			30.0	Sankey (2008)
UCMP128913	cf. *Richardoestesia gilmorei*	3.80	7.00			30.0	Sankey (2008)
UCMP120153	cf. *Richardoestesia gilmorei*	3.00	4.80			25.0	Sankey (2008)
UCMP120287	cf. *Richardoestesia gilmorei*	5.00	8.00			22.5	Sankey (2008)
UCMP123543	cf. *Richardoestesia gilmorei*	7.00	6.00			20.0	Sankey (2008)
UCMP123565	cf. *Richardoestesia gilmorei*	4.00	7.00			30.0	Sankey (2008)
UCMP119718	cf. *Richardoestesia gilmorei*	6.00	10.00			25.0	Sankey (2008)
UCMP187163	cf. *Richardoestesia gilmorei*	2.50	5.00			35.0	Sankey (2008)
John Henry Member of Straight Cliffs Formation (85.8-?84 Ma)							
UMNH424-17371	cf. *Richardoestesia isosceles*	3.10	8.27	1.62	56.5	40.5	this study
UMNH424-14403	cf. *Richardoestesia isosceles*	1.88	5.01	1.12		54.0	this study
UMNH424-17220	cf. *Richardoestesia isosceles*	2.47	6.18	1.39	54.5		this study
UMNH424-17220	cf. *Richardoestesia isosceles*	2.50	5.53	1.35		55.0	this study
Milk River Formation (~83.5 Ma)							
UALVP48279	cf. *Richardoestesia isosceles*	2.40	5.11	1.12	45.0	37.5	Larson (2008)
UALVP48287	cf. *Richardoestesia isosceles*	3.82	7.72	1.58	45.0	30.0	Larson (2008)
UALVP48290	cf. *Richardoestesia isosceles*	4.65	11.03	2.20	36.3	35.0	Larson (2008)
UALVP48291	cf. *Richardoestesia isosceles*	4.57	11.38	2.20	40.0	35.0	Larson (2008)
UALVP48295	cf. *Richardoestesia isosceles*	2.36	5.15	1.20		37.5	Larson (2008)
UALVP48312	cf. *Richardoestesia isosceles*	3.98	11.73	2.44	40.0	35.0	Larson (2008)
UALVP48323	cf. *Richardoestesia isosceles*	1.92	4.00	1.00	62.5	47.5	Larson (2008)
UALVP48324	cf. *Richardoestesia isosceles*	3.57	10.68	1.82	32.5	35.0	Larson (2008)
UALVP48325	cf. *Richardoestesia isosceles*	4.48	13.30	2.20	40.0	35.0	Larson (2008)
UALVP48326	cf. *Richardoestesia isosceles*	3.32	7.80	1.70	55.0	40.0	Larson (2008)
UALVP48327	cf. *Richardoestesia isosceles*	5.40	14.88	2.96	35.0	32.5	Larson (2008)
UALVP48328	cf. *Richardoestesia isosceles*	2.91	6.64	1.48		50.0	Larson (2008)
UALVP48329	cf. *Richardoestesia isosceles*	4.23	10.50	2.24	36.5	31.3	Larson (2008)
UALVP48330	cf. *Richardoestesia isosceles*	5.78	14.00	2.80		32.5	Larson (2008)

UALVP48331	cf. *Richardoestesia isosceles*	4.81	13.13	2.32	30.0	28.8	Larson (2008)
UALVP48343	cf. *Richardoestesia isosceles*	5.89	15.58	3.00	38.8	32.5	Larson (2008)
UALVP48344	cf. *Richardoestesia isosceles*	3.20	9.45	1.84	55.0	40.0	Larson (2008)
UALVP48345	cf. *Richardoestesia isosceles*	1.96	4.57	1.12		45.0	Larson (2008)
UALVP48355	cf. *Richardoestesia isosceles*	2.80	9.63	1.62	53.8	50.0	Larson (2008)
UALVP50136	cf. *Richardoestesia isosceles*	2.82	7.14	1.34	50.0	38.0	Larson (2008)
UALVP50137	cf. *Richardoestesia isosceles*	2.00	3.40	1.00		52.5	Larson (2008)
UALVP50138	cf. *Richardoestesia isosceles*	4.55	14.00	2.36	65.0	31.0	Larson (2008)
UALVP50139	cf. *Richardoestesia isosceles*	2.74	7.14	1.28	38.5	35.0	Larson (2008)
UALVP50140	cf. *Richardoestesia isosceles*	2.91	5.98	1.38		55.0	Larson (2008)
UALVP50141	cf. *Richardoestesia isosceles*	1.99	4.40	0.96		52.5	Larson (2008)
UALVP50142	cf. *Richardoestesia isosceles*	3.15	7.47	1.46	38.5	35.0	Larson (2008)
UALVP50143	cf. *Richardoestesia isosceles*	3.24	5.40	1.40		42.0	Larson (2008)
UALVP50144	cf. *Richardoestesia isosceles*	1.56	2.72	0.80		70.0	Larson (2008)
UALVP50145	cf. *Richardoestesia isosceles*	3.07	8.93	1.74	48.0	41.5	Larson (2008)
UALVP50146	cf. *Richardoestesia isosceles*	1.83	4.07	0.78		57.5	Larson (2008)
UALVP50147	cf. *Richardoestesia isosceles*	2.32	3.65	1.10		51.0	Larson (2008)
UALVP50148	cf. *Richardoestesia isosceles*	2.82	6.39	1.04		38.5	Larson (2008)
UALVP50149	cf. *Richardoestesia isosceles*	2.57	4.81	1.32	40.0	40.0	Larson (2008)
UALVP50150	cf. *Richardoestesia isosceles*	3.70	9.50	2.00		40.0	Larson (2008)
UALVP50151	cf. *Richardoestesia isosceles*	3.90	9.20	1.90			Larson (2008)
UALVP50152	cf. *Richardoestesia isosceles*	2.41	3.82	1.08	56.5	38.5	Larson (2008)
UALVP50153	cf. *Richardoestesia isosceles*	2.57	5.64	1.56	60.0	44.5	Larson (2008)
UALVP50154	cf. *Richardoestesia isosceles*	5.31	13.21	2.68	45.0	32.5	Larson (2008)
UALVP50155	cf. *Richardoestesia isosceles*	3.57	9.80	1.80	44.0	38.5	Larson (2008)
UALVP50156	cf. *Richardoestesia isosceles*	3.49	9.45	1.92	43.0	31.5	Larson (2008)
UALVP50157	cf. *Richardoestesia isosceles*	2.91	6.14	1.54	51.5	41.0	Larson (2008)
UALVP50158	cf. *Richardoestesia isosceles*	2.12	5.56	1.34		45.0	Larson (2008)
UALVP50159	cf. *Richardoestesia isosceles*	1.72	2.72	0.94		65.0	Larson (2008)
UALVP50160	cf. *Richardoestesia isosceles*	2.04	2.44	0.90	46.0	40.0	Larson (2008)

UALVP50161	cf. *Richardoestesia isosceles*	3.57	9.28	1.96	49.0	37.0	Larson (2008)
UALVP50162	cf. *Richardoestesia isosceles*	2.57	6.14	1.66	62.5	40.0	Larson (2008)
UALVP50163	cf. *Richardoestesia isosceles*	2.66	7.06	1.60			Larson (2008)
UALVP50164	cf. *Richardoestesia isosceles*	3.40	8.75	1.82	42.5	32.5	Larson (2008)
UALVP48187	cf. *Richardoestesia isosceles*	2.68	2.68	0.98		40.0	Larson (2008)
UALVP48207	cf. *Richardoestesia isosceles*	3.24	7.30	1.20		37.5	Larson (2008)
UALVP48218	cf. *Richardoestesia isosceles*	3.98	4.48	2.16	40.0	31.5	Larson (2008)
UALVP48222	cf. *Richardoestesia isosceles*	2.44	3.00	1.04		50.0	Larson (2008)
UALVP48227	cf. *Richardoestesia isosceles*	2.04	2.94	0.78		41.0	Larson (2008)
UALVP48228	cf. *Richardoestesia isosceles*	3.57	7.14	1.84	36.3	35.0	Larson (2008)
UALVP48229	cf. *Richardoestesia isosceles*	3.08	7.14	1.76		41.3	Larson (2008)
UALVP48269	cf. *Richardoestesia isosceles*	2.64	7.06	1.28		38.8	Larson (2008)
UALVP50199	cf. *Richardoestesia isosceles*	1.79	4.40	1.04		43.5	Larson (2008)
UALVP50200	cf. *Richardoestesia isosceles*	1.79	4.40	0.94		45.0	Larson (2008)
UALVP50201	cf. *Richardoestesia isosceles*	2.95	6.56	1.74		36.5	Larson (2008)
UALVP50202	cf. *Richardoestesia isosceles*	1.99	3.98	0.96	45.0	42.5	Larson (2008)
UALVP50203	cf. *Richardoestesia isosceles*	2.41	3.98	1.08	60.0	47.0	Larson (2008)
UALVP50204	cf. *Richardoestesia isosceles*	1.60	3.36	0.90	56.0	50.0	Larson (2008)
UALVP50205	cf. *Richardoestesia isosceles*	2.16	3.60	0.98		40.0	Larson (2008)
UALVP50206	cf. *Richardoestesia isosceles*	2.24	3.74	0.94	47.5	45.0	Larson (2008)
UALVP50207	cf. *Richardoestesia isosceles*	1.92	3.28	0.90		53.5	Larson (2008)
UALVP50208	cf. *Richardoestesia isosceles*	3.90	9.89	2.08	38.5	46.0	Larson (2008)
UALVP50209	cf. *Richardoestesia isosceles*	2.40	3.00	1.00		56.5	Larson (2008)
Foremost Formation (79.5-77 Ma)							
TMP88.86.44	cf. *Richardoestesia isosceles*	3.50	8.50	1.40		39.0	Sankey et al. (2002)
Oldman Formation (77-76 Ma)							
TMP86.159.62	cf. *Richardoestesia isosceles*	3.50	7.50	1.50		32.5	Sankey et al. (2002)
TMP90.79.31	cf. *Richardoestesia isosceles*	2.80	6.80	1.30		40.0	Sankey et al. (2002)
TMP95.177.49a	cf. *Richardoestesia isosceles*	3.20	8.50	1.20		50.0	Sankey et al. (2002)
TMP95.180.5a	cf. *Richardoestesia isosceles*	1.90	5.20	0.90		60.0	Sankey et al. (2002)

TMP96.48.11	cf. *Richardoestesia isosceles*	2.50	5.00	1.30		40.0	Sankey et al. (2002)
TMP96.62.30a	cf. *Richardoestesia isosceles*	3.60	12.50	1.70		30.0	Sankey et al. (2002)
TMP89.103.25	cf. *Richardoestesia isosceles*	3.90	5.40	2.50		37.5	Sankey et al. (2002)
TMP95.177.79	cf. *Richardoestesia isosceles*	1.90	3.00	0.70		60.0	Sankey et al. (2002)
TMP86.172.53	cf. *Richardoestesia isosceles*	1.90	2.90	0.70		60.0	Sankey et al. (2002)
Dinosaur Park Formation (76-75 Ma)							
TMP84.1.12	cf. *Richardoestesia isosceles*	4.50	11.00	2.10		30.0	Sankey et al. (2002)
TMP86.23.105	cf. *Richardoestesia isosceles*	2.30	5.80	1.10		42.5	Sankey et al. (2002)
TMP86.33.54	cf. *Richardoestesia isosceles*	2.10	4.50	1.10		40.0	Sankey et al. (2002)
TMP86.45.46	cf. *Richardoestesia isosceles*	2.30	5.50	1.20		50.0	Sankey et al. (2002)
TMP88.36.199	cf. *Richardoestesia isosceles*	3.70	9.50	1.70		35.0	Sankey et al. (2002)
TMP95.181.10	cf. *Richardoestesia isosceles*	3.00	7.20	1.60		35.0	Sankey et al. (2002)
TMP96.142.19	cf. *Richardoestesia isosceles*	3.10	9.70	1.50		35.0	Sankey et al. (2002)
TMP87.158.76	cf. *Richardoestesia isosceles*	2.40	3.30	0.80		50.0	Sankey et al. (2002)
TMP84.92.205	cf. *Richardoestesia isosceles*	2.00	2.70	0.70		60.0	Sankey et al. (2002)
TMP86.21.68	cf. *Richardoestesia isosceles*	2.00	3.70	1.00		60.0	Sankey et al. (2002)
TMP95.174.52	cf. *Richardoestesia isosceles*	1.80	2.30	0.70		60.0	Sankey et al. (2002)
TMP95.181.10c	cf. *Richardoestesia isosceles*	2.20	3.30	0.80		60.0	Sankey et al. (2002)
TMP95.181.60e	cf. *Richardoestesia isosceles*	1.40	2.40	0.60		60.0	Sankey et al. (2002)
TMP95.181.60f	cf. *Richardoestesia isosceles*	1.90	2.50	0.70		60.0	Sankey et al. (2002)
BB86 uncat.	cf. *Richardoestesia isosceles*	3.00	6.00			45.0	Farlow et al. (1991)
p741067no1	cf. *Richardoestesia isosceles*	2.30	5.00		40.0	24.0	Farlow et al. (1991)
p741067no2	cf. *Richardoestesia isosceles*	3.00	6.00			22.5	Farlow et al. (1991)
p741067no3	cf. *Richardoestesia isosceles*	3.30	5.00		35.0	20.0	Farlow et al. (1991)
p83331	cf. *Richardoestesia isosceles*	4.80	7.00			23.0	Farlow et al. (1991)
p8219366	cf. *Richardoestesia isosceles*	3.10	6.00	1.80		22.0	Farlow et al. (1991)
p83368no3	cf. *Richardoestesia isosceles*	3.60	7.00			35.0	Farlow et al. (1991)
p663182	cf. *Richardoestesia isosceles*	3.80	7.00			20.0	Farlow et al. (1991)
nmckno23b	cf. *Richardoestesia isosceles*	5.90	10.00			20.0	Farlow et al. (1991)
hjohnson4	cf. *Richardoestesia isosceles*	2.00	4.00			25.0	Farlow et al. (1991)

Judith River Group (Formation) (79.5-75 Ma)							
"b	cf. *Richardoestesia isosceles*	1.70	4.20	0.90			Sankey et al. (2002)
"b	cf. *Richardoestesia isosceles*	4.20	10.70	2.30		25.0	Sankey et al. (2002)
Aguja Middle Campanian (~79 Ma)							
LSUMG489:6237	*Richardoestesia isosceles*	2.00	2.50	0.90		50.0	Sankey et al. (2005)
LSUMG489:6235	*Richardoestesia isosceles*	1.70	3.00	0.70		55.0	Sankey et al. (2005)
LSUMG489:6050	*Richardoestesia isosceles*	1.70	3.50	1.00		50.0	Sankey et al. (2005)
Aguja Upper Campanian (?76-71? Ma)							
LSUMG741:5933	cf. *Richardoestesia isosceles*	1.80	2.30	0.90		45.0	Sankey et al. (2005)
LSUMG113:5939	cf. *Richardoestesia isosceles*	2.00	4.00	1.00		60.0	Sankey et al. (2005)
Lance Formation (65.5-66.5 Ma)							
UCMP213984	V5620	4.40	8.60	1.80		32.5	Sankey (2008)
UCMP214012	cf. *Richardoestesia isosceles*	3.80	7.30	1.80		32.5	Sankey (2008)
UCMP187102	cf. *Richardoestesia isosceles*	2.50	5.20	1.80		42.5	Sankey (2008)
UCMP214013	cf. *Richardoestesia isosceles*	2.50	5.40	1.40		42.5	Sankey (2008)
UCMP214016	cf. *Richardoestesia isosceles*	2.70	3.90	1.20		45.0	Sankey (2008)
UCMP214020	cf. *Richardoestesia isosceles*	2.70	5.00	1.40		60.0	Sankey (2008)
UCMP214021	cf. *Richardoestesia isosceles*	2.90	5.40	1.40		50.0	Sankey (2008)
UCMP214022	cf. *Richardoestesia isosceles*	3.50	7.20	1.50		40.0	Sankey (2008)
UCMP214023	cf. *Richardoestesia isosceles*	3.20	6.30	1.40		40.0	Sankey (2008)
UCMP214035	cf. *Richardoestesia isosceles*	2.20	4.00	1.00		45.0	Sankey (2008)
UCMP214039	cf. *Richardoestesia isosceles*	2.80	6.50	1.60		32.5	Sankey (2008)
UCMP214043	cf. *Richardoestesia isosceles*	3.20	7.30	1.60		40.0	Sankey (2008)
	cf. *Richardoestesia isosceles*	4.10	12.00		35.0	32.5	Farlow et al. (1991)
AMNH5366	cf. *Richardoestesia isosceles*	4.75	12.36	2.18	39.9	35.4	Longrich (2008)
AMNH5370	cf. *Richardoestesia isosceles*	4.35	13.50	2.21	38.1	31.6	Longrich (2008)
AMNH5370.2	cf. *Richardoestesia isosceles*	4.02	13.71	2.12	43.7	32.3	Longrich (2008)
AMNH5376.1	cf. *Richardoestesia isosceles*	4.98	16.38	2.26	41.5	33.8	Longrich (2008)
AMNH5376.2	cf. *Richardoestesia isosceles*	4.40	13.86	2.09	39.8	36.7	Longrich (2008)
AMNH5380.1	cf. *Richardoestesia isosceles*	4.74	15.10	2.29	38.5	33.6	Longrich (2008)

AMNH5380.2	cf. *Richardoestesia isosceles*	3.85	13.63	2.04	35.2	31.8	Longrich (2008)
AMNH5382.1	cf. *Richardoestesia isosceles*	5.55	17.20	2.39	39.7	30.1	Longrich (2008)
AMNH5382.2	cf. *Richardoestesia isosceles*	5.74	16.65	2.53	37.8	31.5	Longrich (2008)
AMNH5386.3	cf. *Richardoestesia isosceles*	4.24	9.46	1.96	46.5	31.0	Longrich (2008)
AMNH5386.2	cf. *Richardoestesia isosceles*	3.46	11.26	1.83		38.2	Longrich (2008)
AMNH5386.2	cf. *Richardoestesia isosceles*	4.31	14.37	2.11	35.4	31.4	Longrich (2008)
AMNH5390.2	cf. *Richardoestesia isosceles*	4.22	9.04		45.8	34.2	Longrich (2008)
AMNH5390.3	cf. *Richardoestesia isosceles*	3.35	9.57		71.2	52.2	Longrich (2008)
AMNH5390.1	cf. *Richardoestesia isosceles*	2.85	5.50		45.8	30.9	Longrich (2008)
AMNH5556.1	cf. *Richardoestesia isosceles*	5.57	17.13		39.7	34.1	Longrich (2008)
AMNH5556.2	cf. *Richardoestesia isosceles*	5.80	16.80		38.9	28.8	Longrich (2008)
Upper Hell Creek Formation (65.5-66.75 Ma)							
UCMP186837	cf. *Richardoestesia isosceles*	3.30	6.70	1.70		52.5	Sankey (2008)
UCMP186842	cf. *Richardoestesia isosceles*	2.70	5.30	1.40		40.0	Sankey (2008)
UCMP186825	cf. *Richardoestesia isosceles*	3.30	9.10	1.80		40.0	Sankey (2008)
UCMP213927	cf. *Richardoestesia isosceles*	3.20	6.20	1.50		32.5	Sankey (2008)
UCMP213933	cf. *Richardoestesia isosceles*	3.00	4.80	1.50		40.0	Sankey (2008)
UCMP213935	cf. *Richardoestesia isosceles*	2.30	4.40	1.40		40.0	Sankey (2008)
UCMP213951	cf. *Richardoestesia isosceles*	4.20	13.00	1.80		40.0	Sankey (2008)
UCMP213953	cf. *Richardoestesia isosceles*	3.80	8.90	1.70		37.5	Sankey (2008)
UCMP213960	cf. *Richardoestesia isosceles*	3.90	9.10	1.80		37.5	Sankey (2008)
UCMP213972	cf. *Richardoestesia isosceles*	4.10	8.50	2.00		40.0	Sankey (2008)
UCMP213975	cf. *Richardoestesia isosceles*	4.40	8.90	2.00		35.0	Sankey (2008)
UCMP213994	cf. *Richardoestesia isosceles*	2.90	5.80	1.40		50.0	Sankey (2008)
UCMP213995	cf. *Richardoestesia isosceles*	3.50	8.60	1.80		27.5	Sankey (2008)
UCMP213997	cf. *Richardoestesia isosceles*	2.90	5.90	1.50		50.0	Sankey (2008)
UCMP186842	cf. *Richardoestesia isosceles*	2.70	5.90	1.40		45.0	Sankey (2008)
UCMP123525	cf. *Richardoestesia isosceles*	3.90	7.30	1.50		50.0	Sankey (2008)
UCMP186840	cf. *Richardoestesia isosceles*	4.40	9.20	2.00		32.5	Sankey (2008)
UCMP213980	cf. *Richardoestesia isosceles*	2.70	5.20	1.40		32.5	Sankey (2008)

Judith River? Formation (79.5-75 Ma)							
MOR 553	*Troodon formosus*	4.92	7.22	2.43	18.8	11.3	Smith et al. (2005)
MOR 554	*Troodon formosus*	6.22	9.61	2.95	10.0	10.0	Smith et al. (2005)
MOR 555	*Troodon formosus*	6.00	9.39	3.03	10.0	8.8	Smith et al. (2005)
MOR 556	*Troodon formosus*	5.60	8.47	2.71	10.0	12.5	Smith et al. (2005)
MOR 557	*Troodon formosus*	5.20	7.84	2.33	12.5	12.5	Smith et al. (2005)
MOR 558	*Troodon formosus*	4.45	7.25	1.62	12.5	12.5	Smith et al. (2005)
Dinosaur Park Formation (76-75 Ma)							
TMP00.19.1	cf. *Pectinodon*	2.80	5.50	1.20		10.0	Longrich (2008)
TMP00.21.1	cf. *Pectinodon*	3.10	5.20	1.20		7.5	Longrich (2008)
TMP79.8.635	cf. *Pectinodon*	2.40	3.30	0.90		10.0	Longrich (2008)
p849114	cf. *Troodon*	5.20	9.00		7.5	7.5	Farlow et al. (1991)
p798498	cf. *Troodon*	5.00	7.00		7.1	8.1	Farlow et al. (1991)
p841832	cf. *Troodon*	5.20	9.00		7.5	8.3	Farlow et al. (1991)
p80161370	cf. *Troodon*	5.70	8.00		7.1	6.8	Farlow et al. (1991)
p8219370	cf. *Troodon*	4.80	9.00		7.7	8.3	Farlow et al. (1991)
p80161950	cf. *Troodon*	5.10	8.00		9.4	9.7	Farlow et al. (1991)
p8561	cf. *Troodon*	4.30	8.00		5.4	7.1	Farlow et al. (1991)
p7412	cf. *Troodon*	6.20	9.00	3.40	4.7	7.8	Farlow et al. (1991)
p8116501	cf. *Troodon*	5.90	8.00		9.3	8.3	Farlow et al. (1991)
p841685	cf. *Troodon*	5.60	8.00		10.7	9.4	Farlow et al. (1991)
TMP2000.12.117	cf. *Troodon*	4.51	6.67	2.22	12.0	11.2	Longrich (2008)
TMP1996.12.72	cf. *Troodon*	4.96	8.61	2.55	10.0	8.9	Longrich (2008)
TMP1995.12.11	cf. *Troodon*	5.35	8.01	2.65		10.8	Longrich (2008)
TMP1995.21.10	cf. *Troodon*	4.99	6.92	2.81	9.2	10.0	Longrich (2008)
TMP1989.89.4	cf. *Troodon*	2.97	3.89	1.53		16.9	Longrich (2008)
TMP1987.50.34	cf. *Troodon*	3.26	4.55	1.79		10.3	Longrich (2008)
TMP1986.216.4	cf. *Troodon*	4.88	6.56	2.32		10.5	Longrich (2008)
TMP1987.36.139	cf. *Troodon*	5.91	8.36	2.72	13.2	11.3	Longrich (2008)
TMP1989.50.129	cf. *Troodon*	4.01	4.16	1.99		9.9	Longrich (2008)

TMP1986.177.8	cf. *Troodon*	3.45	3.37	1.55		14.9	Longrich (2008)
TMP1985.66.73	cf. *Troodon*	3.31	4.57	1.69		12.1	Longrich (2008)
TMP1989.116.63	cf. *Troodon*	3.39	4.48	1.83	11.7	10.8	Longrich (2008)
TMP184.89.275	cf. *Troodon*	5.21	8.76	2.44	11.4	9.8	Longrich (2008)
TMP1986.23.(91)	cf. *Troodon*	2.86	3.56	1.25		16.1	Longrich (2008)
TMP1986.8.93	cf. *Troodon*	3.62	3.33	1.73		14.8	Longrich (2008)
TMP1986.130.16	cf. *Troodon*	5.02	7.44	2.42	15.2	12.7	Longrich (2008)
TMP1983.36.214	cf. *Troodon*	4.29	6.50	2.73	7.0	8.2	Longrich (2008)
TMP1985.56.182	cf. *Troodon*	5.85	10.38	3.33	12.1	9.6	Longrich (2008)
TMP1985.56.179	cf. *Troodon*	5.83	7.72	2.93		10.2	Longrich (2008)
TMP1986.54.66	cf. *Troodon*	1.53	2.33	1.10	13.8	11.0	Longrich (2008)
TMP1994.16.15	cf. *Troodon*	3.62	5.40		8.7	12.1	Longrich (2008)
TMP1987.36.301	cf. *Troodon*	4.18	5.24	1.94	7.1	8.1	Longrich (2008)
TMP1987.77.135	cf. *Troodon*	3.58	3.46	1.69		14.7	Longrich (2008)
Horseshoe Canyon Formation (68-72 Ma)							
TMP1997.44.4	cf. *Troodon*	5.67	7.40	3.31	8.1	10.5	Longrich (2008)
TMP1994.9.4	cf. *Troodon*	5.68	7.36	2.76	5.3	8.6	Longrich (2008)
TMP1987.12.14	cf. *Troodon*	5.25	7.83	2.79	4.7	6.4	Longrich (2008)
TMP1988.96.07	cf. *Troodon*	6.29	8.92	3.12	5.0	6.7	Longrich (2008)
TMP1998.63.43	cf. *Troodon*	6.13	10.68	3.57	8.0	7.0	this study
TMP99.50.115	cf. *Troodon*	5.78	10.68	3.68	5.0	6.5	this study
TMP99.50.114	cf. *Troodon*	5.56	6.81	2.82	7.5	10.0	this study
TMP00.45.90	cf. *Troodon*	3.49	5.23	1.99		12.0	this study
TMP00.45.24	cf. *Troodon*	3.57	4.40	2.24		11.0	this study
TMP00.45.91	cf. *Troodon*	5.43	9.98	3.40	4.5	8.5	this study
TMP01.45.80	cf. *Troodon*	7.00	12.08	4.07	5.5	8.0	this study
TMP01.45.81	cf. *Troodon*	4.81	6.64	2.82	9.0	11.0	this study
TMP02.45.48	cf. *Troodon*	5.56	7.72		7.5	10.0	this study
TMP03.45.58	cf. *Troodon*	4.98	7.06	2.66	8.0	9.5	this study
Lance Formation (65.5-66.5 Ma)							

UCMP187076	*Pectinodon bakkeri*	2.20	3.00	1.00		20.0	Sankey (2008)
UCMP187075	*Pectinodon bakkeri*	2.70	4.50	1.00		18.8	Sankey (2008)
UCMP187073	*Pectinodon bakkeri*	2.90	4.30	1.10		17.5	Sankey (2008)
UCMP187074	*Pectinodon bakkeri*	2.70	4.20	1.10		20.0	Sankey (2008)
UCMP187067	*Pectinodon bakkeri*	2.70	3.80	1.00		17.5	Sankey (2008)
UCMP187068	*Pectinodon bakkeri*	2.60	3.10	1.00		22.5	Sankey (2008)
UCMP187069	*Pectinodon bakkeri*	2.70	4.10	1.00		20.0	Sankey (2008)
UCMP187066	*Pectinodon bakkeri*	3.00	3.50	1.00		15.0	Sankey (2008)
UCMP187063	*Pectinodon bakkeri*	2.40	3.90	0.90		20.0	Sankey (2008)
UCMP187065	*Pectinodon bakkeri*	2.00	4.10	1.00		15.0	Sankey (2008)
UCMP187059	*Pectinodon bakkeri*	2.10	3.20	0.80		25.0	Sankey (2008)
UCMP214059	*Pectinodon bakkeri*	1.90	3.40	1.30		15.0	Sankey (2008)
UCMP186886	*Pectinodon bakkeri*	3.20	4.00	1.00		15.0	Sankey (2008)
IMG 1675	*Pectinodon bakkeri*	2.78	3.83			15.7	Longrich (2008)
AMNH5731 #2	*Pectinodon bakkeri*	2.52	4.43	1.09		9.6	Longrich (2008)
AMNH5731 #1	*Pectinodon bakkeri*	2.44	3.93	0.91		10.1	Longrich (2008)
AMNH5731 #3	*Pectinodon bakkeri*	2.39	4.22	1.00		9.9	Longrich (2008)
AMNH5728.1	*Pectinodon bakkeri*	2.47	4.90	1.12	25.3	14.5	Longrich (2008)
AMNH5728.2	*Pectinodon bakkeri*	2.89	4.99	1.12		16.0	Longrich (2008)
AMNH5728.3	*Pectinodon bakkeri*	2.93	4.85	1.10	32.4	15.9	Longrich (2008)
AMNH5719.1	*Pectinodon bakkeri*	2.74	3.88	0.96		15.3	Longrich (2008)
AMNH5719.2	*Pectinodon bakkeri*	2.53	3.25	0.87		18.7	Longrich (2008)
AMNH5719.3	*Pectinodon bakkeri*	2.64	3.19	0.82		16.4	Longrich (2008)
AMNH5502.1	*Pectinodon bakkeri*	2.74	5.55	1.15		17.0	Longrich (2008)
AMNH5502.2	*Pectinodon bakkeri*	2.63	4.80	1.18	29.7	16.9	Longrich (2008)
AMNH5502.3	*Pectinodon bakkeri*	2.52	4.30	1.22	57.9	19.1	Longrich (2008)
AMNH5733.1	*Pectinodon bakkeri*	2.31	4.26	0.93		10.0	Longrich (2008)
AMNH5706.1	*Pectinodon bakkeri*	2.21	2.62	0.62		19.8	Longrich (2008)
AMNH5706.2	*Pectinodon bakkeri*	2.36	2.73	0.63		20.2	Longrich (2008)
AMNH5706.3	*Pectinodon bakkeri*	2.35	2.60	0.70		19.5	Longrich (2008)

AMNH5489.1	*Pectinodon bakkeri*	3.12	5.63	1.46		7.8	Longrich (2008)
AMNH5489.2	*Pectinodon bakkeri*	2.93	4.35	1.17		10.5	Longrich (2008)
AMNH5489.3	*Pectinodon bakkeri*	2.56	4.50	1.07		8.7	Longrich (2008)
AMNH5725.1	*Pectinodon bakkeri*	2.69	3.72	1.12		14.4	Longrich (2008)
AMNH5725.2	*Pectinodon bakkeri*	2.51	3.10	1.05		18.7	Longrich (2008)
AMNH5725.3	*Pectinodon bakkeri*	2.35	3.16			12.6	Longrich (2008)
AMNH5722.1	*Pectinodon bakkeri*	2.53	3.22			17.6	Longrich (2008)
AMNH5722.2	*Pectinodon bakkeri*	2.40	3.90		46.9	23.3	Longrich (2008)
AMNH5722.3	*Pectinodon bakkeri*	2.33	3.56		39.0	22.1	Longrich (2008)
IMG 1672	*Pectinodon bakkeri*	2.69	3.12			16.1	Longrich (2008)
Upper Hell Creek Formation (65.5-66.75 Ma)							
UCMP186904	cf. *Pectinodon bakkeri*	2.00	3.00	0.70		17.5	Sankey (2008)
UCMP128845	cf. *Pectinodon bakkeri*	3.20	4.60	1.10		20.0	Sankey (2008)
UCMP128787	cf. *Pectinodon bakkeri*	3.60	4.60	1.70		12.5	Sankey (2008)
UCMP186868	cf. *Pectinodon bakkeri*	2.20	2.90	0.90		20.0	Sankey (2008)
UCMP186885	cf. *Pectinodon bakkeri*	2.10	3.00	0.70		22.5	Sankey (2008)