

Albertosaurus bone bed = upper half of the Sulphur Formation

Faunal assemblages from the upper Horseshoe Canyon Formation, an early Maastrichtian cool-climate assemblage from Alberta, with special reference to the *Albertosaurus sarcophagus* bonebed¹

Derek W. Larson, Donald B. Brinkman, and Phil R. Bell

Calyp is ~51°

Upper half

cool, dry
→
warm, wet

Abstract: The faunal assemblage from the early Maastrichtian portion of the Horseshoe Canyon Formation is described on the basis of four new vertebrate microfossil localities and remains from the *Albertosaurus* bonebed. All of the localities sampled were deposited during a cool, dry climate at a palaeolatitude of ~58°N. Thus, these assemblages provide insight into a northern cool-climate assemblage in the early Maastrichtian of western North America. This fauna is characterized by the presence of taxa with more northern affinities, such as *Holosteus A*, champsosaurs, *Troodon*, and toothed birds. Warm-climate taxa, such as crocodylians, large and diverse turtles, and albanerpetontids are notable in their absence. The *Albertosaurus* bonebed locality at the top of unit 4 of the Horseshoe Canyon Formation was deposited during the initial stages of a trend to a warmer and wetter climate that is represented in unit 5. The bonebed shares many taxa with the underlying vertebrate microfossil localities. However, a notable difference is the presence of *Atrociraptor marshalli* from the *Albertosaurus* bonebed but not the other localities in the upper Horseshoe Canyon Formation. The presence of *Atrociraptor* may be attributable to this change in climate rather than local ecological conditions. Also, the assemblages are different in the paucity of fish remains in the bonebed, and the relative rarity of shed hadrosaur teeth. The low abundance of aquatic taxa and rarity of shed teeth of hadrosaurs indicate that the locality is largely autochthonous, with little material being transported into the site.

Résumé : L'assemblage faunique de la portion du Maastrichtien précoce de la Formation de Horseshoe Canyon est décrit à la lumière de quatre nouvelles localités de microfossiles de vertébrés et de restes provenant du gisement d'ossements d'*Albertosaurus*. Toutes les localités échantillonnées témoignent d'un dépôt en climat sec et frais à une paléolatitude d'environ 58°N. Ainsi, ces assemblages offrent une fenêtre sur un assemblage de climat nordique frais du Maastrichtien précoce de l'ouest de l'Amérique du Nord. Cette faune est caractérisée par la présence de taxons présentant des affinités plus nordiques, tels que des holostéens A, des champsosaurs, *Troodon* et des oiseaux à dents. L'absence de taxons de climat chaud, tels que des crocodyliens, diverses tortues dont de grandes espèces et des albanerpetontidés, est notable. Les sédiments de la localité du gisement d'ossements d'*Albertosaurus* au sommet de l'unité 4 de la Formation de Horseshoe Canyon ont été déposés durant les stades initiaux d'une transition vers le climat plus chaud et plus humide représenté dans l'unité 5. Le gisement d'ossements présente bon nombre des mêmes taxons que les localités à microfossiles de vertébrés sous-jacentes. Toutefois, le fait qu'*Atrociraptor marshalli* soit présent dans le gisement d'ossements d'*Albertosaurus*, mais absent des autres localités de la partie supérieure de la Formation de Horseshoe Canyon constitue une différence notable. La présence d'*Atrociraptor* pourrait être attribuable au changement climatique susmentionné plutôt qu'à des conditions écologiques locales. La paucité de restes de poissons dans le gisement d'ossements et la rareté relative des dents d'hadrosaure tombées distinguent également le gisement d'ossements. La faible abondance de taxons aquatiques et la rareté de dents d'hadrosaure tombées indiquent qu'il s'agit d'une localité principalement autochtone caractérisée par une faible proportion de matériel apporté sur les lieux.

[Traduit par la Rédaction]

Received 20 November 2009. Accepted 20 January 2010. Published on the NRC Research Press Web site at cjes.nrc.ca on 2 September 2010.

Paper handled by Associate Editor H.-D. Sues.

D.W. Larson² and **P.R. Bell**. CW405 Biological Sciences Building, University of Alberta, Edmonton, AB T6G 2E9, Canada.

D.B. Brinkman. Royal Tyrrell Museum of Palaeontology, Box 7500, Drumheller, AB T0J 0Y0, Canada.

¹This article is one of a series of papers published in this Special Issue on the theme *Albertosaurus*.

²Corresponding author (e-mail: dlarson@ualberta.ca).

Introduction

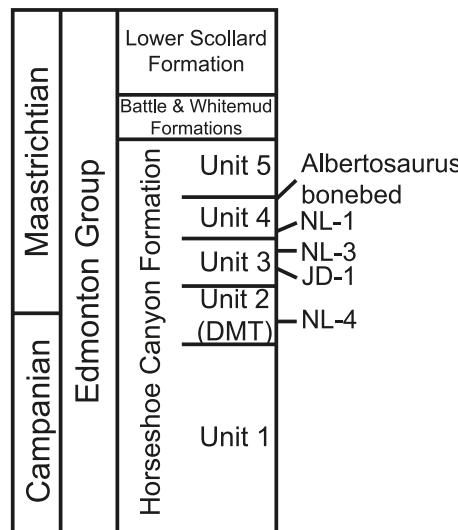
Vertebrate microfossil localities are an important source of palaeoecological data because they provide information about the diversity and relative abundance of many taxa not represented by articulated skeletons. While studies of vertebrate microfossil assemblages have been conducted in many mid Campanian and late Maastrichtian localities in the Western Interior Basin (Estes 1964; Estes and Berberian 1970; Sahni 1972; Baszio 1997; Brinkman 1990; Brinkman et al. 2004), the vertebrate microfossil assemblages of early Maastrichtian age are poorly known. The upper Horseshoe Canyon Formation (units 2–5 of Eberth 2004) is one of the few units that preserve a non-marine record of this age. The Horseshoe Canyon Formation was deposited during late Campanian and early Maastrichtian time, with the boundary between these two stages approximately equivalent to the boundary between a lower coal- and mudstone-dominated succession and an overlying unit generally referred to as the Drumheller Marine Tongue (Lerbekmo and Braman 2002; Eberth and Deino 2005). Previous studies of vertebrate microfossil assemblages have not dealt with the Maastrichtian upper Horseshoe Canyon Formation but have rather reported on material from the Campanian lower Horseshoe Canyon Formation (Ryan et al. 1998) or have combined the assemblages from the Campanian and Maastrichtian portions of the formation (Baszio 1997).

As well as documenting the vertebrate assemblages from a poorly known time interval, the assemblages from the Horseshoe Canyon Formation provide a basis for considering the effect of climate change on vertebrates at a relatively high palaeolatitude (58°N palaeolatitude). The Horseshoe Canyon Formation was deposited under three distinct climatic regimes: warm and wet (unit 1), cool and dry (units 2–4), and warm and wet (unit 5; Eberth 2004; Brinkman and Eberth 2006). Studies of turtles have demonstrated that there is a correlation between the changes in climate and changes in these vertebrates (Brinkman 2003). The vertebrate microfossils from units 2–4, sampled during the course of this study, provide insight into the effect of cool mean annual temperatures on other aspects of the vertebrate assemblages. The *Albertosaurus* bonebed was deposited during the initial phases of the shift between the climatic regimes of units 4 and 5. Thus, the vertebrate microfossils from this locality provide a basis for interpreting the effect of this climatic change on the assemblage. The vertebrate microfossil assemblage of the *Albertosaurus* bonebed is also of interest because the kinds, relative abundances, and modes of preservation provide information that contributes to an understanding of the processes involved in the formation of this locality.

Geologic setting

The Horseshoe Canyon Formation is the lowest of the Edmonton Group, and is overlain successively by the Whitemud, Battle, and Scollard formations (Fig. 1). Five informal subdivisions (units) have been described within the Horseshoe Canyon Formation based on the presence-absence of coal and stratigraphic architecture (Eberth and O'Connell 1995; Eberth 2004). Unit 1 (lower Horseshoe Canyon Formation) comprises more than half the total thickness of the

Fig. 1. Stratigraphic positions of vertebrate microfossil localities and the *Albertosaurus* bonebed within the upper Horseshoe Canyon Formation of Alberta.



Horseshoe Canyon Formation and includes all beds below the Drumheller Marine Tongue. It is a coal- and mudstone-dominated succession deposited during a warm and wet phase in a lower coastal plain setting. $^{40}\text{Ar}/^{39}\text{Ar}$ dates for a bentonite layer that directly overlies coal seam #10 near the base of the overlying Drumheller Marine Tongue (unit 2) were obtained by Eberth and Deino (2005). Their date of 70.44 ± 0.17 Ma is correlated with the Campanian–Maastrichtian boundary (Eberth and Deino 2005). Thus, all but the basal few metres of the Upper Horseshoe Canyon Formation is early Maastrichtian in age. The upper Horseshoe Canyon Formation is subdivided into four units, three of which (units 2–4) are non-coaly intervals deposited during time of cool, dry temperatures. Unit 2 is marked by the presence of a brackish water assemblage of invertebrates; unit 3 is comprised of stacked palaeochannel sandstones; unit 4 is an overbank-mudstone and palaeosol-dominated interval.

Unit 5 is a coaly interval characterized by locally thick palaeochannel sandstones and patchy occurrences of extra-basinal conglomerate clasts. Evidence that this unit was deposited under warm conditions is provided by the presence of *Adocus*, a large turtle that is typically more southern in its distribution (Brinkman and Eberth 2006) and crocodylian remains. The initial phases of the shift in climates from the cool, dry climates typical of units 2–4 to the warmer wet climate typical of unit 5 is documented in the uppermost beds of unit 4. The *Albertosaurus* bonebed was deposited in this transitional zone.

Materials and methods

Data on the vertebrate microfossils from units 2–4 (Fig. 1) of the Horseshoe Canyon Formation were derived from both surface collected specimens recovered during surveys of the formation and samples recovered from screenwashing vertebrate microfossil localities. Four vertebrate microfossil localities were sampled by screenwashing using a #18 screen (holes 1 mm measured diagonally). Counts of

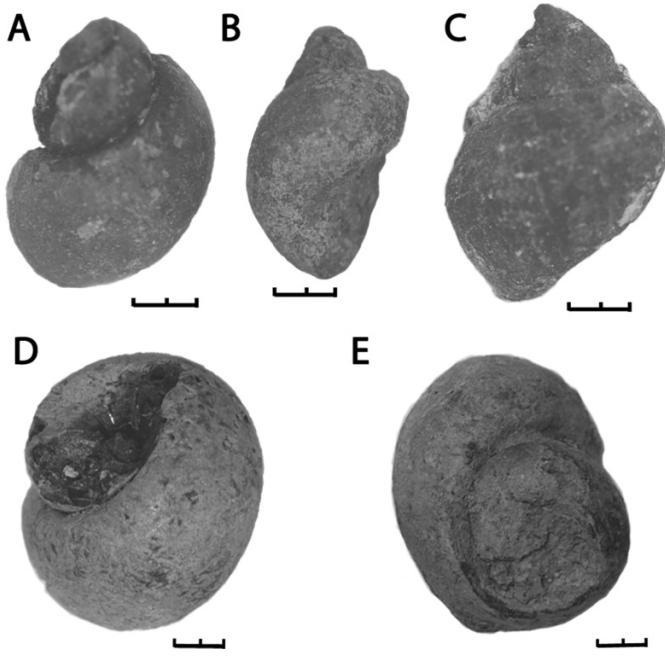
Table 1. Counts of vertebrate microfossil minimum numbers of major elements from localities in units 2–4 of the Horseshoe Canyon Formation that were recovered by underwater screenwashing operations and from the *Albertosaurus* bonebed. Localities are ordered from lowest (NL-4) to highest (*Albertosaurus* bonebed) in section.

Taxon	Element	NL-4 2003	JD-1 2003	NL-3 2004	NL-1 2003	<i>Albertosaurus</i> bonebed
(?) <i>Ischyrrhiza</i>	Tooth			1		
<i>Myledaphus</i>	Teeth		4	2		
	Centra		1	3		
Rhinobatoidei	Tooth (smooth)			1		
Acipenseridae	Fin spine					1
Polyodontidae	Denticles				2	
<i>Belonostomus</i>	Jaw				1	
	Scales				3	
Holostean A	Scales	106	500	44	437	1
<i>Cyclurus</i>	Centra				18	3
	Tooth-bearing elements		2		10	
	Teeth	1	7	1	6	
<i>Coriops</i>	Centrum				1	
	Tooth plates				5	
	Dentaries		1	1		
Elopiformes	Centrum				1	
Ellimmichthyo- formes	All major elements					55
Esocoidea	Dentaries		5		5	
Teleost indet.	Centra type U-5			1	2	
Acanthomorph	Centra		1		56	
	Dentaries				2	
	Fin spines		1	1	12	
	Saber fin spines		28	3	4	
Anura	All elements	8	5	4	76	3
Scapherpetontidae	Vertebra					1
<i>Scapherpeton</i>	Centra	9	10	6	68	
<i>Opisthotriton</i>	Centra	3	29		61	
Chelydridae	Shell fragments	1			9	
Borioteiioidea	Jaws				14	1
<i>Champsosaurus</i>	Teeth			1		3
	Vertebrae					2
<i>Parksosaurus</i>	Tooth				1	
Hadrosauridae	Teeth	59	4	11	58	17
Ceratopsidae	Teeth	17			2	3
Ankylosauridae	Teeth	1				2
Tyrannosauridae	Teeth	1		1	1	232
Ornithomimidae	Phalanges					5
<i>Albertonykus</i>	All elements					11
Dromaeosaurinae	Teeth			1		10
<i>Atrociraptor</i>	Teeth					6
<i>Troodon</i>	Teeth	5				13
<i>Paronychodon</i>	Tooth	1				
<i>Richardoestesia</i>	Teeth				1	5
Avialae indet.	Teeth	1		1	1	2
Archosauria indet.	Teeth		2		11	
Metatheria	Teeth and jaws	1			2	1

identifiable elements from these sites, along with material from the *Albertosaurus* bonebed, are listed in Table 1. Specimens collected from the *Albertosaurus* bonebed and curated by the Royal Tyrell Museum of Palaeontology (TMP) and the University of Alberta Laboratory for Verte-

brate Paleontology (UALVP) were also identified in this study. Specimens previously described are given brief summary descriptions. While representative taxa from all of the vertebrate microfossil localities are mentioned, the taxa present in the *Albertosaurus* bonebed are explicitly refer-

Fig. 2. *Viviparus prudentius* steinkerns from the *Albertosaurus* bonebed. (A–C) TMP 1998.064.0004 (three elements), abapertural views; (D–E) TMP 2004.056.0069 (in part); (D) abapertural view; (E) apertural view. Scale bar equals 2 mm.



enced. Mammals are present in both vertebrate microfossil localities and the *Albertosaurus* bonebed and are included in Table 1. However, this material is currently under study by C. Scott and R.C. Fox and is not described here.

Systematic palaeontology

Phylum Mollusca Linnaeus, 1758
Class Gastropoda Cuvier, 1797
Family Viviparidae Gray, 1847
Genus *Viviparus* de Montfort, 1810

Viviparus prudentius White, 1877

DIAGNOSIS: (modified from Tozer 1956) A medium-sized shell, depressed turbinate shape with the aperture height slightly greater than the altitude of the shell. Body whorl is significantly larger than those of the spire. Whorls are evenly convex with deeply impressed sutures. Aperture is obliquely ovate and lacks a reflected inner lip.

REFERENCE SPECIMENS: TMP 1998.064.0004, steinkerns; TMP 1999.050.0121 (in part), steinkern; TMP 1999.050.0153, steinkern; TMP 1999.050.0165, steinkern; TMP 2004.056.0069, steinkern.

COMMENTS: Several species of freshwater molluscs are present within unit 4 of the Horseshoe Canyon Formation. However, only *Viviparus prudentius* and an unidentified bivalve are known from the *Albertosaurus* bonebed. These steinkerns represent the first documented gastropods from unit 4 (Fig. 2). Although the species is documented in penecontemporaneous beds in the St. Mary River Formation, and from the upper Maastrichtian Laramie Formation of Colorado, and Willow Creek Formation of Alberta, it does not occur in the upper Campanian portion of the Horseshoe Canyon

Formation (Tozer 1956), where the species *V. westoni* and *V. tasgina* occur. The occurrence of *V. prudentius* is probably indicative of a still-to-slow freshwater environment (Tozer 1956).

Phylum Chordata Balfour, 1880

Class Chondrichthyes Huxley, 1880

Superfamily Hybodontoidea Owen, 1846

Family Hybodontidae Owen, 1846

Genus *Hyodus* Agassiz, 1837

Hyodus sp. *This must not be a hybodont*

REFERENCE SPECIMEN: TMP 2003.054.0011, tooth

COMMENTS: *Hyodus* is represented by a single surface-collected specimen that preserves the central cusp and a portion of the base of the crown (Fig. 3A). Because of the incompleteness of this specimen, it cannot be identified to species.

Order Lamniformes Berg, 1958

Family Cretoxyrhinidae Glückman, 1958

Genus *Cretoxyrhina* Glückman, 1958

Cretoxyrhina sp.

REFERENCE SPECIMEN: TMP 2003.038.0001, tooth.

COMMENTS: A single tooth of a lamnid shark collected during surface surveys of unit 2 (Fig. 3B) was referred to *Cretoxyrhina* because it has a smooth crown, lacks lateral cusplets, and lacks a nutrient groove, having instead a small central lingual foramen.

Order Rajiformes Berg, 1940

Family Sclerorhynchidae Capetta, 1974

Genus *Ischyrhiza* Leidy, 1856a

(?)*Ischyrhiza* sp.

REFERENCE SPECIMEN: TMP 2009.138.0001, tooth.

COMMENTS: A single incomplete tooth is tentatively attributed to *Ischyrhiza* (Fig. 3C). This specimen preserved the base of the tooth and a portion of the crown. The crown is expanded and has long medial and distal shoulders lacking cusplets, and the root is strongly bilobate and is subdivided by a deep nutrient groove.

Suborder Rhinobatoidei Fowler, 1941

Genus *Myledaphus* Cope, 1876a

Myledaphus sp.

REFERENCE SPECIMENS: TMP 2003.054.0007, tooth; TMP 2009.136.0001, tooth.

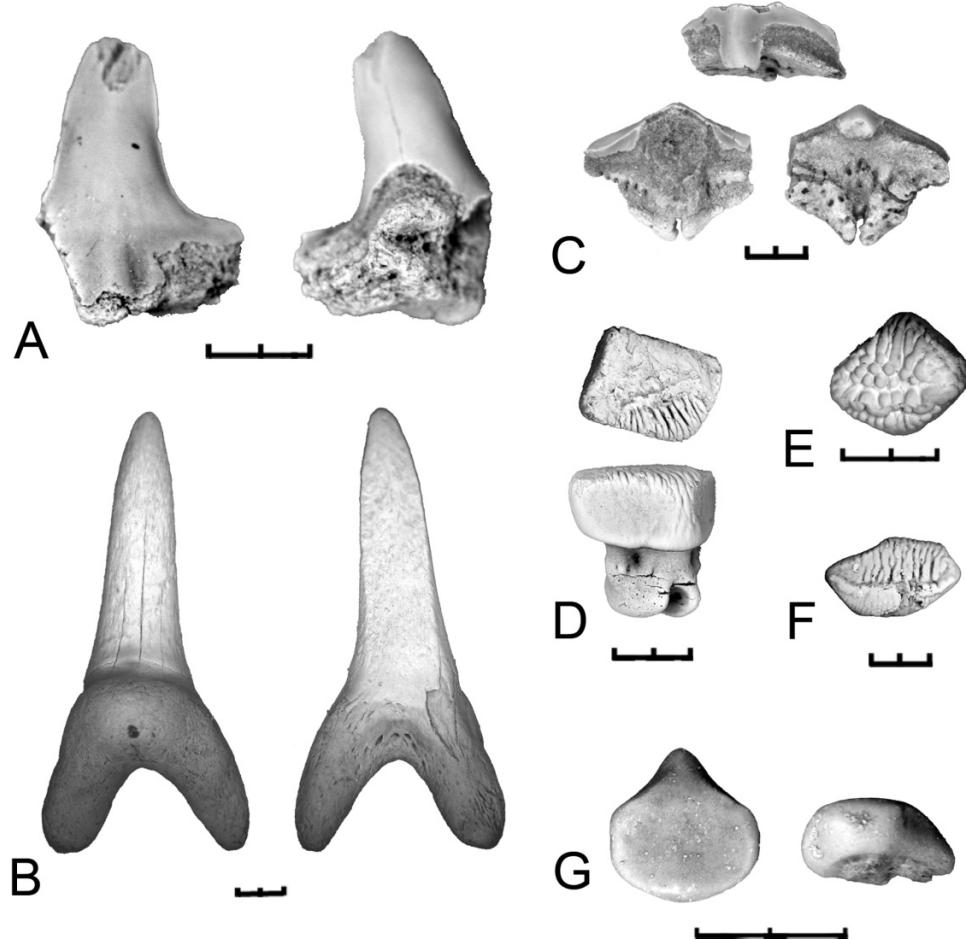
COMMENTS: The most abundant ray is *Myledaphus* (Figs. 3D–3F). Unworn teeth seem to be distinct from those of *Myledaphus bipartitus* in that the ornamentation on the occlusal surface of the tooth is more strongly developed; and therefore, the *Myledaphus* specimens may represent a distinct species.

Gen. et sp. indet.

REFERENCE SPECIMEN: TMP 2009.136.0002, tooth.

COMMENTS: The presence of a second ray is represented by tooth crowns that are small and smooth and sometimes have distinct lingual flanges (Fig. 3G). These teeth are generally similar to *Protoplatyrhina* in these features, although the lingual flange

Fig. 3. Chondrichthyan teeth from units 2–4 of the Horseshoe Canyon Formation. (A) *Hybodus* sp., tooth, TMP 2003.054.0011; (B) *Cretoxyrhina* sp., tooth, TMP 2003.038.0001; (C) (?)*Ischyrhiza* sp., tooth, TMP 2009.138.0001; (D–F) *Myledaphus* sp., teeth; (D) TMP 2003.054.0007 (in part) in lateral and occlusal views; (E) TMP 2009.136.0001 in occlusal view; (F) TMP 2003.054.0007 (in part) in occlusal view; (G) Rhinobatoidei gen. et sp. indet., tooth, TMP 2009.136.0002 in occlusal and lateral views. Scale bar equals 2 mm.



is more strongly developed than is typical in that genus, so this ray is referred to as Rhinobatoidei gen. et sp. indet.

Clade Osteichthyes Huxley, 1880
Subclass Actinopterygii Cope, 1887
Clade Chondrostei Müller, 1846
Order Acipenseriformes Berg, 1940
Family Acipenseridae Bonaparte, 1831

Gen. et sp. indet.

REFERENCE SPECIMENS: TMP 1999.050.0150, fin spine; TMP 2003.034.0002, fin spine.

COMMENTS: The presence of a sturgeon is documented by a spine fragment of moderate size found during surface collections (Fig. 4A) and a fin spine from the *Albertosaurus* bonebed. No sturgeon elements were recovered from screen-washed vertebrate microfossil localities that were sampled.

Family Polyodontidae Bonaparte, 1838

Gen. et sp. indet.

REFERENCE SPECIMENS: TMP 2009.137.0001, denticle; TMP 2009.137.0002, denticle.

COMMENTS: Paddlefish are represented by denticles with char-

acteristic tubercles oriented at right angles to the dorsal plate and by the comb-like development of projections from the posterior edge of the plate (Figs. 4B–4C).

Superorder Halecomorpha Cope, 1872
Order Amiiformes Hay, 1929
Family Amiidae Bonaparte, 1837
Genus *Cyclurus* Agassiz, 1836

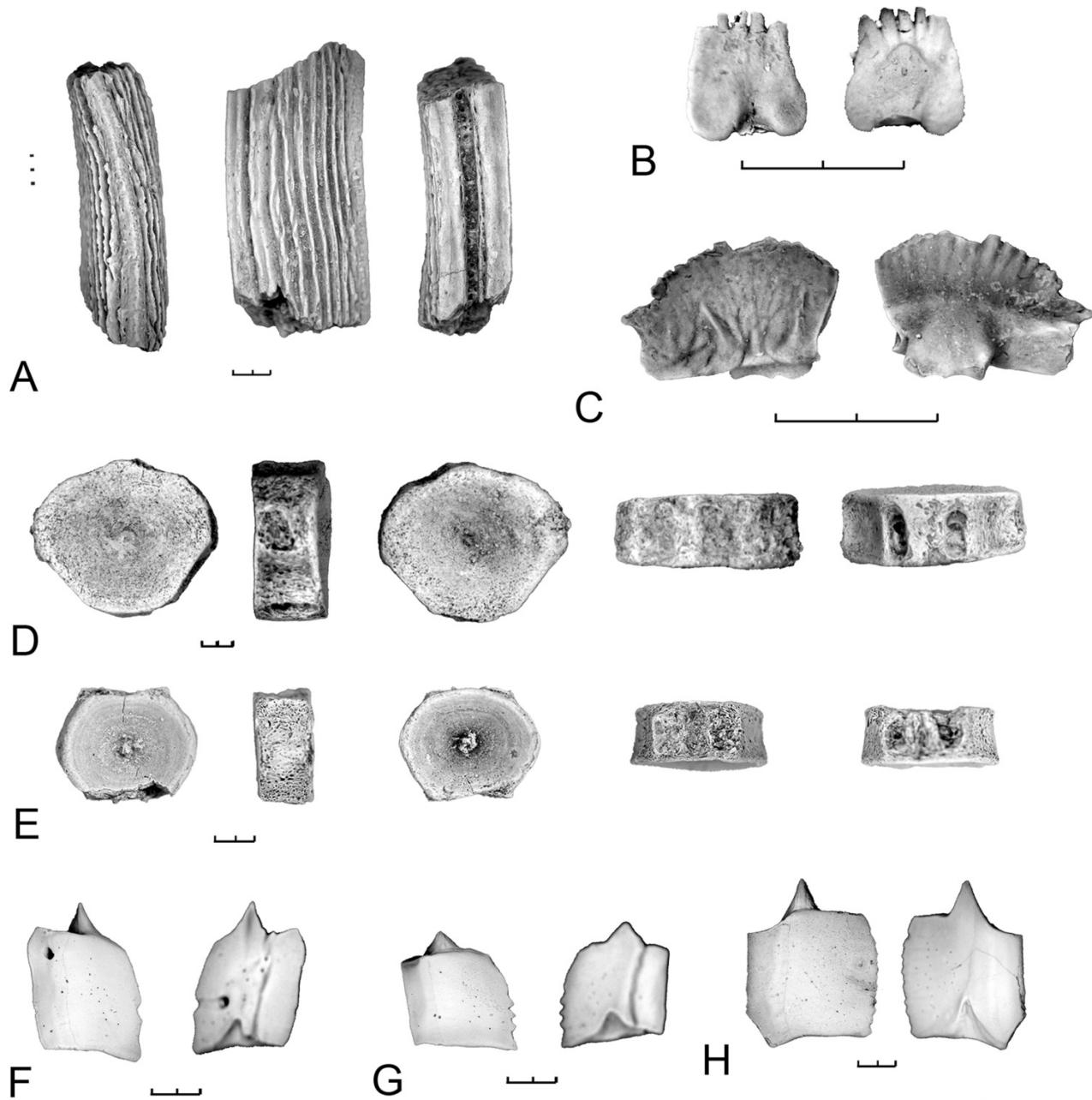
Cyclurus sp.

REFERENCE SPECIMENS: TMP 1999.050.0144, centrum; TMP 1999.050.0146, centrum; TMP 1999.050.0148, centrum; TMP 2003.045.0062, frontal; TMP 2004.079.0001, mid-dorsal centrum; TMP 2003.029.0001, caudal centrum.

COMMENTS: The amiid (Figs. 4D–4E) is represented by centra of size generally comparable to that of *Cyclurus*. Isolated pillar-like teeth typical of *Cyclurus* are also present, demonstrating that the amiid present belongs to that genus. This taxon is the most abundant fish known from the *Albertosaurus* bonebed from disarticulated, identifiable remains (Table 1). In addition to centra, a complete frontal of an amiid was recovered from the *Albertosaurus* bonebed.

Clade Neopterygii Regan, 1923

Fig. 4. Chondrostean- and holostean-grade fish elements from units 2–4 of the Horseshoe Canyon Formation. (A) Acipenseridae, spine, TMP 2003.034.0002 in anterior, lateral, and medial views; (B–C) Polyodontidae, denticles in dorsal and ventral views; (B) TMP 2009.137.0002; (C) TMP 2009.137.0001; (D–E) *Cyclurus*, centra; (D) mid-dorsal centrum, TMP 2004.079.0001 in anterior, lateral, posterior, dorsal, and ventral views; (E) caudal centrum TMP 2003.029.0001 in anterior, lateral, posterior, dorsal, and ventral views; (F–H) scales of Holostean A, TMP 2009.136.0003 (three elements) in lateral and internal views. Scale bars equals 2 mm.



What is a
holostean?

Order Aspidorhynchiformes Bleeker, 1859

Family Aspidorhynchidae Nicholson and Lydekker, 1889
Genus *Belonostomus* Agassiz, 1834

Belonostomus sp.

REFERENCE SPECIMEN: TMP 2009.137.0027, jaw fragment.

COMMENTS: *Belonostomus* is represented by jaw fragments and by characteristic deep flank scales.

Order Semionotiformes Arambourg and Bertini, 1958
Family incertae sedis

Gen. et sp. indet. (Holostean A)

REFERENCE SPECIMENS: TMP 2005.050.0064, scale; TMP 2009.136.0003, scales.

COMMENTS: The most abundant taxon in vertebrate microfossil assemblages from the units 2–4 of the Horseshoe Canyon Formation is the probable semionotiform referred to by Brinkman (1990) as Holostean A. The scales are all of small size (Figs. 4F–4H). Variation is present in the shape of the scales, which is assumed to represent variation along the body. The scales of this fish dominate all of the vertebrate

microfossil localities that were observed. However, it is one of the least abundant elements of the four fish taxa known from the *Albertosaurus* bonebed (Table 1).

Clae Teleostei Müller, 1846

COMMENTS: As is generally the case in Late Cretaceous vertebrate microfossil assemblages, teleosts are one of the most taxonomically challenging groups present. Following the approaches of Brinkman and Neuman (2002) and Neuman and Brinkman (2005), isolated centra, jaws, and spines were examined in an attempt to estimate the diversity and relationships of teleosts present and to document patterns of distribution.

Superorder Osteoglossomorpha Greenwood, Rosen, Weitzman, and Myers, 1966

Order incertae sedis

Genus *Coriops* Estes, 1969

Coriops sp.

REFERENCE SPECIMENS: TMP 2003.055.0007, centra; TMP 2009.137.0007, dentaries.

COMMENTS: Osteoglossomorphs are represented by a single centrum comparable to centra that Neuman and Brinkman (2005) referred to *Coriops* because of the shape of the neural arch articular pits (Fig. 5A).

Osteoglossomorph dentaries similar to those from the Dinosaur Park Formation that Neuman and Brinkman (2005) referred to *Coriops* are well represented (Fig. 6A). As in the Dinosaur Park specimens, these are short and deep and have multiple rows of teeth, with the largest teeth on the labial side of the dentary. No teeth are preserved in place, but isolated conical, recurved teeth similar to those on the lateral surface of *Coriops* are present.

Order Elopiformes Sauvage, 1875

Family incertae sedis

Gen. et sp. indet.

REFERENCE SPECIMEN: TMP 2009.137.0025, centrum.

COMMENTS: One vertebra was identified as an elopiform of relatively small size, although this identification is tentative because the centrum is incomplete.

Order Ellimmichthyiformes Grande, 1982

Family Sorbinichthyidae Bannikov and Bacchia, 2000

Gen. et sp. nov.

REFERENCE SPECIMENS: TMP 2009.137.0003, centrum; TMP 2009.137.0008, dentary.

COMMENTS: In the *Albertosaurus* bonebed, teleost fish are represented by indeterminate skull bones and a new species of articulated ellimmichthyiform described by Newbrey et al. (2010). This ellimmichthyiform is represented in one surface-collected locality by an isolated anterior precaudal centrum (Fig. 5B). As well, a dentary tentatively attributed to this taxon has a single row of widely spaced teeth on its dorsal edge, with the anterior-most tooth in this series being the largest (Fig. 6B).

Order Salmoniformes Bleeker, 1859

Suborder Esocoidea Bleeker, 1859

Family Esocidae Cuvier, 1817

Genus *Oldmanesox* Wilson, Brinkman, and Neuman, 1992

Oldmanesox sp.

REFERENCE SPECIMENS: TMP 2009.136.0004, dentary; TMP 2009.136.0006, vomer.

COMMENTS: Dentaries that are elongated and have single rows of relatively large teeth, with gaps between groups of one to two teeth on the posterior half of each dentary, are referred to *Oldmanesox* sp. (Fig. 6C). As well as conforming to the type specimen in the size of teeth and presence of replacement teeth, this specimen shows the feature of lateral trigeminal foramen located mid-way on the side of the dentary and facing posteriorly. It differs from *O. canadensis* in having a single row of teeth anteriorly and a reduced symphysis. The single esocoid vomer that was recovered has two rows of relatively large teeth (Fig. 6G). In the relatively low number of rows and large size of teeth on this element, this esocoid vomer differs from those most frequently encountered in Campanian vertebrate microfossil localities which have four to five rows of relatively small teeth. Thus, it is likely that this vomer is from *Oldmanesox* sp.

Genus *Estesesox* Wilson, Brinkman, and Neuman, 1992

Estesesox sp.

REFERENCE SPECIMEN: TMP 2009.137.0009, dentary.

COMMENTS: The presence of a species of *Esetesesox* is documented by a dentary that has multiple rows of teeth near the symphysis, a well developed ventral flange at the anterior end of the dentary, no obvious gaps for replacement teeth, and the lateral trigeminal foramen located just below the tooth row (Fig. 6D). It differs from *Estesesox foxi*, the only described species in the genus, in that the teeth are larger.

Family indet.

Gen. et sp. indet. #1

REFERENCE SPECIMEN: TMP 2009.136.0005, dentary.

COMMENTS: Esocoid indet. #1 is relatively large and has multiple rows of teeth on a broad, flat anterior end (Fig. 6E).

Gen. et sp. indet. #2

REFERENCE SPECIMEN: TMP 2003.054.0009, dentary.

COMMENTS: Esocoid indet. #2 is relatively short, deeper posteriorly, and has multiple rows of teeth (Fig. 6F).

Gen. et sp. indet.

REFERENCE SPECIMEN: TMP 2009.139.0001, precaudal centrum.

A salmoniform centrum from the Horseshoe Canyon Formation (Fig. 5C) matches those illustrated by Neuman and Brinkman (2005, fig. 9.8B). These are simple spools with unfused parapophyses and neural spines, close neural arch and parapophyseal pits being close together, and centra that are about as long as they are wide. The relatively large size of the centrum suggests that it is from either Esocoid indet #1 or *Oldmanesox canadensis*, but there is no basis for associating it with one or the other of these taxa.

Order indet.

Gen. et sp. indet. (teleost centrum type U-5)

REFERENCE SPECIMEN: TMP 2009.138.0002, centra.

COMMENTS: An indeterminate non-acanthopterygian teleost is documented by a distinctive centrum, designated U-5, that cannot be referred to any extant group. In teleost centrum

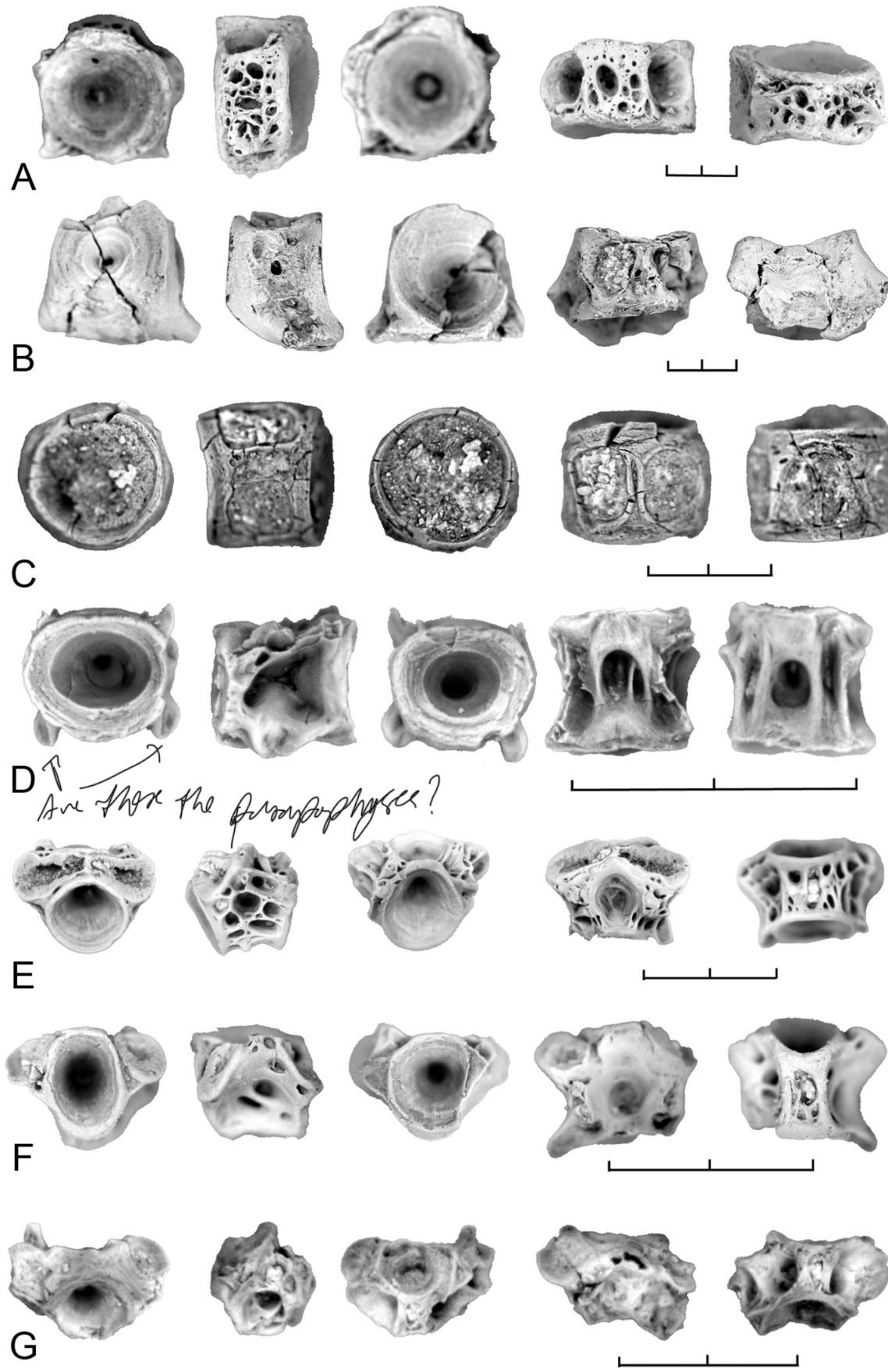
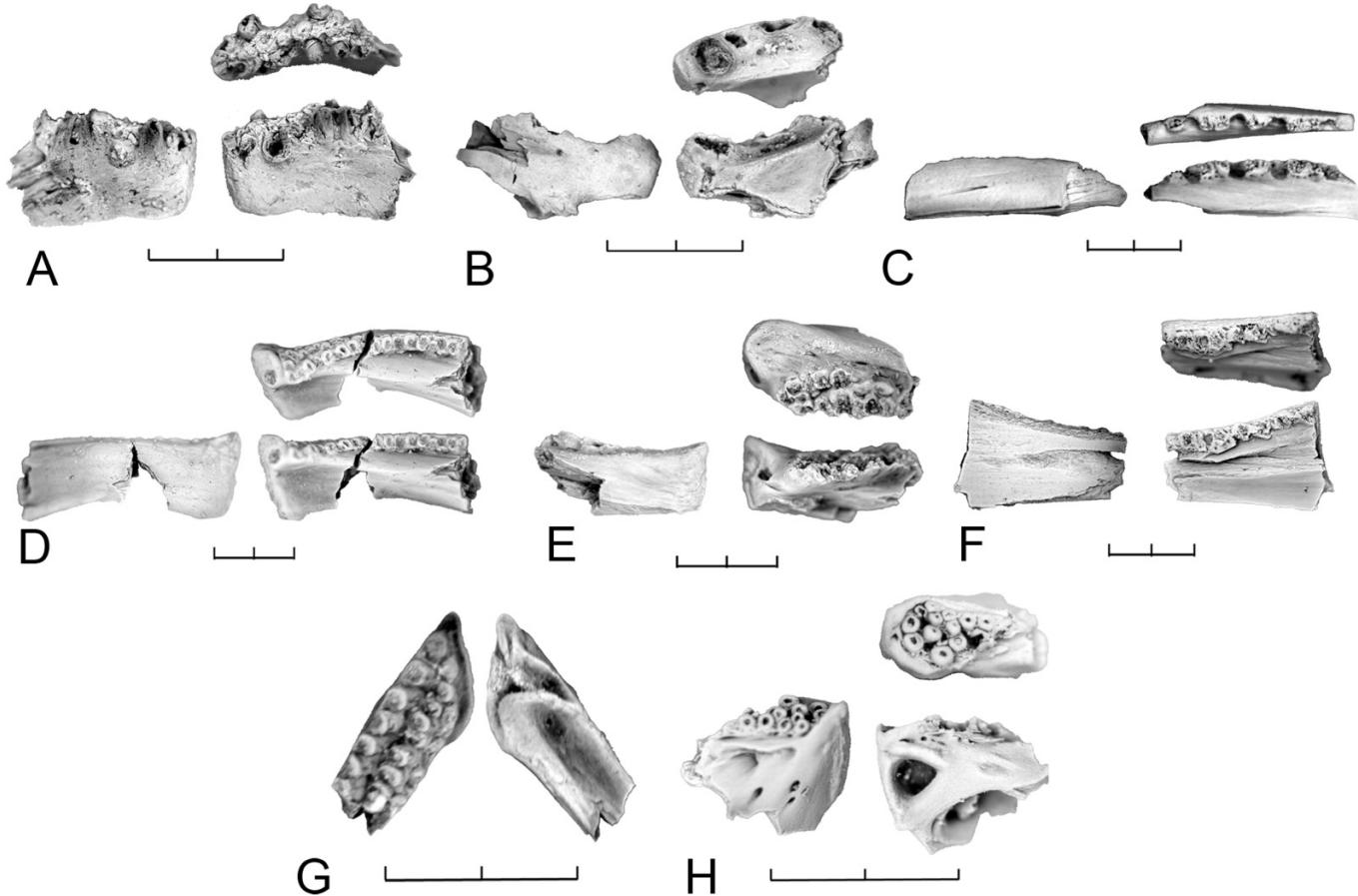


Fig. 5. Teleost precaudal centra from units 2–4 of the Horseshoe Canyon Formation in anterior, lateral, posterior, dorsal, and ventral views. (A) *Coriops*, anterior precaudal, centrum TMP 2003.055.0007; (B) Ellimmichthyiformes, anterior precaudal centrum, TMP 2009.137.0003; (C) Esocoidea, precaudal centrum, TMP 2009.139.0001; (D) centrum morphotype U-5, TMP 2009.138.0002; (E) Acanthomorph #1 atlas, TMP 2009.137.0004; (F) Acanthomorph #2 atlas, TMP 2009.137.0005; (G) Acanthomorph #3 atlas, TMP 2009.137.0006. Scale bar equals 2 mm.

Fig. 6. Teleost tooth-bearing elements from units 2–4 of the Horseshoe Canyon Formation. (A) *Coriops*, dentary, TMP 2009.137.0007. (B) Ellimmichthyiformes, dentary, TMP 2009.137.0008; (C) *Oldmanesox canadensis*, dentary, TMP 2009.136.0004; (D) *Esetesox* sp., dentary, TMP 2009.137.0009; (E) Esocoidea gen. et sp. indet. #1, dentary, TMP 2009.136.0005; (F) Esocoidea gen. et sp. indet. #2, dentary, TMP 2003.054.0009; (G) Esocoidea, vomer, TMP 2009.136.0006; (H) Acanthomorpha, dentary, TMP 2009.137.0013. Scale bar equals 2 mm.



type U-5 (Fig. 5D), the neural arch and parapophyses are fused to the centrum, but in contrast with centrum morphotypes with this feature that were described previously (Brinkman and Neuman 2002; Neuman and Brinkman 2005), the parapophyses are short and face ventrally, and mid-dorsal and mid-ventral pits are present. Because this is a morphologically distinct centrum with a distinct stratigraphic distribution pattern, it is concluded that this is from a distinct kind of teleost.

Clade Acanthomorpha Rosen, 1973

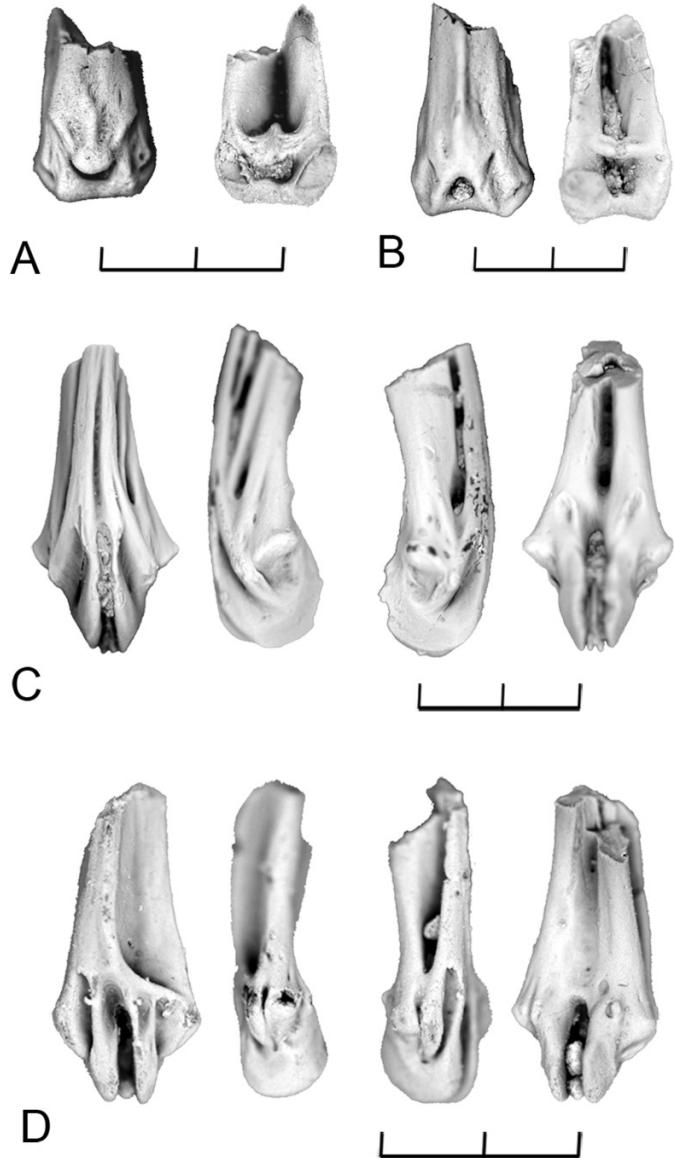
Order indet.

REFERENCE SPECIMENS: TMP 2009.137.0004, atlas; TMP 2009.137.0005, atlas; TMP 2009.137.0006, atlas; TMP 2009.137.0013, dentary; TMP 2009.137.0011, fin spine; TMP 2009.137.0012, fin spine; TMP 2009.137.0010, fin spine; TMP 2009.136.0009, fin spine.

COMMENTS: Three distinct kinds of acanthomorphs are documented by variation in atlas centra. These are designated Acanthomorpha #1, Acanthomorpha #2, and Acanthomorpha #3 (Figs. 5E–5G). Acanthomorpha #1 is represented by centra that are generally wedge-shaped in lateral view, are covered laterally by a network of bone, and have exoccipital articular surfaces that meet above the anterior articular surface (Fig. 5E). Centra of Acanthomorpha #2 are relatively more elongate, have smoother lateral surfaces, and exoccipital articular surfaces that are widely separated by the anterior articular surfaces (Fig. 5F). Acanthomorpha #3 centra are low and wide, have exoccipital articular surfaces that are widely separated by the anterior articular surfaces, and have dorsal processes, apparently representing the base of incomplete neural arches (Fig. 5G). There are no mid-dorsal and mid-ventral pits.

Acanthomorph dentaries from the Horseshoe Canyon For-

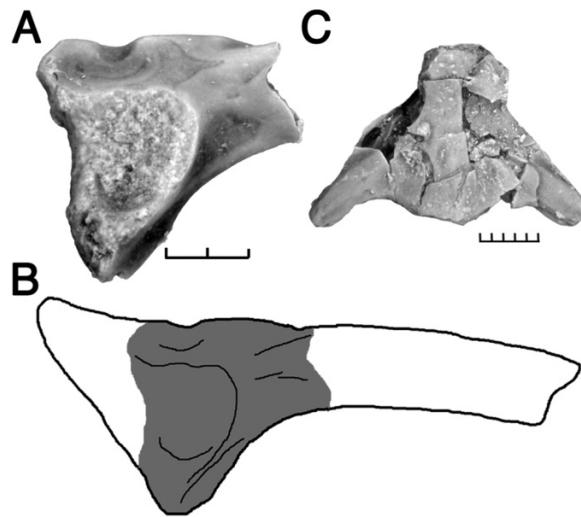
Fig. 7. Acanthomorph fin spines from units 2–4 of the Horseshoe Canyon Formation. (A–B) type one where base of fin spine with solid basal bar of bone ventrally joining the paired articular limbs; (A) TMP 2009.137.0011; (B) TMP 2009.137.0012; (C–D) type two in which the bases of the spine are paired flanges; (C) symmetrical fin spine, TMP 2009.136.0009; (D) asymmetrical fin spine, TMP 2009.137.0010.



mation (Fig. 6H) are generally similar to the type that Newman and Brinkman (2005) referred to as Acanthomorph dentary #4. A pad of small teeth is present dorsally, and the lateral line canal is widely open laterally. A bar of bone extends across this canal from the anteroventral edge of the dentary to the base of the tooth row. Among the extant acanthopterygians that were examined, this morphology is most closely approached in perciforms, suggesting that they were the dominant group present. However, it is uncertain which of the atlas centra are associated with these dentaries.

Additional data on the acanthomorph teleosts present are provided by fin spines. Two kinds of fin spines are present.

Fig. 8. Amphibians from the *Albertosaurus* bonebed. (A–B) (?)*Palaeobatrachus occidentalis*, ilium in lateral view; (A) specimen, TMP 2000.045.0038; (B) line drawing; (C) Scapherpetontidae, vertebra in dorsal view, TMP 1999.050.0131. Scale bar equals 2 mm in A and 5 mm in C.



Type one is typical of those of many derived acanthomorphs, including perciforms, in being smooth and having a solid basal bar of bone that extends between the paired articular limbs (Figs. 7A–7B). The second type of fin spine is distinctive in being striated and in having a distinctive basal articular surface in which the base of the spine is a pair of flanges that are not joined by a basal bar of bone (Figs. 7C–7D). Two general morphologies are present in the second type of fish spine, one that is generally symmetrical (Fig. 7C) and a second that is strongly assymetrical (Fig. 7D). The symmetrical fin spines are like spines described by Becker et al. (2009) from the Hornerstown and New Egypt formations and referred to as saber fin spines. Becker et al. (2009) concluded that these spines were from a basal or stem group acanthopterygian. They noted that some of the fin spines were assymetrical, although these were not illustrated, so it is uncertain whether the assymetrical spines present in the Horseshoe Canyon Formation are also present in the material from the Hornerstown and New Egypt formations. The degree of assymmetry in the saber fin spines from the Horseshoe Canyon Formation suggests that they were associated with paired fins, rather than median fins.

Class Amphibia Linnaeus, 1758

Order Salientia Laurenti, 1768

Family Palaeobatrachidae Cope, 1865

Genus *Palaeobatrachus* Tschudi, 1839

(?)*Palaeobatrachus occidentalis* Estes and Sanchíz, 1982

DIAGNOSIS: (modified from Gardner 2008) Bell-shaped acetabulum, straight dorsal border of shaft approaching dorsal acetabular expansion in lateral view, and a sulcus wrapping around anterior margin of dorsal tubercle to separate it from the iliac shaft.

REFERENCE SPECIMENS: TMP 2000.045.0038, partial right ilium; TMP 2000.045.0101, urostyle.

COMMENTS: A specimen of a partial ilium (TMP 2000.045.0038; Figs. 8A–8B) compares well with the type

and referred material of (?)*P. occidentalis*. However, this species has previously only been reported from the late Maastrichtian of North America, and all other putative members of this genus are from the Palaeogene of Europe. This extends the range of the species back to the early Maastrichtian. A urostyle from the *Albertosaurus* bonebed has not been sufficiently prepared or examined to permit accurate identification but may well be referable to (?)*P. occidentalis*.

Fused vertebrae

Family indet.

Gen. et sp. indet.

REFERENCE SPECIMENS: TMP 2009.137.0023, jaw elements; TMP 2009.137.0024, skull elements; TMP 2009.139.0006, humeri.

COMMENTS: In vertebrate microfossil localities that were screenwashed, frogs are surprisingly abundant (Table 1). They are represented by skull elements and the distal ends of humeri. The skull elements are ornamented by a fine network of ridges with tuberculate prominences on the ridges. No more than one species of frog is indicated from the known material. No ilia or urostyles were recovered, so it is not possible to determine if this material is also from (?)*P. occidentalis*.

What is this?

Order Caudata Scopoli, 1777

Family Scapherpetontidae Auffenberg and Goin, 1959

Gen. et sp. indet.

REFERENCE SPECIMENS: TMP 1999.050.0131, dorsal vertebra.

COMMENTS: A dorsal vertebra (TMP 1999.050.0131; Fig. 8C) from the *Albertosaurus* bonebed is referable to the Scapherpetontidae based on the following characteristics: bicipital transverse processes, lack of basapophyses, and amphicoely. It differs from *Scapherpeton tectum* because of its highly excavated and sub-rounded centrum and highly divergent transverse processes, from *Lisserpeton bairdi* in lacking ventral fossae on either side of the subcentral keel and having lower transverse processes, and from *Piceoerpeton willwoodense* in having a narrow subcentral keel that extends below the cotyles. Also of note is its large size, which at 14 mm in centrum length is over twice the size of the largest known *S. tectum* specimens and 1.5 times the size of the largest known *L. bairdi* specimen (Gardner 2000). Such a large size is more comparable to *P. willwoodense*, but that species is known from the Paleocene to Eocene, and a species of that genus known from the Maastrichtian is much smaller (Gardner 2000).

Genus *Scapherpeton* Cope, 1876b

Scapherpeton sp.

REFERENCE SPECIMENS: TMP 2009.137.0021, dorsal vertebrae.

COMMENTS: Scapherpetontids of small size referred to the genus *Scapherpeton* are known from abundant centra from vertebrate microfossil localities in units 2–4 of the Horseshoe Canyon Formation (Table 1).

Family Batrachosauroididae Auffenberg, 1958

Genus *Opisthotriton* Auffenberg, 1961

Opisthotriton sp.

REFERENCE SPECIMEN: TMP 2009.137.0022, dorsal vertebra.

COMMENTS: *Opisthotriton* sp. is known from abundant centra from vertebrate microfossil localities only.

Class Reptilia Laurenti, 1768

Subclass Anapsida Osborn, 1903

Order Testudinata Oppel, 1811

Family Chelydridae Swainson, 1839

Gen. et sp. indet.

REFERENCE SPECIMEN: TMP 2009.137.0020, shell fragments.

COMMENTS: Turtles of the Horseshoe Canyon Formation were reviewed by Brinkman (2003). Only one kind of turtle is present in units 2–4. This is a small *eucryptodire* tentatively identified as a chelydrid by Brinkman (2003). Material recovered from the screenwashed samples is consistent with this identification.

Subclass Diapsida Osborn, 1903

Order Squamata Oppel, 1811

Infraorder Scincomorpha, Camp, 1923

Clade Borioteioidae Nydam, Eaton, and Sankey, 2007

Family incertae sedis

Genus *Leptochamops* Estes, 1964

Leptochamops sp.

What does this species mean?

REFERENCE SPECIMEN: TMP 2009.137.0016, partial dentary.

COMMENTS: Lizards from vertebrate microfossil localities are represented by dentaries, which, although fragmentary, indicate the presence of at least two distinct kinds (Fig. 9). Partial dentaries (Figs. 9A–9B) referable to *Leptochamops* have only been recovered from vertebrate microfossil localities. Anteriorly, specimens possess slender, non-striated, unicuspid teeth and weak ventral buttresses below the symphyses. There are incipient tricuspid teeth posteriorly. The parapets are one-third to one-half the height of the crowns. The three most anterior teeth are oblique in their orientations to the long axes of the jaws. In dental morphology, specimens resemble *L. denticulatus* more closely than *L. thrinax*.

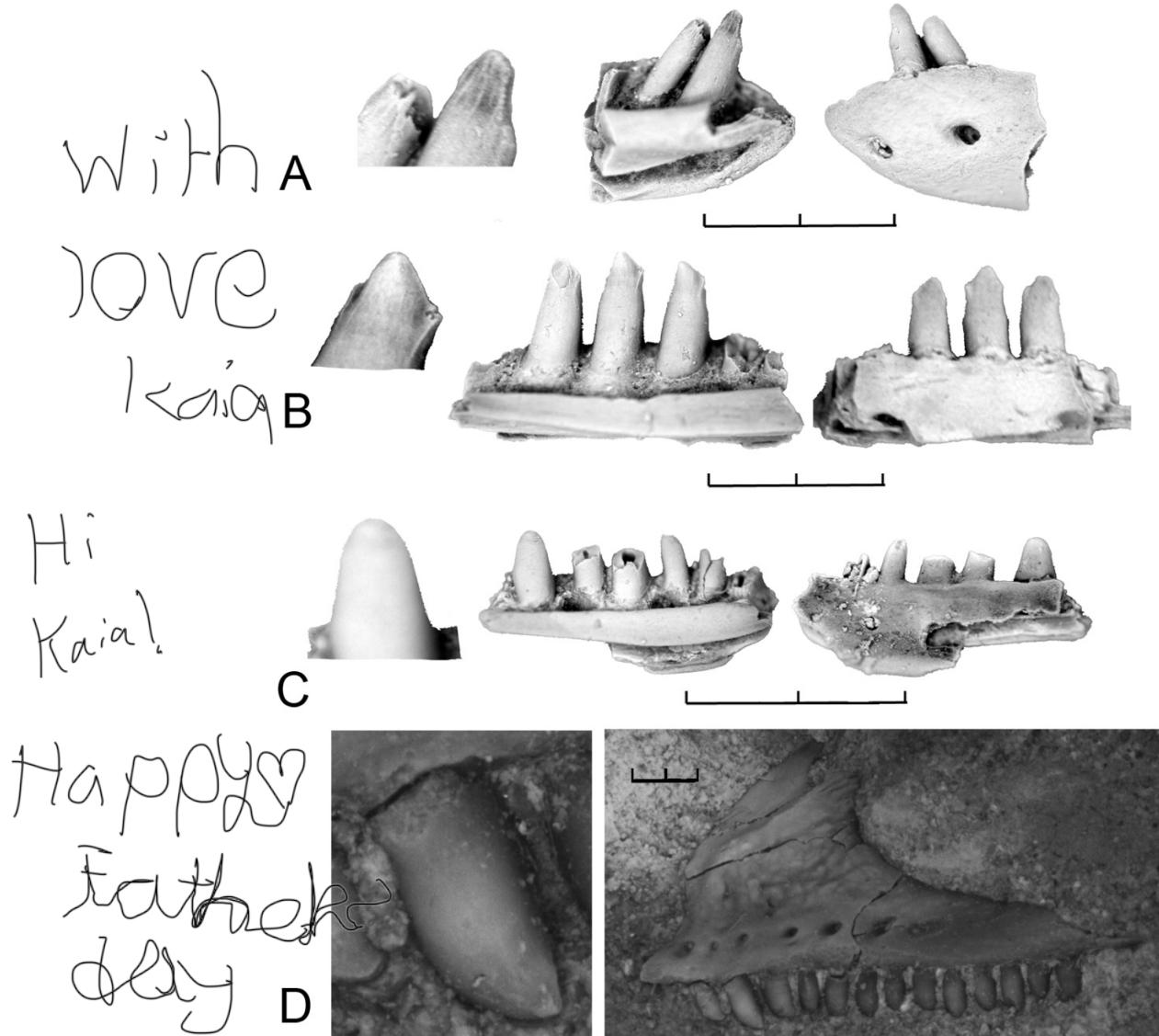
Gen. et sp. indet.

REFERENCE SPECIMENS: TMP 2009.137.0014, partial dentary; TMP 2003.045.0072, left maxilla.

COMMENTS: Dentaries from the vertebrate microfossil assemblage with robust, blunt teeth without surface features on the crowns (Fig. 9C) indicate the presence of a second lizard in the assemblage. It is unclear whether or not the lack of surface features is preservational, but the proportions of the teeth indicate that it is distinct from *Leptochamops*. The dentaries resemble *Gerontoceps irvinensis* of the Campanian Dinosaur Park Formation in exhibiting relatively widely spaced teeth and posterior teeth having swollen bases, so if the tooth crowns are smooth because of erosion of surface features, the dentaries may be those of *Gerontoceps*.

A left maxilla (TMP 2003.045.0072; Fig. 9D) recovered from the *Albertosaurus* bonebed is quite complete but remains imbedded in matrix with its medial side completely obscured. It has at least 15 maxillary tooth positions, with much of the crown exposed below the parapet. The anterior three crowns are more posteriorly inclined than the remainder of the teeth. The lateral premaxillary process of the maxilla is blunt rather than pointed. The contact between the maxilla and the nasal extends farther anteriorly than

Fig. 9. Lizard jaws from units 2–4 of the Horseshoe Canyon Formation. (A–B) Borioteioid *Leptochamops* sp., dentaries in lateral and medial view, with enlarged image of tooth, TMP 2009.137.0016: (A) specimen showing symphyseal region; (B) specimen showing mid-dentary tooth row. (C) Borioteiioidea, dentary with smooth tooth crown, TMP 2009.137.0014. (D) Borioteiioidea, maxilla in external view, TMP 2003.045.0072. Scale bar equals 2 mm.



even in *Chamops segnis*. The posterior narial margin descends steeply, the prefrontal process is prominent and robust, and the jugal process is elongate (probably at least the length of two tooth positions). It is similar to the indeterminate dentaries of the vertebrate microfossil localities in having unicuspids teeth. However, the dentaries exhibit greater heterodonty with posterior teeth having more swollen bases than the straight-sided teeth of the maxillary teeth. Therefore, it is likely that these are from two separate taxa. In most respects, the maxilla resembles the larger of the referred maxillary specimens of *Socognathus unicuspis* from the Dinosaur Park Formation (Gao and Fox 1996). Both maxillae have unicuspids teeth with pronounced anterior carinae and reduced posterior carinae, and the teeth lack the longitudinal ridges that characterize some other genera. Also, in both specimens, the crowns have various angles and spacing between the teeth, and heterodonty is poorly de-

fined, with only one minor “step” present on maxillary crowns 6–9. However, TMP 2003.045.0072 differs from the Dinosaur Park Formation specimens referred to *S. unicuspis* in having a relatively straight ventral margin rather than one that is dorsally flexed. While most features between the maxillary specimen and *Socognathus* suggest that it belongs to that genus, no maxillae are known for *G. irvinensis*, so the possibility that it is from this or some other borioteioid for which maxillae are not known cannot be excluded.

Order Choristodera Cope, 1876b

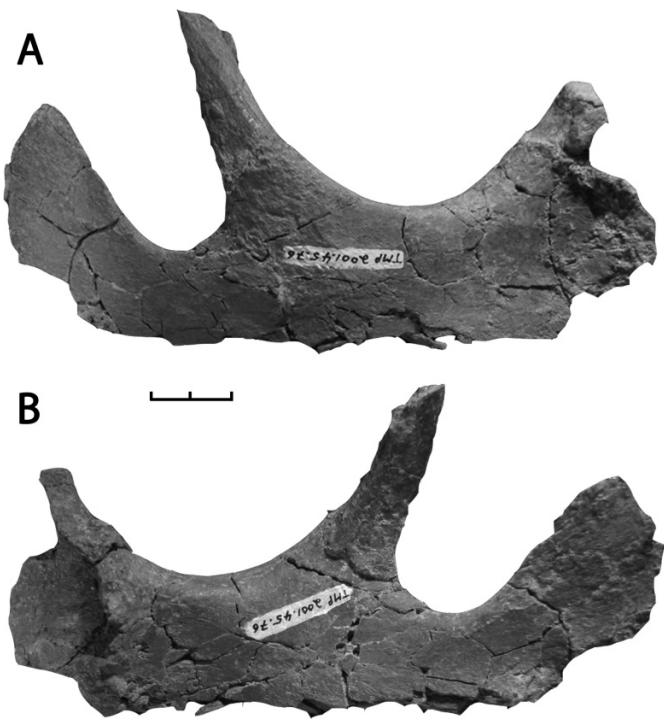
Family Champsosauridae Cope, 1876b

Genus *Champsosaurus* Cope, 1876b *what are*

Champsosaurus sp. *the origins?*

REFERENCE SPECIMENS: TMP 2001.045.0079, tooth; TMP 2003.045.0061, tooth; TMP 2003.045.0067, tooth; TMP 1999.050.0139, vertebra; TMP 1999.076.0001, vertebra;

Fig. 10. Juvenile *Hypacrosaurus altispinus* jugal (TMP 2001.045.0076) from the *Albertosaurus* bonebed in (A) lateral and (B) medial views. Scale bar equals 2 cm.



TMP 1999.050.0138, coracoid; TMP 2004.056.0065, scapula.

COMMENTS: The presence of champsosaurs is documented by teeth that are tall, straight, round in cross section, striated at the base, and have apical carinae on either side of the crown. Postcranial elements, particularly centra and girdle elements, were recovered during surface prospecting surveys and from the *Albertosaurus* bonebed but were not present in the screenwashed samples. *C. albertensis* is the only named species of *Champsosaurus* from the Horseshoe Canyon Formation (Gao and Fox 1998), but none of the material collected for this study is diagnostic to species.

Superorder Archosauria Cope, 1870

Clade Dinosauria Owen, 1842

Order Ornithischia Seeley, 1888

Suborder Ankylosauria Osborn, 1923

Family Ankylosauridae Brown, 1908

Gen. et sp. indet.

REFERENCE SPECIMENS: TMP 2000.045.0037, tooth; TMP 2003.045.0055, tooth; TMP 2009.139.0003, tooth; TMP 2009.139.0004, tooth.

COMMENTS: Ankylosaurid teeth have phylliform crowns with a simple, peg-like root, low cingula on only one side, and surface ornamentation that is longitudinally ridged on one side and smooth on the other (Coombs 1990). TMP 2000.045.0037 does not match the teeth of *Ankylosaurus magniventris* (Coombs 1990) in that it is smaller and crown height is roughly equal to mesiodistal length. It is more comparable in these features to teeth of *Euoplocephalus tutus*. As in specimens from the Dinosaur Park Formation, two

distinct wear patterns are present, one with a vertical wear surface that extends the height of the crown (Fig. 11B) and one in which an oblique surface extends across the crown (Fig. 11C).

Clade Neornithischia Cooper, 1985

Suborder Ornithopoda Marsh, 1881a

Family indet.

Genus *Parksosaurus* Sternberg, 1937

Parksosaurus warreni (Parks, 1926)

REFERENCE SPECIMEN: TMP 2009.137.0017, tooth.

COMMENTS: Basal ornithopods are represented by a single tooth from a vertebrate microfossil locality in unit 4. The tooth matches those of *Parksosaurus* in having well-developed vertical ridges that extend from the base of the crown and in that the largest ridge is positioned towards the lateral edge of the tooth (Fig. 11D). The type and only other known specimen of *Parksosaurus* was also recovered from unit 4 in the upper Horseshoe Canyon Formation.

Family Hadrosauridae Cope, 1870

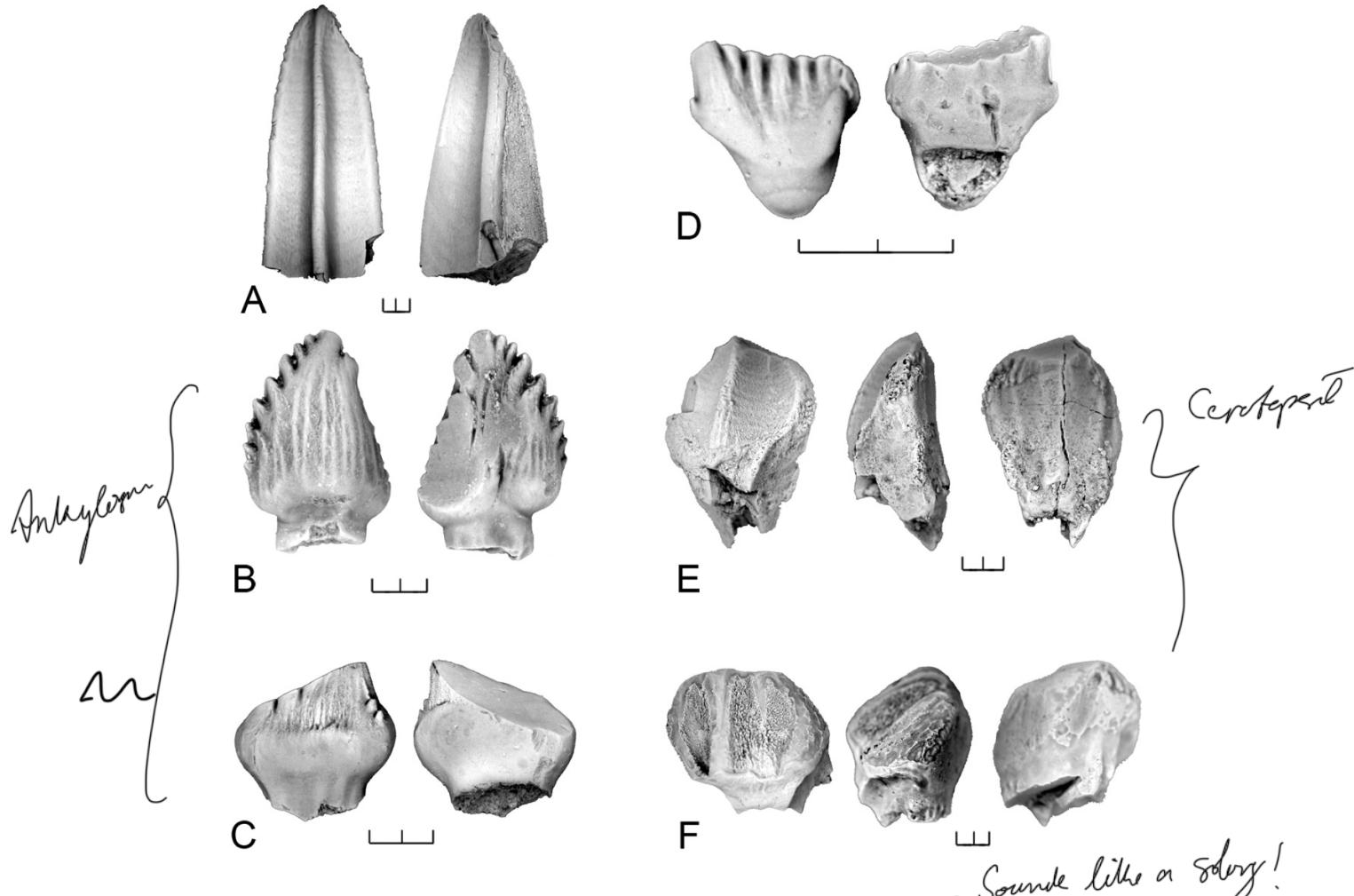
Subfamily Lambeosaurinae Parks, 1923

Genus *Hypacrosaurus* Brown, 1913

Hypacrosaurus altispinus Brown, 1913

REFERENCE SPECIMENS: TMP 1998.063.0008, tooth; TMP 1998.063.0017, metatarsal; TMP 1998.063.0018, caudal vertebra; TMP 1998.063.0033, caudal vertebra; TMP 1998.063.0072, caudal vertebrae; TMP 1998.063.0080, tooth; TMP 1998.063.0086, vertebra, TMP 1999.050.0011, vertebra; TMP 1999.050.0119, tooth; TMP 1999.050.0120, tooth; TMP 1999.050.0122, tooth; TMP 1999.050.0123, tooth; TMP 1999.050.0124, tooth; TMP 1999.050.0125, metacarpal; TMP 1999.050.0126, vertebra; TMP 1999.050.0137, vertebra; TMP 1999.050.0154, vertebra; TMP 1999.050.0170, pubis; TMP 2000.045.0013, phalanx; TMP 2000.045.0029, phalanx; TMP 2000.045.0042, tooth; TMP 2000.045.0051, phalanx; TMP 2000.045.0081, tooth; TMP 2000.045.0105, tooth; TMP 2001.045.0055, metatarsal; TMP 2001.045.0076, jugal; TMP 2001.045.0086, tooth; TMP 2001.045.0087, tooth; TMP 2001.045.0088, phalanx; TMP 2002.045.0054, tooth; TMP 2002.045.0055, phalanx; TMP 2002.045.0056, caudal vertebra; TMP 2002.045.0057, limb bone; TMP 2002.045.0058, jaw; TMP 2002.045.0059, ilium; TMP 2003.045.0022, metatarsal; TMP 2003.045.0040, tooth; TMP 2003.045.0041, tooth; TMP 2003.045.0042, humerus; TMP 2003.045.0043, vertebra; TMP 2003.045.0044, cervical vertebra; TMP 2003.045.0045, pedal phalanx; TMP 2003.045.0046, phalanx; TMP 2003.045.0047, tooth; TMP 2003.045.0048, caudal vertebra; TMP 2003.045.0075, pubis; TMP 2003.045.0077, limb bone; TMP 2003.045.0078, cervical vertebra; TMP 2003.045.0080, ischium; TMP 2003.045.0082, tibia; TMP 2004.056.0058, tooth; TMP 2004.056.0059, vertebra; TMP 2004.056.0060, dorsal vertebra (not prepared); TMP 2004.056.0061, dorsal vertebra; TMP 2004.056.0062, ischium; TMP 2004.056.0063, metatarsal; TMP 2005.050.0062, limb bone; TMP 2005.050.0065, phalanx; TMP 2005.050.0066, caudal vertebra; TMP 2005.050.0068, caudal vertebra; TMP 2003.043.0002, tooth; UALVP52076, phalanx; UALVP52089, phalanx; UALVP52091, caudal vertebra;

Fig. 11. Ornithischian teeth from units 2–4 of the Horseshoe Canyon Formation. (A) unshed hadrosaurid tooth, TMP 2003.043.0002. (B–C) Ankylosauridae, teeth; (B) specimen showing vertical wear pattern, TMP 2009.139.0003; (C) specimen showing oblique wear pattern, TMP 2009.139.0004. (D) *Parksosaurus warreni*, tooth, TMP 2009.137.0017. (E–F) Ceratopsidae, teeth; (E) TMP 2003.058.0009; (F) small ceratopsid tooth, TMP 2003.054.0014. Scale bar equals 2 mm.



UALVP52092, caudal vertebra; UALVP52094, caudal vertebra; UALVP52095, caudal vertebra; UALVP52100, fibula; UALVP52105, caudal; UALVP52116, femur.

COMMENTS: Disarticulated cranial and postcranial hadrosaur elements (Fig. 10) from the *Albertosaurus* bonebed are the second most numerous in the taphocoenosis. However, most specimens have not been prepared. Dorsal vertebrae with neural spines that are five-to-seven times the height of the corresponding centrum are attributable to *Hypacrosaurus altispinus* (Brown 1913). While it is conceivable that some of the non-diagnostic hadrosaur remains from the bonebed belong to *Sauropeltes*, which is only known from unit 4, all diagnostic hadrosaur bones are assignable to *H. altispinus* and we conservatively assign all other material to this species. The juvenile jugal is essentially identical to that described for an immature specimen of *Hypacrosaurus altispinus* (Lambe 1917) in having a relatively large orbital margin and a foreshortened infratemporal fenestra. The anterior process shows signs of anteroposterior shortening, which is a feature of the adults (Gilmore 1924b), although this is apparently not the case in young individuals (Horner and Currie 1994). The jugal flange and ventral half of the ante-

rior process are not preserved. A large sacrum with high neural spines recovered in 2003 was unfortunately destroyed in a helicopter lift during which it had to be jettisoned. Teeth are relatively rare but are dominated by unshed teeth.

From the vertebrate microfossil localities, hadrosaur teeth are the most abundant identifiable dinosaurian remains. Both shed and unshed teeth are present, but shed teeth are overwhelmingly dominant. The unshed teeth are tall and anteroposteriorly short, as is typical for lambeosaurines (Fig. 11A). In the absence of marginal crenulations, these teeth are similar to those of *Hypacrosaurus altispinus*, as represented by TMP 2006.015.0001.

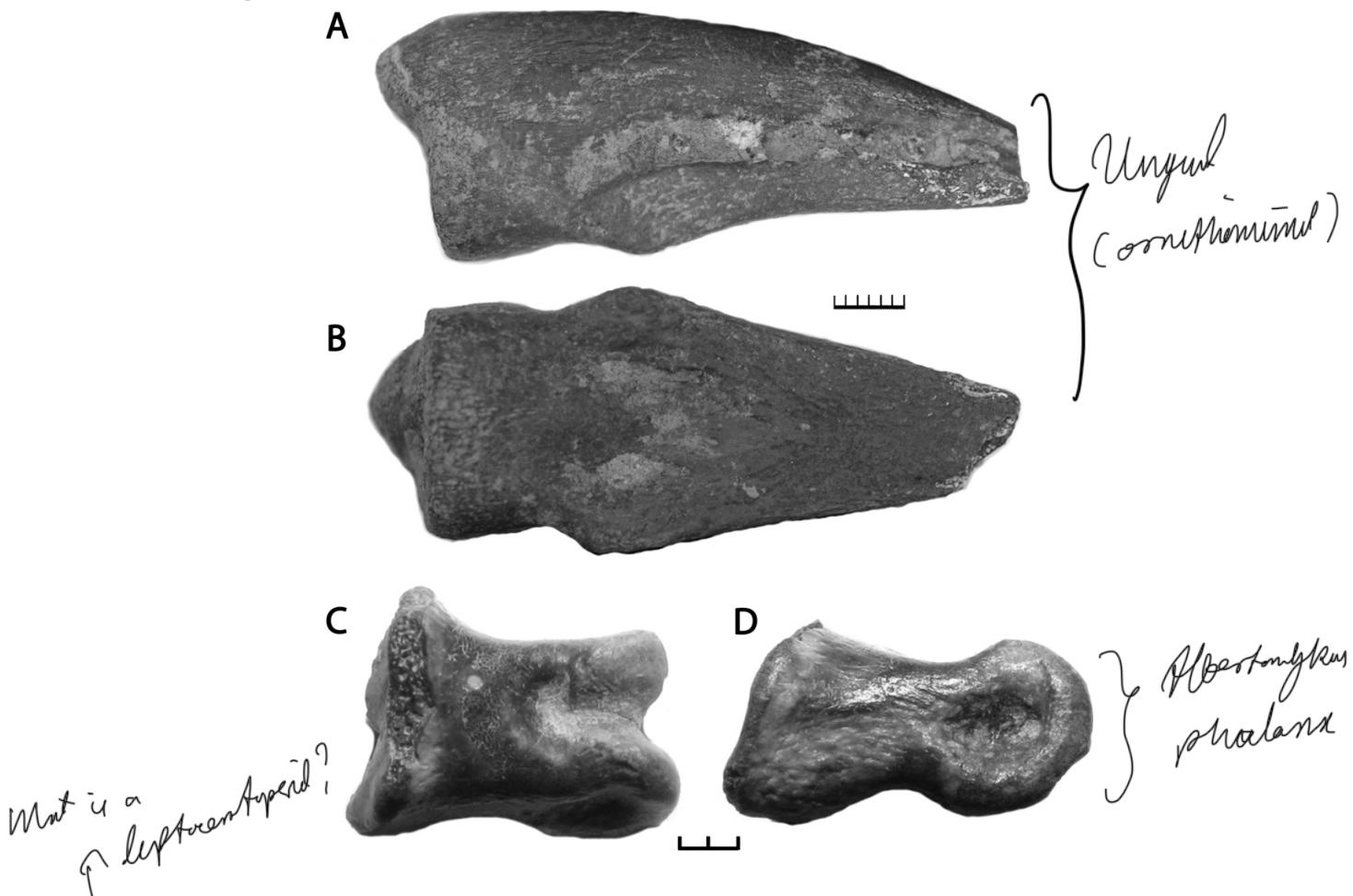
Suborder Ceratopsia Marsh, 1890b
Family Ceratopsidae Marsh, 1888

Gen. et sp. indet.

REFERENCE SPECIMENS: TMP 1999.050.0121 (in part), tooth; TMP 1999.050.0164, tooth; TMP 2000.045.0036, tooth; UALVP52093, femur; TMP 2003.058.0009, tooth; TMP 2003.054.0014, tooth.

COMMENTS: Ceratopsid teeth are differentiated from leptocera-

Fig. 12. Small theropod postcrania from units 2–4 of the Horseshoe Canyon Formation. (A–B) Ornithomimidae, ungual, TMP 2001.045.0085, in (A) lateral and (B) ventral views; (C–D) *Albertonykus borealis*, phalanx, UALVP48636, in (C) dorsal and (D) lateral views. Scale bar equals 6 mm in A–B and 2 mm in C–D.



topsid teeth by the lack of secondary ridges and the possession of double roots, and from leptoceratopsid and hadrosaurid teeth by their characteristic cross-sectional shape of a flattened triangle when worn (Baszio 1997). The range in morphology of ceratopsid teeth matches that of ceratopsid teeth from the Dinosaur Park Formation (Figs. 11E–11F). Small ceratopsid teeth with well-developed crenulations on the edge of the tooth are present in the vertebrate microfossil localities. One has a low, wide crown and one has a crown that is higher than its width (Fig. 11F). They are identified as ceratopsid, rather than leptoceratopsid because they have double roots typical of ceratopsids and because the crenulations do not extend along the ventral edge of the crown of the lateral surface of the tooth as they do in leptoceratopsids. Although isolated ceratopsid teeth are undiagnostic to species level, the only ceratopsid known from unit 4 is *Anchiceratops* (Russell and Chamney 1967). Two other ceratopsid taxa, *Pachyrhinosaurus* and *Arrhinosaurus*, are known only from unit 1. The recently described *Eotriceratops* is known only from a single specimen from unit 5. The abundance of ceratopsid teeth relative to hadrosaur teeth in vertebrate microfossil localities (1:7) is similar to that in the *Albertosaurus* bonebed (1:6). In addition to the teeth, a ceratopsid femur (UALVP52093) was recovered from the *Albertosaurus* bonebed.

Order Saurischia Seeley, 1888
Suborder Theropoda Marsh, 1881b
Clade Coelurosauria von Huene, 1914
Family Ornithomimidae Marsh, 1890a

Gen. et sp. indet.

REFERENCE SPECIMENS: TMP 1998.064.0002, phalanx; TMP 1999.050.0127, ungual; TMP 2001.045.0085, pedal ungual; TMP 2004.056.0064, pedal ungual; TMP 2005.050.0060, ungual.

COMMENTS: Two pedal unguals (Figs. 12A–12B) found in the bonebed (TMP 2001.045.0085 and TMP 2004.056.0064) are referable to the Ornithomimidae on the basis of their relatively straight, triangular shape. Isolated ornithomimid material is known from throughout the Horseshoe Canyon Formation. *Ornithomimus*, *Struthiomimus*, and *Dromiceiomimus* have all been reported from the formation.

Clade Maniraptora Gauthier, 1986

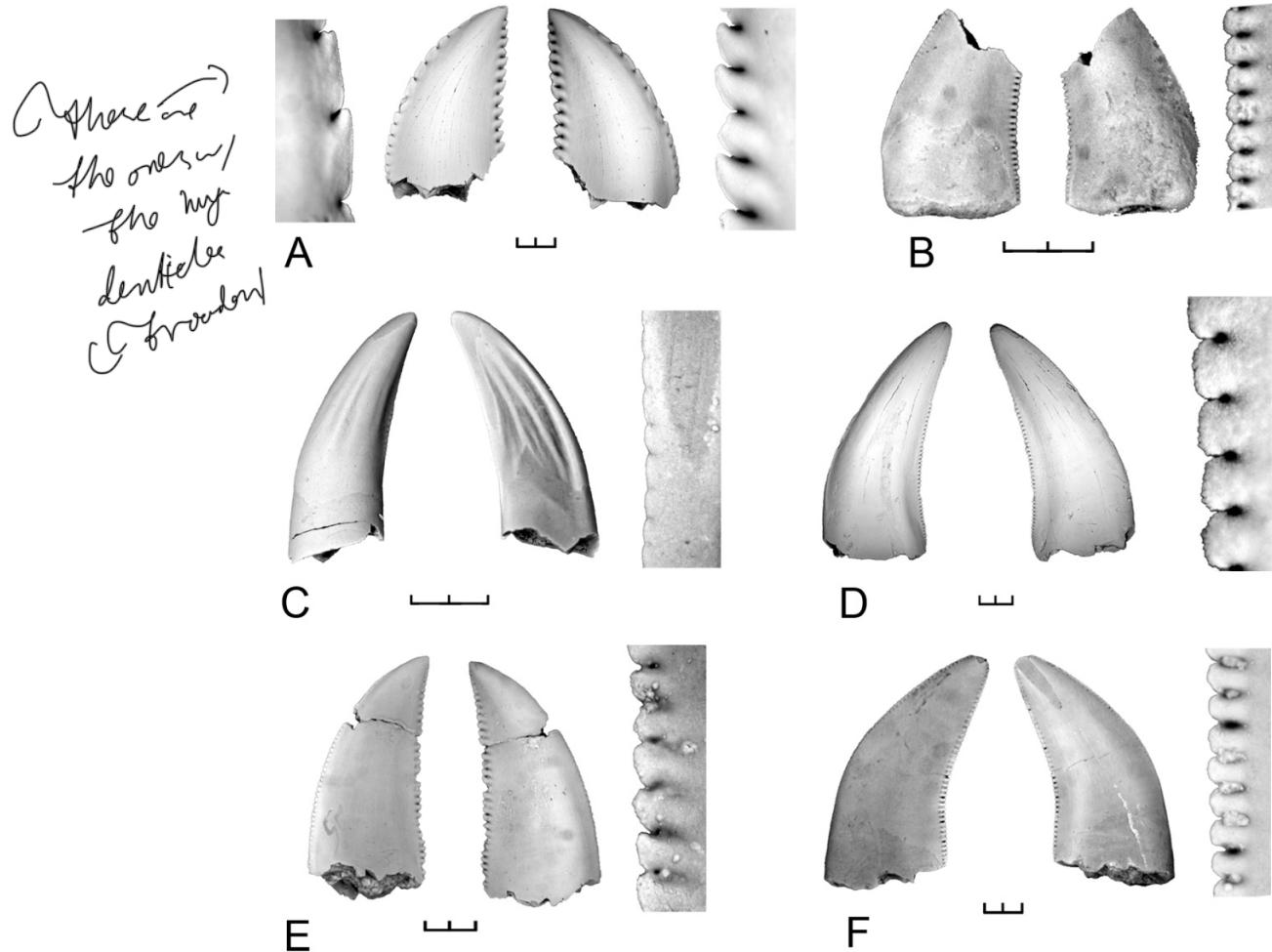
Family Alvarezsauridae Bonaparte, 1991

Genus *Albertonykus* Longrich and Currie, 2008

Albertonykus borealis Longrich and Currie, 2008

REFERENCE SPECIMENS: TMP 2001.045.0091, left ulna (holotype); TMP 2000.045.0086, manual ungual I; TMP

Fig. 13. Small theropod teeth from units 2–4 of the Horseshoe Canyon Formation. (A) *Troodon*, tooth, TMP 2003.034.0001; (B) Dromaeosaurinae gen. et sp. indet., tooth, TMP 2009.136.0008; (C) *Paronychodon*, tooth with flat surface showing faint developments of denticles, TMP 2009.139.0004; (D) *Richardoestesia* sp., tooth, TMP 2003.015.0002; (E–F) *Atrociraptor marshalli*, teeth; (E) TMP 2000.045.0103; (F) TMP 2003.045.0060. Scale bar equals 2 mm. Denticles not to scale.



2000.045.0012, right metatarsal III; TMP 1999.050.0010, ungual; TMP 2000.045.0031, tibia; TMP 2000.045.0061, phalanx; TMP 2000.045.0085, metatarsal; TMP 2000.045.0097, phalanx; TMP 2000.045.0098, tibia; TMP 2002.045.0052, phalanx; TMP 2003.045.0051, pedal phalanx; UALVP48636, phalanx.

COMMENTS: The recently described alvarezsaur, *Albertonykus borealis*, is known from fourteen isolated cranial and postcranial elements all recovered from unit 4. Of these specimens, only two were surface collected (Figs. 12C–12D), whereas the remainder were found within the *Albertosaurus* bonebed, including an ulna (holotype), a manual ungual, two tibiae, metatarsals, and several pedal phalanges. *Albertonykus* is distinguished from other alvarezsaurs by the presence of a particularly broad ulna (35% of the length) that has a tuber on the medial surface (Longrich and Currie 2008). The presence of two right third metatarsals indicates at least two individuals were present within the bonebed itself.

Family Dromaeosauridae Colbert and Russell, 1969
Subfamily Dromaeosaurinae Colbert and Russell, 1969

Gen. et sp. indet.

REFERENCE SPECIMENS: TMP 1998.063.0032, tooth; TMP 1998.063.0071, tooth; TMP 1998.064.0017, tooth; TMP 1999.050.0116, tooth; TMP 2000.045.0040, TMP 2000.045.0082, tooth; TMP 2000.045.0102, tooth; TMP 2001.045.0083, tooth; TMP 2002.045.0050, tooth; TMP 2003.045.0060, tooth; TMP 2009.136.0008, tooth.

COMMENTS: Teeth resembling those of *Dromaeosaurus albertensis* of Dinosaur Provincial Park (Currie et al. 1990) have relatively large (3.0–4.3 denticles/mm on distal carina), rounded denticles. However, these teeth lack the lingually hooked mesial carinae that characterize the species. They are like those of more typical small theropod teeth in being blade-like and curved with the anterior carina located on the anterior edge of the tooth (Fig. 13B).

Subfamily Saurornitholestinae Longrich and Currie, 2009

Genus *Atrociraptor* Currie and Varricchio, 2004

Atrociraptor marshalli Currie and Varricchio, 2004

DIAGNOSIS: (modified from Currie and Varricchio 2004) Den-

tal characters of *Atrociraptor marshalli* include posteriorly inclined tooth crowns and large (3–5 denticles/mm on distal carina), pointed, and apically hooked denticles. The teeth differ from *Saurornitholestes langstoni* by generally larger basal width and denticle size, and smaller crown heights relative to fore-aft basal length.

REFERENCE SPECIMENS: TMP 1998.063.0004, tooth; TMP 1999.050.0117, tooth; TMP 2000.045.0035, tooth; TMP 2000.045.0103, tooth; TMP 2003.045.0049, tooth; TMP 2003.045.0052, tooth.

COMMENTS: All shed teeth attributed to *A. marshalli* (Figs. 13E–13F) were collected from the *Albertosaurus* bonebed and fall within the range of variation seen in the type specimen. These teeth have been shown to be quantitatively distinct from taxa such as *Saurornitholestes langstoni* from the Dinosaur Park Formation and other dromaeosaurs (Larson 2009). It would seem, based on the stratigraphic distribution of these specimens, that this species occurs throughout the formation and spans the Campanian–Maastrichtian boundary.

Family Troodontidae Gilmore, 1924a

Genus *Troodon* Leidy, 1856b

Troodon sp.

REFERENCE SPECIMENS: TMP 1998.063.0043, tooth; TMP 1999.050.0114, tooth; TMP 1999.050.0115, tooth; TMP 2000.045.0010, tooth; TMP 2000.045.0024, tooth; TMP 2000.045.0041, tooth; TMP 2000.045.0090, tooth; TMP 2000.045.0091, tooth; TMP 2001.045.0080, tooth; TMP 2001.045.0081, tooth; TMP 2002.045.0048, tooth; TMP 2003.045.0057, tooth; TMP 2003.045.0058, tooth; TMP 2003.034.0001, tooth.

COMMENTS: *Troodon* teeth are characterized by their relatively large and apically pointed denticles with prominent interdental pits. *Troodon* was reported from the Horseshoe Canyon Formation previously (Currie 1987; Baszio 1997; Ryan et al. 1998) and is easily identified by the large, hooked denticles (Fig. 13A). Based on the occurrence of teeth in the vertebrate microfossil sites that were screenwashed, *Troodon* is the most abundant small theropod in the Horseshoe Canyon Formation. Although Currie (1987) identified all troodontid material from North America as belonging to *T. formosus* and such identifications are still common (Fiorillo et al. 2009), referral of isolated teeth to named taxa with represented skeletal material is problematic. Therefore, no specific epithet was identified for the known material.

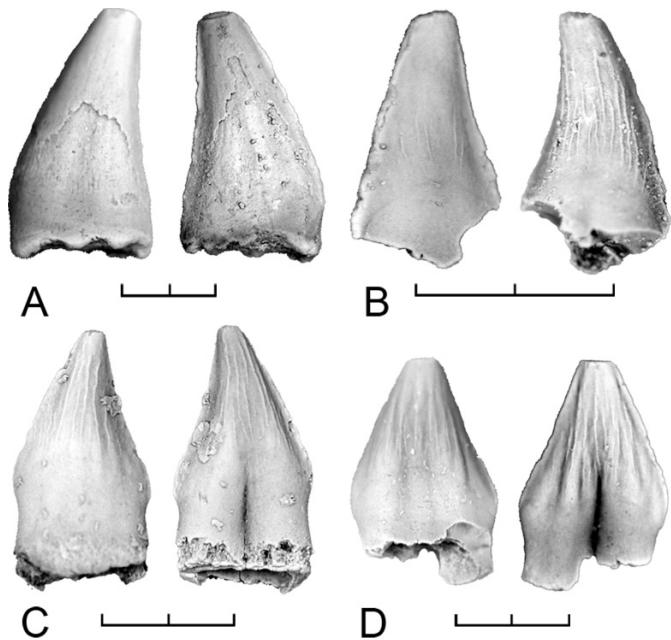
Genus *Paronychodon* Cope, 1876a

Paronychodon sp.

REFERENCE SPECIMEN: TMP 2009.139.0004, tooth.

COMMENTS: *Paronychodon*, perhaps one of the most enigmatic of the small theropods from the Cretaceous of the Western Interior, is documented in the Horseshoe Canyon Formation by a single tooth from unit 2 that has the characteristic feature of being flat on one side with strong plications extending the length of the tooth (Fig. 13C). Some *Paronychodon* teeth of the late Maastrichtian sometimes have small denticles (Longrich 2008), whereas those of the Belly River Group and Milk River Formation do not (Sankey et al. 2002; Larson 2008). The tooth of *Paronychodon* from the

Fig. 14. Other archosaur teeth from units 2–4 of the Horseshoe Canyon Formation. (A) Avialae indet., tooth, TMP 2003.057.0002. (B–D) Archosauria indet., teeth: (B) tooth showing twisted crown, TMP 2009.137.0018; (C) tooth showing reduced twisting and moderately developed ventral groove subdividing the root into two lobes, TMP 2009.139.0005; (D) tooth showing blade-like condition with well developed groove subdividing the root into two lobes, TMP 2009.137.0019. Scale bar equals 2 mm.



Horseshoe Canyon Formation appears intermediate in that it shows faintly developed denticles (Fig. 13C).

Family incertae sedis

Genus *Richardoestesia* Currie, Rigby, and Sloan, 1990

Richardoestesia sp.

REFERENCE SPECIMENS: TMP 1999.050.0113, tooth; TMP 2000.045.0080, tooth; TMP 2001.045.0082, tooth; TMP 2002.045.0049, tooth; TMP 2002.045.0053, tooth; TMP 2003.015.0002, tooth.

COMMENTS: Teeth referable to *Richardoestesia* sp. (Fig. 13D) are characterized by rounded, small denticles (in this case 5.0–6.6 denticles/mm on distal carina) and a curved tooth crown (Currie et al. 1990). They differ from *R. gilmorei* in being taller and differ from *R. isosceles* in being more recurved. In some cases, they have weakly developed plications. These teeth have been attributed to *Paronychodon* (Estes et al. 1969; Longrich 2008). However, as weak plications occur on many different theropod teeth (Larson 2008) and appear to be distinct from the strong plications on the lingual and often labial sides of teeth of *Paronychodon*, these morphotypes are treated as separate taxa in this study. There are no known teeth from the upper Horseshoe Canyon Formation that exhibit the straight, isosceles triangle morphology of *R. isosceles* (Sankey 2001) or the low triangular teeth of *R. gilmorei* (Currie et al. 1990).

Clade Avialae

Gen. et sp. indet.

REFERENCE SPECIMENS: TMP 2000.045.0052, tooth; TMP 2000.045.0057, tooth; TMP 2003.057.0002, tooth.

COMMENTS: Teeth included in Avialae indet. correspond generally to those teeth reported in Sankey et al. (2002) in having gently curved, triangular, labiolingually flattened crowns with no development of denticles on the carinae and with constrictions at the base of the crown (Fig. 14A). Avian teeth from the *Albertosaurus* bonebed are greater than twice the size of those from the Campanian beds at Dinosaur Provincial Park.

Archosauria indet.

REFERENCE SPECIMENS: TMP 2009.137.0018, tooth; TMP 2009.139.0005, tooth; TMP 2009.137.0019, tooth.

COMMENTS: A morphotype, designated as Archosauria indet., includes curved teeth that have twisted crowns, well developed carina, and fine crenulations on the enamel (Figs. 14B–14D). Teeth with this morphology from the Lance Formation were described as Archosauria incertae sedis by (Longrich 2008), who felt that they could be either bird or crocodile.

Discussion

(A) Comparison of the vertebrate microfossil assemblages of units 2–4 with the *Albertosaurus* bonebed assemblage

Abundances of specimens of each taxon from the vertebrate microfossil sites samples and the *Albertosaurus* bonebed are given in Table 1. The vertebrate microfossil sites are dominated by aquatic taxa with the scales of Holostein A being particularly abundant. Vertebrate microfossil elements recovered from the *Albertosaurus* bonebed differ from the typical Horseshoe Canyon Formation assemblage most obviously in the dominance of terrestrial vertebrates. In the *Albertosaurus* bonebed assemblage, 75% of the vertebrate microfossil elements recovered are from terrestrial taxa; whereas in the screenwashed samples, 10% of the elements recovered are from terrestrial taxa. Chondrichthyans are absent from the bonebed. Much of the non-*Albertosaurus* component of the bonebed is composed of large hadrosaurid elements and shed small theropod teeth.

Differences are also apparent in the relative abundance of the different kinds of terrestrial taxa. In the *Albertosaurus* bonebed, nearly half the vertebrate microfossil specimens recovered were small theropod teeth, which constitute <5% of the specimens recovered from the screenwashed samples. Furthermore, in the *Albertosaurus* bonebed, *Atrociraptor* is well-represented by multiple specimens, although this taxon is absent in the screenwashed samples and was not encountered in surface collections of units 2–4. Because the *Albertosaurus* bonebed was deposited during the initial phases of a change from a cool, dry climate to a warm, wet climate (Eberth and Currie 2010), the occurrence of *Atrociraptor marshalli* in the *Albertosaurus* bonebed and in unit 1, but not the vertebrate microfossil localities of units 2–4, may be associated with this change in climate.

The relative rarity of aquatic taxa in the *Albertosaurus* bonebed, which dominate the vertebrate microfossil localities of the Horseshoe Canyon Formation, suggests that little

vertebrate material was transported into the locality through normal fluvial processes. This interpretation is also supported by the relative rarity of shed hadrosaur teeth in the *Albertosaurus* bonebed. In the vertebrate microfossil localities that were sampled, the majority of hadrosaur teeth recovered were shed teeth. In the vertebrate microfossil sites, only 13% of the teeth were unshed teeth; whereas in the *Albertosaurus* bonebed, 90% of the hadrosaur teeth recovered are unshed teeth. This indicates that, unlike the transported accumulation in vertebrate microfossil localities, the non-*Albertosaurus* remains from the *Albertosaurus* bonebed were mostly derived from an accumulation of remains of animals that died at the site. The high abundance of shed teeth of small theropods can be explained by scavenging done by individuals that were attracted to the *Albertosaurus* bonebed by temporarily abundant food resources.

(B) Comparison of the vertebrate microfossil assemblages of the upper and lower Horseshoe Canyon Formation

As far as can be determined, no microfossil remains document non-marine extinctions across the Campanian–Maastrichtian boundary in Alberta. However, differences in the relative abundances and taxonomic compositions between unit 1 and units 2–4 are present. These can be interpreted as a result of biogeographic shifts associated with the cooling of the climate during this time. One of these differences is the occurrence of crocodylians. Crocodylians are present in the basal (unit 1) and uppermost (unit 5) units but not in units 2–4. As well, turtle diversity is low in units 2–4 and the turtle present is much smaller than those in unit 1 (Brinkman 2003; Brinkman and Eberth 2006). A striking feature of the assemblage is the abundance of amphibians, particularly frogs, in units 2–4. Amphibian remains from this unit are significant in that they represent the northernmost occurrence of the Amphibia during late Campanian – early Maastrichtian times in North America (Gardner 2000; Fanti and Miyashita 2009), and their abundance indicates that their distribution was not as strongly limited by climate as were some ectothermic mesoreptiles.

The *Albertosaurus* bonebed, however, does bear a striking resemblance in both composition and relative abundances of taxa (apart from *Albertosaurus* itself) to the assemblage reported by Ryan et al. (1998) from the uppermost lower Horseshoe Canyon Formation. The *Albertosaurus* bonebed shares with this assemblage a paucity of aquatic taxon elements and a dominance of terrestrial taxa. Moreover, in both assemblages, *Troodon* dominates amongst small theropods, with *Atrociraptor* and *Richardoestesia* making up similar proportions of the assemblage. The only notable differences are that in the *Albertosaurus* bonebed turtles and embryonic hadrosaurs are absent; *Dromaeosaurinae* indet. is present; and, of course, *Albertosaurus* remains are dominant. This mixture of similarities and differences suggests that both of these localities preferentially preserved terrestrial taxa and are largely non-transported assemblages.

(C) Comparison of the vertebrate microfossil assemblages of the Dinosaur Park and Horseshoe Canyon formations

The vertebrate microfossil assemblage of units 2–4 of the

Horseshoe Canyon Formation is of particular interest because the animals represented lived in a relatively northern locality (palaeolatitude 58°N) at a time of relatively cool mean annual temperatures (Wolfe and Upchurch 1987; Brinkman 2003; Eberth 2004; Brinkman and Eberth 2006). Brinkman (2003) argued that the vertebrates of this unit represent a more northerly assemblage that has shifted south because of the cooler climate. Thus, it provides a basis for interpreting the nature of high-latitude assemblages during the Late Cretaceous.

Among the fish, the most striking aspect of the assemblage is the overwhelming abundance of Holostean A and the absence of *Lepisosteus*. Because the scales of these fish are taphonomically equivalent, this difference is easily interpreted as a result of the presence of Holostean A and absence of *Lepisosteus* in the original palaeocommunities. The absence of *Lepisosteus* and the abundance of Holostean A may reflect latitudinal patterns of distribution. That the abundance of Holostean A in units 2–4 of the Horseshoe Canyon Formation is a reflection of its more northern distribution, rather than local ecology, is supported by distribution patterns during the mid-Campanian and late Maastrichtian. During the mid-Campanian, it is present in the Belly River Group of Alberta but is absent in the Judith River Formation of Montana (Sahni 1972). Similarly, a more southern distribution of *Lepisosteus* is supported by its absence in a vertebrate microfossil assemblage from the Wapiiti Formation of northern Alberta described by Fanti and Miyashita (2009). This locality includes Holostean A but not *Lepisosteus*, whereas penecontemporaneous localities from more southern regions of the province consistently include both *Lepisosteus* and Holostean A. The possibility that the presence of Holostean A and absence of *Lepisosteus* in units 2–4 of the Horseshoe Canyon Formation is a result of difference in local environments of deposition can be rejected because units 2–4 were deposited in suites of environmental settings comparable with the Belly River Group. Both of these units include coastal and more inland deposits as well as both quiet water and more high-energy conditions. At present, neither *Lepisosteus* nor Holostean A are known from unit 5 of the Horseshoe Canyon Formation. Because aspects of the vertebrate assemblage of unit 5 indicate that it was deposited in warm water conditions (specifically the presence of the turtle *Adocus* and a crocodylian), the hypothesis of latitudinal restrictions of *Lepisosteus* and Holostean A presented here leads to the predictions that this unit will include a high proportion of *Lepisosteus* scales.

The teleost assemblage differs from that of the Dinosaur Park Formation in several respects, including the presence of previously unrecognized taxa of teleost fish. Because teleost fish assemblages of vertebrate microfossil localities of the late Maastrichtian are poorly understood, it is unclear if this difference is a result of latitudinal patterns of distribution or evolutionary change in teleost assemblages. One aspect of the teleost assemblage that is of particular interest for biogeographic reasons is the abundant presence of the saber-like (?)acanthomorph fin spines. The presence of these spines in both the Horseshoe Canyon and Hornerstown – New Egypt Formation of New Jersey indicates a connection between these areas.

Among the amphibians, a taxon conspicuous by its ab-

sence in units 2–4 is *Albanerpeton*, which is present in both mid-Campanian and late Maastrichtian localities of Alberta and Montana.

Tarduno et al. (1998) argued that ectothermic mesoreptiles are particularly sensitive to climate change at high latitudes because of the reduced growing season associated with the seasonal variation in photoperiod at high latitudes. The low diversity and small size of turtles present in units 2–4 of the Horseshoe Canyon Formation are reflections of this (Brinkman 2003, Brinkman and Eberth 2006). Another aspect of the mesoreptile assemblage of units 2–4 that can be interpreted as a reflection of its high-latitude location during a time of relatively cool temperatures is the absence of crocodiles. This absence is striking because they are typically represented in vertebrate microfossil localities by teeth, which are well represented in every vertebrate microfossil locality in the Dinosaur Park Formation that has been sampled. The absence of crocodiles in units 2–4 of the Horseshoe Canyon Formation suggests that they are more sensitive to climate than are turtles and champsosaurs because both these mesoreptiles are present. Champsosaurs are typically members of a more northern vertebrate assemblage (Tarduno et al. 1998), which is suggested by their consistent presence in the Campanian beds in Alberta and Montana and absence in beds of this time period in Mexico, Texas, and Utah. The presence of crocodylian remains at the top of unit 5, therefore, indicates the presence of warm climatic conditions at that time.

Ornithischian dinosaur remains from vertebrate microfossil sites mirror the assemblage as represented by articulated specimens. Hadrosaurs are overwhelmingly dominant, and ankylosaurids and basal ornithopods are present but rare members of the assemblage. However, ceratopsian remains are more abundant in the vertebrate microfossil localities than they are as macrofossils. Ceratopsian macrofossils are rare in units 2–4 of the Horseshoe Canyon Formation, while they are well-represented as teeth in vertebrate microfossil localities.

Differences in the saurischian dinosaur assemblages of the Horseshoe Canyon Formation and Dinosaur Park Formation were noted by Baszio (1997). Of particular significance was the higher abundance of *Troodon*, and this taxon was subsequently suggested to be more northern in its distribution because of its abundance in Alaska (Fiorillo and Gangloff 2000). Assemblages from vertebrate microfossil sites sampled by underwater screenwashing methods agree with the results of Baszio (1997) in having a high abundance of *Troodon* relative to other small theropods. This is the reverse in the Belly River Group. Thus, the high abundance in the Horseshoe Canyon Formation is consistent with the idea that this formation preserves a high-latitude assemblage that has extended to more southern latitudes because of the relatively cool temperatures of this time. Another difference between the theropod assemblages of the Horseshoe Canyon Formation and the Dinosaur Park Formation is the presence of *Dromaeosaurinae* indet. teeth and not *Dromaeosaurus albertensis*. It is unclear whether or not these differences are a result of climate-controlled shifts in distribution patterns or evolutionary changes in the small theropods.

A striking aspect of the vertebrate assemblage of units 2–4 of the Horseshoe Canyon Formation is the presence of

bird teeth and Archosauria indet. The abundance of birds in this assemblage is consistent with previous suggestions that birds are more abundant in high-latitude assemblages (Nicholls and Russell 1990).

(D) Comparison of the vertebrate microfossil assemblages of units 2–4 with the late Maastrichtian Scollard, Lance, and Hell Creek formations

The non-mammalian vertebrate assemblage of the late Maastrichtian Scollard Formation is not well understood, preventing a detailed comparison of these assemblages. However, the faunal assemblages are well described from the American Lance and Hell Creek formations.

Holostean A was not recognized in the late Maastrichtian Hell Creek and Lance formations of Montana and Wyoming (Estes 1964; Estes and Berberian 1970), but it is abundant in the temporally equivalent Scollard Formation of Alberta (D.B. Brinkman, personal observation, 2009).

The presence of abundant ectothermic mesoreptiles and *Lepisosteus* in the Scollard Formation is a marked deviation from the assemblages from units 2–4 of the Horseshoe Canyon Formation. This difference is consistent with the suggestions that these taxa had a more southern distribution because leaf margin analysis has provided evidence for a climatic warming in the late Maastrichtian (Wolfe and Upchurch 1987).

The Scollard, Lance, and Hell Creek formations are all similar to one another and different from the Campanian Belly River Group and unit 1 of the Horseshoe Canyon Formation in a low abundance of hadrosaurs. The greater abundance of hadrosaurid teeth relative to ceratopsid teeth in units 2–4 of the Horseshoe Canyon Formation (Table 1) is similar to that of Campanian assemblages rather than those of the late Maastrichtian. This difference suggests that the shift from a megaherbivore fauna dominated by hadrosaurs to one dominated by ceratopsians occurred in the mid-Maastrichtian, at least after the deposition of unit 4 of the Horseshoe Canyon Formation.

The only taxa that are present in both the early and late Maastrichtian (but not the Campanian) assemblages are the frog (?)*Palaeobatrachus occidentalis* and a *Leptochamops* sp. similar to *L. denticulatus*. Only in the occurrence of these taxa does the early Maastrichtian assemblage appear transitional between the late Campanian and late Maastrichtian assemblages.

Summary and conclusions

The vertebrate microfossil assemblages of units 2–4 document a cool-climate, northern fauna. The presence in these assemblages of abundant remains of Holostean A and the absence of *Lepisosteus*, *Albanerpeton*, crocodylians, and diverse turtles are aspects of the assemblage that can be interpreted as related to the cool climate. The *Albertosaurus* bonebed assemblage differs from that of the vertebrate microfossil localities in the dominance of terrestrial taxa, indicating an assemblage with little transport. As well, the bonebed differs in the presence of *Atrociraptor marshalli*. Because the bonebed was deposited during the onset of a transition between a cool, dry climate and a warm, wet climate, the presence of *Atrociraptor* in the bonebed but not

elsewhere in units 2–4 may be a result of climatic controls on the distribution of this small theropod.

A comparison of the assemblages from the vertebrate microfossil localities and the *Albertosaurus* bonebed with the well-known mid-Campanian and late Maastrichtian assemblages of western North America allow for large-scale patterns to be observed. In contrast to the few similarities to the overlying assemblage, the relatively minor change within communities between the late Campanian and early Maastrichtian, despite changing climatic conditions, indicates that observed faunal changes in the early Maastrichtian are likely due to climatic response and not faunal turnover, providing additional data on the changes in the non-marine vertebrate assemblages through the latest Cretaceous.

Acknowledgements

The authors would like to thank the staff and volunteers of the TMP who were involved in locating and sampling vertebrate microfossil localities from the Horseshoe Canyon Formation. In particular, we would like to thank N. Longrich, who found three of the vertebrate microfossil localities that were sampled here, and J. Divay, who located locality JD-1. Thanks also to J. Maccagno, who has spent many hours of sorting vertebrate microfossil concentrate on a volunteer basis. The authors would also like to thank the crews, preparators, and collections staff from the TMP and the UALVP who have worked on material from the *Albertosaurus* bonebed. This manuscript benefited greatly from discussion with and suggestions from P. Currie and E. Koppelhus, as well as comments from the Journal Associate Editor H.-D. Sues and reviewers J. Eaton and T. Lehman.

References

- Agassiz, J.L.R. 1833–1844. Recherches sur les poissons fossiles. Imprimerie Petitpierre, Neuchâtel, Switzerland, 1420 p. [In French.]
- Arambourg, C., and Bertini, L. 1958. Super-ordre des Holostéens et des Halecostomi (Holostei et Halecostomi). In *Traité de Zoologie: Anatomie, Systématique, Biologie*. Edited by P.-P. Grassé. Masson et Cie, Paris, pp. 2173–2203. [In French.]
- Auffenberg, W. 1958. A new family of Miocene salamanders from the Texas Coastal Plain. *Quarterly Journal of the Florida Academy of Sciences*, **21**: 169–176.
- Auffenberg, W. 1961. A new genus of fossil salamander from North America. *American Midland Naturalist*, **66**(2): 456–465. doi:10.2307/2423045.
- Auffenberg, W., and Goin, C.J. 1959. The status of the salamander genera *Schapherpeton* and *Hemitypus* of Cope. *American Museum Novitates* 1979, pp. 1–12.
- Balfour, F.M. 1880. Larval forms: their nature, origin, and affinities. *The Quarterly Journal of Microscopical Science*, **20**: 381–407.
- Bannikov, A.F., and Bacchia, F. 2000. A remarkable clupeomorph fish (Pisces, Teleostei) from a new Upper Cretaceous marine locality in Lebanon. *Senckenbergiana Lethaea*, **80**(1): 3–11. doi:10.1007/BF03043659.
- Baszio, S. 1997. Systematic palaeontology of isolated dinosaur teeth from the latest Cretaceous of south Alberta, Canada. *Courier Forschungsinstitut Senckenberg*, **196**: 33–77.
- Becker, M.A., Chamberlain, J.A., Jr., Lundberg, J.R., L'Amoreaux, W.J., Chamberlain, R.B., and Holden, T. 2009. Beryciform-like fossils (Teleostei: Acanthomorpha: Euacanthopterygii) from the

- late Cretaceous – early Tertiary of New Jersey. Proceedings of the Academy of Natural Sciences of Philadelphia, **158**(1): 159–181. doi:10.1635/053.158.0108.
- Berg, L.S. 1940. Classification of fishes both recent and fossil. Transactions of the Zoological Academy of Sciences, **5**: 85–517.
- Berg, L.S. 1958. System der Rezenten und fossilen Fischartigen und Fische. Hochschulbuecher fur Biologie. Vol. 4, pp. 1–310. [In German.]
- Bleeker, P. 1859. Enumeratio specierum piscium hucusque in Archipelago indico observatarum adjectis habitationibus citationibusque, ubi descriptiones earum recentiores reperiuntur, nec non speciebus Musei Bleekeriani Bengalensis, Japonicis, Capensis, Tasmanicisque. Acta Societatis Regiae Scientiarum Indo-Neerlandicae. Vol. 6, pp. 1–276. [In Latin.]
- Bonaparte, C.L. 1831. Saggio di una distribuzione metodica degli animali vertebrati. Giornale Arcadico di Scienze Lettere ed Arti. Vol. 52, pp. 155–189. [In Italian.]
- Bonaparte, C.L. 1837. Iconographia della Fauna Italica per le quattro classi degli animali vertebrati. Iconographia, **3**: 6–11.
- Bonaparte, C.L. 1838. Selachorum tabula analytica. Nouvelles Annales des Sciences Naturelles (Bologna), **2**: 195–214.
- Bonaparte, J.F. 1991. Los vertebrados fosiles de la Formacion Rio Colorado de Neuquen y cercanias, Cretacio Superior, Argentina. Revista del Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’ (Paleontologia). Vol. 4, pp. 17–123.
- Brinkman, D.B. 1990. Paleoecology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: evidence from vertebrate microfossil localities. Palaeogeography, Palaeoclimatology, Palaeoecology, **78**(1–2): 37–54. doi:10.1016/0031-0182(90)90203-J.
- Brinkman, D.B. 2003. A review of nonmarine turtles from the Late Cretaceous of Alberta. Canadian Journal of Earth Sciences, **40**(4): 557–571. doi:10.1139/e02-080.
- Brinkman, D.B., and Eberth, D.A. 2006. Turtles of the Horseshoe Canyon and Scollard Formations, further evidence for a biotic response to Late Cretaceous climate change. Fossil Turtle Research, **1**: 11–18.
- Brinkman, D.B., and Neuman, A.G. 2002. Teleost centra from uppermost Judith River Group (Dinosaur Park Formation, Campanian) of Alberta, Canada. Journal of Paleontology, **76**(1): 138–155. doi:10.1666/0022-3360(2002)076<0138:TCFUR>2.0.CO;2.
- Brinkman, D.B., Russell, A.P., Eberth, D.A., and Peng, J.H. 2004. Vertebrate palaeocommunities of the lower Judith River Group (Campanian) of southeastern Alberta, Canada, as interpreted from vertebrate microfossil assemblages. Palaeogeography, Palaeoclimatology, Palaeoecology, **213**: 295–313.
- Brown, B. 1908. The Ankylosauridae, a new family of armored dinosaurs from the Upper Cretaceous. Bulletin of the American Museum of Natural History, **24**: 187–201.
- Brown, B. 1913. A new trachodont dinosaur, *Hypacrosaurus*, from the Edmonton Cretaceous of Alberta. Bulletin of the American Museum of Natural History, **32**: 395–406.
- Camp, C.L. 1923. Classification of the lizards. Bulletin of the American Museum of Natural History, **48**: 289–481.
- Capetta, H. 1974. Sclerorhynchidae nov. fam., Prestidae et Pristiphoridae: un exemple de parallélisme chez Sélaçiens. Comptes Rendus de l'Académie des Sciences de Paris (Série D), **278**: 225–228. [In French.]
- Colbert, E.H., and Russell, D.A. 1969. The small Cretaceous dinosaur *Dromaeosaurus*. American Museum Novitates 2380, pp. 1–49.
- Coombs, W.P., Jr. 1990. Teeth and taxonomy in ankylosaurs. In Dinosaur Systematics: Approaches and Perspectives. Edited by K. Carpenter and P.J. Currie. Cambridge University Press, Cambridge, UK, pp. 269–279.
- Cooper, M.R. 1985. A revision of the ornithischian dinosaur *Kangnasaurus coetzeei* Haughton, with a classification of the Ornithischia. Annals of the South African Museum, **95**: 281–317.
- Cope, E.D. 1865. Sketch of the primary groups of Batrachia Salientia. Natural History Review, **1**: 97–120.
- Cope, E.D. 1870. Synopsis of the extinct Batrachia, Reptilia, and Aves of North America. Transactions of the American Philosophical Society, **14**(1): 1–252. doi:10.2307/1005355.
- Cope, E.D. 1872. Observations on the systematic relationships of the fishes. Proceedings of the American Association for the Advancement of Science, **20**: 317–343.
- Cope, E.D. 1876a. Descriptions of some vertebrate remains from the Fort Union beds of Montana. Proceedings of the Academy of Sciences of Philadelphia, **28**: 248–261.
- Cope, E.D. 1876b. On some extinct reptiles and Batrachia from the Judith River and Fox Hills beds of Montana. Proceedings of the Academy of Natural Sciences of Philadelphia, **28**: 340–359.
- Cope, E.D. 1887. Geology and paleontology. American Naturalist, **21**(11): 1014–1019. doi:10.1086/274597.
- Currie, P.J. 1987. Bird-like characteristics of the jaws and teeth of troodontid theropods (Dinosauria, Saurischia). Journal of Vertebrate Paleontology, **7**: 72–81.
- Currie, P.J., and Varricchio, D.J. 2004. A new dromaeosaurid from the Horseshoe Canyon Formation (Upper Cretaceous) of Alberta, Canada. In Feathered Dragons. Edited by P.J. Currie, E.B. Koppelhus, M.A. Shugar, and J.L. Wright. Indiana University Press, Bloomington, Ind., pp. 112–132.
- Currie, P.J., Rigby, J.K., Jr., and Sloan, R.E. 1990. Theropod teeth from the Judith River Formation of Southern Alberta, Canada. In Dinosaur Systematics: Approaches and Perspectives. Edited by K. Carpenter and P.J. Currie. Cambridge University Press, Cambridge, UK, pp. 107–125.
- Cuvier, G. 1797. Tableau Élémentaire de l'Histoire des Animaux. Paris. [In French.]
- Cuvier, G. 1817. Le Règne Animal Distribué d'après son Organisation Pour Servir de Base à L'histoire Naturelle des Animaux et D'introduction à L'anatomie Comparée. Les Reptiles, les Poissons, les Molusques et les Annélides. 1 ed. P.F. Didot le jeune, Paris. [In French.]
- de Montfort, D. 1810. Conchyliologie systématique, et classification méthodique des coquilles; offrant leurs figures, leur arrangement générique, leurs descriptions caractéristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. Ouvrage destiné à faciliter l'étude des coquilles, ainsi que leur disposition dans les cabinets d'histoire naturelle. Coquilles univalves, non cloisonnées. Vol. 2. Schoell, Paris. [In French.]
- Eberth, D.A. 2004. A revised stratigraphy for the Edmonton Group (Upper Cretaceous) and its potential sandstone reservoirs. In Proceedings of the CSPG–CHOA–CWLS Joint Conference, Calgary, Alta., 31 May – 4 June 2004, 44 p.
- Eberth, D.A., and Currie, P.J. 2010. Stratigraphy, sedimentology and taphonomy of the *Albertosaurus* bonebed (upper Horseshoe Canyon Formation, Maastrichtian). Canadian Journal of Earth Sciences, **47**(9): This issue.
- Eberth, D.A., and Deino, A. 2005. New $^{40}\text{Ar}/^{39}\text{Ar}$ ages from three bentonites in the Bearpaw, Horseshoe Canyon and Scollard formations (Upper Cretaceous – Paleocene) of southern Alberta, Canada. In Dinosaur Park Symposium — Short Papers, Abstracts, and Program. Edited by D. Braman, F. Therrien, E. Koppelhus, and W. Taylor. Special Publication of the Royal Tyrrell Museum, Drumheller, Alta., pp. 23–24.
- Eberth, D.A., and O'Connell, S.C. 1995. Notes on changing paleoenvironments across the Cretaceous–Tertiary boundary (Scollard Formation) in the Red Deer River valley of southern Alberta. Bulletin of Canadian Petroleum Geology, **43**: 44–53.

- Estes, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, Eastern Wyoming. University of California Publications in Geological Sciences, Berkeley, Calif. Vol. 49, pp. 1–187.
- Estes, R. 1969. Two new late Cretaceous fishes from Montana and Wyoming. *Breviora*, **335**: 1–15.
- Estes, R., and Berberian, P. 1970. Paleoecology of a Late Cretaceous vertebrate community from Montana. *Breviora*, **343**: 1–35.
- Estes, R., and Sanchíz, B. 1982. New discoglossid and palaeobatrachid frogs from the Late Cretaceous of Wyoming and Montana, and a review of other frogs from the Lance and Hell Creek formations. *Journal of Vertebrate Paleontology*, **2**: 9–20.
- Estes, R., Berberian, P., and Meszoely, C.A.M. 1969. Lower vertebrates from the late Cretaceous Hell Creek Formation, McCone County, Montana. *Breviora*, **337**: 1–33.
- Fanti, F., and Miyashita, T. 2009. A high latitude vertebrate fossil assemblage from the Late Cretaceous of west-central Alberta, Canada: evidence for dinosaur nesting and vertebrate latitudinal gradient. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **275**(1–4): 37–53. doi:10.1016/j.palaeo.2009.02.007.
- Fiorillo, A.R., and Gangloff, R.A. 2000. Theropod teeth from the Prince Creek Formation (Cretaceous) of northern Alaska, with speculations on Arctic dinosaur paleoecology. *Journal of Vertebrate Paleontology*, **20**(4): 675–682. doi:10.1671/0272-4634(2000)020[0675:TTFTPC]2.0.CO;2.
- Fiorillo, A.R., Tykoski, R.S., Currie, P.J., McCarthy, P.J., and Flaig, P. 2009. Description of two partial *Troodon* braincases from the Prince Creek Formation (Upper Cretaceous), North Slope Alaska. *Journal of Vertebrate Paleontology*, **29**: 178–187.
- Fowler, H.W. 1941. The George Vanderbilt Oahu survey: the fishes. *Proceedings. Academy of Natural Sciences of Philadelphia*, **93**: 247–279.
- Gao, K., and Fox, R.C. 1996. Taxonomy and evolution of Late Cretaceous lizards (Reptilia: Squamata) from western Canada. *Bulletin of the Carnegie Museum of Natural History*, **33**: 1–107.
- Gao, K., and Fox, R.C. 1998. New choristoderes (Reptilia: Diapsida) from the Upper Cretaceous and Palaeocene, Alberta and Saskatchewan, Canada, and phylogenetic relationships of Choristodera. *Zoological Journal of the Linnean Society*, **124**(4): 303–353. doi:10.1111/j.1096-3642.1998.tb00580.x.
- Gardner, J.D. 2000. Systematics of Albanerpetontids and Other Lissamphibians from the Late Cretaceous of Western North America. Unpublished Ph.D. thesis, University of Alberta, Edmonton, Alta.
- Gardner, J.D. 2008. New information on frogs (Lissamphibia: Anura) from the Lance Formation (Late Maastrichtian) and Bug Creek Anthills (Late Maastrichtian and Early Paleocene), Hell Creek Formation, USA. In *Vertebrate Microfossil Assemblages: Their Role in Paleoecology and Paleobiogeography*. Edited by J.T. Sankey and S. Baszio. Indiana University Press, Bloomington, Ind., pp. 219–249.
- Gauthier, J. 1986. Saurischian monophyly and the origin of birds. *Memoires of the California Academy of Sciences*, **8**: 1–55.
- Gilmore, C.W. 1924a. On *Troodon validus*, an ornithopodous dinosaur from the Belly River Cretaceous of Alberta, Canada. *Bulletin of the Department of Geology, the University of Alberta*, Vol. 1, pp. 1–143.
- Gilmore, C.W. 1924b. On the skull and skeleton of *Hypacrosaurus*, a helmet-crested dinosaur from the Edmonton Cretaceous of Alberta. *Geological Survey of Canada Bulletin*, **38**: 49–64.
- Glückman, L.S. 1958. Rates of evolution in lamnid sharks. *Doklady Akademii Nauk*, **123**: 568–672.
- Grande, L. 1982. A revision of the fossil genus †*Diplomystus*, with comments on the interrelationships of clupeomorph fishes. *American Museum Novitates* 2728, pp. 1–43.
- Gray, J.E. 1847. A list of genera of recent Mollusca, their synonyma and types. *Proceedings of the Zoological Society of London*, **15**: 129–182.
- Greenwood, P.H., Rosen, D.E., Weitzman, S.G., and Myers, G.S. 1966. Phylogenetic studies of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History*, **131**: 339–356.
- Hay, O.P. 1929. Second Bibliography and Catalogue of the Fossil Vertebrata of North America. Carnegie Institution, Washington, D.C.
- Horner, J., and Currie, P.J. 1994. Embryonic and neonatal morphology and ontogeny of a new species of *Hypacrosaurus* (Ornithischia, Lambeosauridae) from Montana and Alberta. In *Dinosaur eggs and babies*. Edited by K. Carpenter, K.F. Hirsch, and J.R. Horner. Cambridge University Press, Cambridge, UK, pp. 312–336.
- Huxley, T.H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London*, **1880**: 649–662.
- Lambe, L.M. 1917. On *Cheneosaurus tolmanensis*, a new genus and species of trachodont dinosaur from the Edmonton Cretaceous of Alberta. *Ottawa Naturalist*, **30**: 117–123.
- Larson, D.W. 2008. Diversity and variation of theropod dinosaur teeth from the uppermost Santonian Milk River Formation (Upper Cretaceous), Alberta: a quantitative method supporting identification of the oldest dinosaur tooth assemblage in Canada. *Canadian Journal of Earth Sciences*, **45**(12): 1455–1468. doi:10.1139/E08-070.
- Larson, D.W. 2009. Multivariate analyses of small theropod teeth and implications for paleoecological turnovers through time. *Journal of Vertebrate Paleontology*, **29**: 132A.
- Laurenti, J.N. 1768. Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium austriacorum. Johann Thomas Edler von Trattner, Vienna, Austria. [In Latin.]
- Leidy, J. 1856a. Notices of remains of extinct vertebrated animals discovered by Professor E. Emmons. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **8**: 255–256.
- Leidy, J. 1856b. Notices of remains of extinct reptiles and fishes, discovered by Dr. F.V. Hayden in the bad lands of the Judith River, Nebraska Territory. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **8**: 72–73.
- Lerbekmo, J.F., and Braman, D.R. 2002. Magnetostratigraphic and biostratigraphic correlation of the late Campanian and Maastrichtian marine and continental strata from the Red Deer Valley to the Cypress Hills, Alberta, Canada. *Canadian Journal of Earth Sciences*, **39**(4): 539–557. doi:10.1139/e01-085.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 10 ed. Holmiae, Stockholm, Sweden. Vol. 1. [In Latin.]
- Longrich, N.R. 2008. Small theropod teeth from the Lance Formation of Wyoming, USA. *Vertebrate Microfossil Assemblages: Their Role in Paleontology and Paleobiogeography*. Edited by J. Sankey and S. Baszio. Indiana University Press, Bloomington, Ind., pp. 135–158.
- Longrich, N.R., and Currie, P.J. 2008. *Albertonykus borealis*, a new alvarezsaur (Dinosauria: Theropoda) from the early Maastrichtian of Alberta, Canada: implications for the systematics and ecology of the Alvarezsauridae. *Cretaceous Research*, **30**(1): 239–252. doi:10.1016/j.cretres.2008.07.005.
- Longrich, N.R., and Currie, P.J. 2009. A microraptorian (Dinosauria — Dromaeosauridae) from the Late Cretaceous of North America. *Proceeding of the National Academy of Sciences USA*, **106**(13): 5002–5007. doi:10.1073/pnas.0811664106.

- Marsh, O.C. 1881a. Principal characters of American Jurassic dinosaurs, Part 4: Spinal cord, pelvis and limbs of *Stegosaurus*. *American Journal of Science*, **21**: 167–170.
- Marsh, O.C. 1881b. Principal characters of American Jurassic dinosaurs. Part 5. *American Journal of Science*, **21**: 417–423.
- Marsh, O.C. 1888. A new family of horned dinosaurs from the Cretaceous. *American Journal of Science*, **36**: 477–478.
- Marsh, O.C. 1890a. Description of new dinosaurian reptiles. *American Journal of Science*, **39**: 81–86.
- Marsh, O.C. 1890b. Additional characters of the Ceratopsidae, with notice of new Cretaceous dinosaurs. *American Journal of Science*, **39**: 418–426.
- Müller, J. 1846. Über den Bau und die Grenzen der Ganoiden, und über das natürliche System der Fische. Königlichen Akademie der Wissenschaften, Berlin. [In German.]
- Neuman, A.G., and Brinkman, D.B. 2005. Fishes of the fluvial beds. In *Dinosaur Provincial Park: A Spectacular Ancient Ecosystem Revealed*. Edited by P.J. Currie and E.B. Koppelhus. Indiana University Press, Bloomington, Ind., pp. 167–185.
- Newbrey, M.G., Murray, A.M., Brinkman, D.B., Wilson, M.V.H., and Neuman, A.G. 2010. A new fish (Clupeomorpha, Ellimichthyiformes) from the Late Cretaceous Horseshoe Canyon Formation, Alberta, Canada. *Canadian Journal of Earth Sciences*, **47**(9): This issue.
- Nicholls, E.L., and Russell, A.P. 1990. Paleobiogeography of the Cretaceous Western Interior Seaway of North America: the vertebrate evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **79**(1–2): 149–169. doi:10.1016/0031-0182(90)90110-S.
- Nicholson, H.A., and Lydekker, R. 1889. A Manual of Palaeontology. 2nd ed. W. Blackwood and Sons, Edinburgh and London, UK.
- Nydam, R.L., Eaton, J.G., and Sankey, J. 2007. New taxa of transversely-toothed lizards (Squamata: Scincomorpha) and new information on the evolutionary history of “teiids.” *Journal of Paleontology*, **81**(3): 538–549. doi:10.1666/03097.1.
- Oppel, M. 1811. Die Ordnungen, Familien und Gattungen der Reptilien, als Prodrom einer Naturgeschichte derselben. Joseph Lindauer, Munich, Germany. [In German.]
- Osborn, H.F. 1903. On the primary division of the Reptilia into two sub-classes, Synapsida and Diapsida. *Science*, **17**(424): 275–276. doi:10.1126/science.17.424.275-b.
- Osborn, H.F. 1923. Two Lower Cretaceous dinosaurs of Mongolia. *American Museum Novitates* 95, pp. 1–10.
- Owen, R. 1842. Report on British fossil reptiles. Part II: Report to the British Association for the Advancement of Science. Vol. 11, pp. 60–204.
- Owen, R. 1846. Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals Delivered at the Royal College of Surgeons, England in 1844 and 1846, Part. 1, Fishes. Longman, Brown, Green, and Longman, London, UK.
- Parks, W.A. 1923. *Corythosaurus intermedius*, a new species of trachodont dinosaur. *University of Toronto Studies. Geology Series*, **15**: 1–57.
- Parks, W.A. 1926. *Thescelosaurus warreni*, a new species of orthopodous dinosaur from the Edmonton Formation of Alberta. *University of Toronto Studies. Geology Series*, **21**: 1–42.
- Regan, C.T. 1923. The skeleton of *Lepidosteus*, with remarks on the origin and evolution of the lower neopterygian fishes. *Proceedings of the Zoological Society of London*, **1923**: 445–461.
- Rosen, D.E. 1973. Interrelationships of higher euteleostean fishes. *Journal of the Linnaean Society*, **53**(Suppl. 1): 397–513.
- Russell, D.A., and Chamney, T.P. 1967. Notes on the biostratigraphy of dinosaurian and microfossil fauna in the Edmonton Formation (Cretaceous), Alberta. *Canadian National Museum of Natural History, Natural History Papers* 35, 22 p.
- Ryan, M.J., Currie, P.J., Gardner, J.D., Vickaryous, M.K., and Lavigne, J.M. 1998. Baby hadrosaurid material associated with an unusually high abundance of *Troodon* teeth from the Horseshoe Canyon Formation, Upper Cretaceous, Alberta, Canada. *Gaia*, **15**: 123–133.
- Sahni, A. 1972. The vertebrate fauna of the Judith River Formation, Montana. *Bulletin of the American Museum of Natural History*, **147**: 321–412.
- Sankey, J.T. 2001. Late Campanian southern dinosaurs, Aguja Formation, Big Bend, Texas. *Journal of Paleontology*, **75**(1): 208–215. doi:10.1666/0022-3360(2001)075<0208:LCSDAF>2.0.CO;2.
- Sankey, J.T., Brinkman, D.B., Guenther, M., and Currie, P.J. 2002. Small theropod and bird teeth from the Late Cretaceous (Upper Campanian) Judith River Group, Alberta. *Journal of Paleontology*, **76**(4): 751–763. doi:10.1666/0022-3360(2002)076<0751:STABTF>2.0.CO;2.
- Sauvage, H.E. 1875. Sur la faune ichthyologique de l’île Saint-Paul. *Comptes Rendus Hebdomadaires des Séances de l’Académie des Sciences*, **81**: 987–989. [In French.]
- Scopoli, G.A. 1777. *Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, characteribus essentialibus donata, in tribus divisa, surinde ad leges naturae*. Wolfgang Gerle, Prague, Czech Republic. [In Latin.]
- Seeley, H.G. 1888. The classification of the Dinosauria. Report to the British Association for the Advancement of Science. Vol. 1888, pp. 698–699.
- Sternberg, C.M. 1937. Classification of *Thescelosaurus*, with a description of a new species. *Proceedings of the Geological Society of America*, **1936**: 375.
- Swainson, W. 1839. *The Natural History and Classification of Fishes, Amphibians, & Reptiles, or Monocardian Animals*. Vol. 2. Spottiswoode & Co., London, UK.
- Tarduno, J.A., Brinkman, D.B., Renne, P.R., Cottrell, R.D., Scher, H., and Castillo, P. 1998. Evidence for extreme climatic warmth from Late Cretaceous Arctic vertebrates. *Science*, **282**(5397): 2241–2243. doi:10.1126/science.282.5397.2241.
- Tozer, E.T. 1956. Uppermost Cretaceous and Paleocene non-marine molluscan faunas of western Alberta. *Geological Survey of Canada. Memoir* 280, pp. 1–125.
- Tschudi, J.J. 1839. Classification der Batrachier, mit Berücksichtigung der Fossilien Thiere dieser Abteilung der Reptilien. *Mémoire de la Société des Sciences Naturelles*. Imprimerie de Petitpierre, Neuchâtel, Switzerland. [In German.]
- von Huene, F. 1914. Das natürliche System der Saurischia. *Zentralblatt für Mineralogie, Geologie und Paläontologie B*, **1914**: 154–158. [In German.]
- White, C.A. 1877. Comparisons of the North American Mesozoic and Cenozoic Unionidae and associated mollusks with living species. *Bulletin of the United States Geological and Geographical Survey of the Territories*, **3**: 615–624.
- Wilson, M.V., Brinkman, D.B., and Neuman, A.G. 1992. Cretaceous esocoidei (Teleostei): early radiation of the pikes in North American fresh waters. *Journal of Paleontology*, **66**: 839–846.
- Wolfe, J.A., and Upchurch, G.R., Jr. 1987. North American non-marine climates and vegetation during the Late Cretaceous. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **61**: 33–77. doi:10.1016/0031-0182(87)90040-X.