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A New Species of Troodontid Theropod (Dinosauria: Maniraptora) from the Horseshoe Canyon Formation (Maastrichtian) of Alberta, Canada.

David C. Evans^{1,2}, Thomas M. Cullen^{1,2}, Derek W. Larson^{2,3}, Adam Rego²

¹, Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6

², Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Ontario, Canada M5S 3B2

³, Philip J. Currie Dinosaur Museum, Box 328 9301-112 Ave, Wembley, Alberta, Canada T0H 3S0

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Abstract

Troodontid material from the Maastrichtian of North America is extremely rare, beyond isolated teeth from microvertebrate sites. Here we describe troodontid frontals from the early Maastrichtian Horseshoe Canyon Formation (Horsethief Member). The most complete specimen, TMP 1993.105.01, is notably foreshortened and robust when compared to numerous specimens referred to *Troodon* from the Dinosaur Park Formation, and exhibits several characteristics that distinguish it from other Late Cretaceous troodontids. Morphometric analyses reinforce shape differences between TMP 1993.105.01 and other North America troodontids, and show that proportional differences are independent of size. We therefore erect a new taxon, *Albertavenator curriei* gen. et. sp. nov., that is diagnosed by the following autapomorphies: 1) primary supraciliary foramen is truncated anteriorly by the lacrimal contact, 2) superficial (ectocranial) surface of the frontal proportionally shorter than all known troodontids, with a length to width ratio under 1.25, and 3) frontoparietal contact in which an enlarged lappet of the frontal extends medially to extensively overlap the lateral region of the anteromedial process of the parietal. Interestingly, tooth and jaw morphology from the single relatively complete dentary recovered from the Horseshoe Canyon cannot be distinguished from dentaries and teeth from the Dinosaur Park Formation. If the dentary and teeth from the Horsethief Member of the Horseshoe Canyon Formation prove to belong to *A. curriei*, extensive overlap in tooth morphology between the Dinosaur Park and Horseshoe Canyon formations reinforce the notion that tooth morphotypes do not exhibit strong correspondence to species alpha diversity, and may encompass multiple closely-related taxa.

Introduction

Troodontidae is a clade of small maniraptoran theropod dinosaurs that occurs in Late Jurassic through end Cretaceous deposits of Laurasia (Makovicky and Norell 2004). Troodontids from the Late Cretaceous of North America are poorly known and have a complex taxonomic history (for reviews, see Currie 1987b; Currie and Koppelhus 2005; Zanno et al. 2011). Since the discovery of *Troodon formosus*, named on the basis of an isolated tooth from the Judith River Formation (Leidy 1856), only four species have been formally named based on material recovered from North America: *T. formosus* (Judith River Formation, Montana), *Stenonychosaurus inequalis* (Dinosaur Park Formation, Alberta), *Pectinodon bakkeri* (Lance Formation, Wyoming) and *Talos sampsoni* (Kaiparowits Formation, Utah). Little skeletal material has been described, and skull material is particularly rare (Carpenter 1982; Fiorillo et al. 2009; Makovicky and Norell 2004; Russell 1969; Zanno et al. 2011), hindering assessments for taxonomic diversity in the group. Despite this, isolated troodontid teeth are relatively common through the Campanian and Maastrichtian of western North America (Cullen and Evans 2016; Larson et al. 2016; Larson and Currie 2013). Historically, the genus *Troodon* has been reported to occur throughout the Campanian and Maastrichtian, and across most of western North America (Makovicky and Norell 2004), based on referrals of isolated teeth and the few, and generally fragmentary, available fossils (Zanno et al. 2011). More recently, some researchers have recognized *T. formosus* as a form taxon based on potentially non-diagnostic tooth morphology, and suggested that the taxon may contain multiple species or genera (Fiorillo et al. 2008, 2009). Zanno et al. (2011) noted morphological variation in materials previously referred to this taxon, and hypothesized that the diversity of Late Cretaceous troodontids in North

America is presently underestimated due to over-synonymization based on fragmentary material, and predicted that closer examination of this material may reveal hidden taxonomic diversity. In a subsequent morphometric study of isolated small theropod teeth from the latest Cretaceous of western North America, Larson and Currie (2013) also concluded that their diversity is underestimated, and that *T. formosus* sensu stricto is only definitively known from the Judith River and Dinosaur Park formations, implying teeth from other units may represent distinct taxa.

Troodontid material from the Maastrichtian of North America is particularly rare, beyond isolated teeth from microvertebrate sites (e.g. Larson and Currie 2013). Previous reports include two troodontid braincases referred to *Troodon formosus* from the Prince Creek Formation of Alaska (Fiorillo 2008; Fiorillo et al. 2009), and a perinate dentary and basioccipital from the Lance Formation (Carpenter 1982). Troodontid cranial material has also been recovered from the Horsethief Member of the Horseshoe Canyon Formation of Alberta (Eberth et al. 2013), which is now classified as early Maastrichtian in age (Gradstein et al. 2012). Currie (1987a) described a relatively complete dentary (TMP 1983.012.0011) and tentatively referred it to *Troodon formosus*. Eberth et al (2013) listed two undescribed troodontid frontals recovered from this unit, which represent the only reported frontals of this clade from the Maastrichtian of North America. Together with the previously described dentary (Currie 1987a), these constitute all of the non-dental troodontid remains from the formation, and some of the only non-dental troodontid remains from the Maastrichtian of North America (Carpenter 1982; Fiorillo et al. 2009). Frontals are generally diagnostic to low taxonomic levels in deinonychosaurs (Averianov 2016; Bell and Currie 2016; Currie 1987b; Evans et al. 2014), and may be useful in distinguishing troodontid taxa (Zanno et al. 2013; Zanno et al. 2011). Here we describe the troodontid frontals from the Horseshoe Canyon Formation and compare them with other Late Cretaceous

troodontids. Comparison of the Horseshoe Canyon Formation frontals to numerous specimens belonging to *Troodon* from the Dinosaur Park Formation, as well as other Late Cretaceous troodontids, suggest that these Horseshoe Canyon Formation frontals can be distinguished and recognized as a new taxon, *Albertavenator curriei* gen. et sp. nov. This corroborates predictions that troodontid diversity in the latest Cretaceous of North America is underestimated due to oversynonymization of fragmentary material (Zanno et al. 2011), and suggests that more detailed studies of collections from the latest Cretaceous of northern Laramidia may reveal more, currently unrecognized taxa.

Institutional abbreviations

AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences of Drexel University; CMN, Canadian Museum of Nature; IGM, Institute of Geology, Mongolian Academy of Sciences; ROM, Royal Ontario Museum; TMP, Royal Tyrrell Museum of Palaeontology; UALVP, University of Alberta Laboratory for Vertebrate Palaeontology; UMNH, Utah Museum of Natural History.

Materials and Methods

The taxonomy of the genus *Troodon* has been historically complex (for reviews, see Currie 1987, 2005; Zanno et al. 2011). Here, we refer to the material collected from the Dinosaur Park Formation as *Troodon inequalis*, following Currie (2005). Furthermore, the frontals from the Dinosaur Park Formation can be linked directly to the holotype foot of *Stenonychosaurus* (= *Troodon*) *inequalis* (Sternberg 1932) through the most complete associated skeleton (CMN 12340) collected from the same unit, which includes skull and pedal material, but no teeth

(Russell 1969). Because the genotype of *Troodon* is an isolated tooth (Leidy 1856) from potentially co-eval beds of the Judith River Formation (Mallon et al. 2016), it remains possible that *T. inequalis* is a junior synonym of *T. formosus* since teeth collected from the Dinosaur Park Formation and Judith River Formation are morphologically indistinguishable (Larson and Currie 2013). However, whether or not this type of tooth morphology is diagnostic to the species-level will require more complete material from both formations. When making comparisons between the Horseshoe Canyon and Dinosaur Park formations, we refer to specimen numbers where appropriate (e.g., Zanno et al. 2011), but for the sake of brevity in the discussion, *T. inequalis* refers only to material from the Dinosaur Park Formation. We also recognize the possibility that more than one taxon may be present in the sample from the Dinosaur Park Formation. If more than one taxon is present, it would only inflate the range of individual variation we are using to assess the distinctiveness of the Horseshoe Canyon material, thereby providing a robust test.

First hand morphological comparisons were made between frontals and dentaries referred to Troodontidae from the Horseshoe Canyon and Dinosaur Park formations. The more complete of the two Horseshoe Canyon Formation frontals, TMP 1993.105.0001, was compared to nine frontals referred to *Troodon inequalis* from the Dinosaur Park Formation of Alberta, and one troodontid frontal from the Kaiparowits Formation of Utah in a series of morphometric analyses (Table 1). Comparisons to Asian troodontid taxa relied upon published descriptions. The frontal length to width ratio in *Zanabazar* and *Gobivenator* were calculated from published photographs in Norell et al. (2009) and Tsuihiji et al. (2014) respectively.

In order to quantitatively determine the range of morphological variation present in North American troodontid frontals, we used several morphometric methods. To this end, six landmarks (Appendices 1-2) were identified on the dorsal surface of each frontal for 2-D

geometric morphometric analyses. Landmarks were selected based on two main criteria: 1) homologous points and/or multiple sutural intersections (sensu Bookstein 1997), and 2) being present on the available specimens. The latter criterion limited the placement of landmarks on the postorbital process and the delicate anterior flange, which are unfortunately broken on both Horseshoe Canyon Formation frontals. While methods do exist to estimate missing points in geometric morphometric analyses (Arbour and Brown 2014), we were concerned that the proportional dominance of *T. inequalis* in the sample relative to the Horseshoe Canyon form would bias the estimated landmarks in a way that minimizes morphological variation between potentially different species. Landmark data were collected and geometric morphometric analyses, including Procrustes superimposition and Principal Component Analyses (PCA), performed using the ‘geomorph’ package (Adams and Otárola-Castillo 2013) in the R programming language (Appendix 5).

Linear measurements (Table 1, Appendix 1, Appendix 3) were taken from a sample of troodontid frontals from North America for comparisons that supplement the geometric morphometric analyses. This series of measurements allows for a multivariate linear Principal Component Analysis (PCA) and for bivariate tests of size-related (e.g. ontogenetic) allometry to be performed (Appendix 5). Reduced Major Axis line fitting was used to describe the relationship between linear measurement variables, and Ordinary Least Squares regression was used to plot PC scores against brain length (Legendre and Legendre 2012).

Isolated troodontid teeth from the Horseshoe Canyon, Dinosaur Park, and Judith River formations were also compared quantitatively. Data was taken from Larson et al. (2016) and updated with data from Torices et al. (2014) with modifications to some of the identifications (Appendices 6-7) (Larson et al. 2016; Torices et al. 2014). Dental variables analyzed include

fore-aft basal length (FABL), crown height (CH), basal width (BW), mesial denticle length (ADL), and distal denticle length, (PDL). Analyses (Appendix 8) were run in R (R-Development-Core-Team 2015) using the core stats and BiodiversityR packages (Kindt and Coe 2008). These two datasets also separate teeth by positional variation, with posterior dentary teeth in North American troodontids lacking denticles, unlike the remainder of the tooth positions (Currie et al. 1990; Currie 1987a; Longrich 2008b). Specimens were grouped into two analyses based on whether or not they possessed mesial denticles because when analyzed together, this trait systematically separates specimens into two groups, and we did not want to exclude mesial denticle measurements from the analysis. Previous studies (Larson et al. 2016) have shown that the teeth from the Dinosaur Park and Horseshoe Canyon formations differ in average size. For the purposes of this study, we wanted to test for differences between the specimens from the Horseshoe Canyon, Dinosaur Park, and Judith River formations based on aspects of shape independent of size. The mesial denticles dataset was size-standardized using residuals that were calculated for CH, BW, ADL, and PDL by regressing log-transformed variables against FABL using ordinary least squares regression. Residuals for the dataset without mesial denticles were conducted in the same way but with ADL excluded. Residuals in the two analyses were analyzed using PCA, and significant variables were calculated using the broken stick method (Frontier 1976; Jackson 1993). Welch two-sample t-tests were conducted on the scores of the significant axes of the Dinosaur Park and Horseshoe Canyon teeth. Convex hulls were calculated to include 95% of specimens closest to the mean of each group along the significant separating axis of each analysis.

Additionally, the eigenvectors of the PCA were used to project in situ teeth from two dentaries into the analyses (Appendix 4, Appendix 7). The dentary TMP 1983.012.0011 was

recovered from the Horseshoe Canyon Formation and preserves three germ teeth, two of which were projected into the dataset with mesial denticles PCA, and one of which was projected into the dataset without mesial denticles PCA. ROM 1445 preserves two dentary teeth, both of which were projected into the dataset without mesial denticles PCA.

Systematic Palaeontology

Dinosauria Owen, 1842

Saurischia Seeley, 1888

Theropoda Marsh, 1881

Troodontidae Gilmore, 1924

Albertavenator gen. nov.

Diagnosis. Monotypic, same as for species.

Albertavenator curriei gen. et. sp. nov.

urn:lsid:zoobank.org:pub:B9267D1C-BFE5-45D6-85B4-2A74958D40D1

Holotype. TMP 1993.105.0001, an incomplete left frontal, lacking the postorbital process.

Referred Material. TMP 1996.005.0008, a fragmentary right frontal from a small individual.

Etymology. The generic name refers to the Canadian province of Alberta, combined with the Latin ‘venator’, for hunter. The species epithet honours Philip J. Currie, who has worked extensively on the Late Cretaceous theropods of Alberta and whose work on the similarities between troodontids and birds advanced the study of paravians.

Locality and Horizon. All specimens were recovered from the Horsethief Member of the Horseshoe Canyon Formation, within the stratigraphic interval of coal zones 7 through 9 (Eberth and Braman 2012; Eberth et al. 2013) (Figure 1). The holotype frontal, TMP 1993.105.0001 (Figure 2), was discovered 25 m northeast of the Day Digs Bleriot Ferry *Edmontosaurus* Bonebed (see Evans et al. 2015), located close to the Bleriot Ferry crossing of the Red Deer River, approximately 22 km northwest of the Town of Drumheller. Stratigraphically, the specimen occurs at the level of coal zone 8 (Eberth et al. 2013; Evans et al. 2015). The referred frontal, TMP 1996.005.0008 (Figure 3), was collected near Morrin Bridge, at the level of coal zones 8-9, also within the Horsethief Member. Detailed locality data for each specimen is on file at the Royal Tyrrell Museum of Palaeontology.

Age. The Horsethief Member of the Horseshoe Canyon Formation occurs within the 32n magnetochron interval, and has an estimated age of ~71.5–71.0 Ma (Eberth and Braman 2012; Eberth et al. 2013). Based on this chronostratigraphic age, this unit is considered earliest Maastrichtian in age (Gradstein et al. 2012).

Diagnosis. Large troodontid diagnosed by the following autapomorphies: 1) primary supraciliary foramen is truncated anteriorly by the lacrimal contact, 2) superficial (ectocranial) surface of the frontal proportionally shorter than all known troodontids, with a length to width ratio less than 1.3, and 3) a frontoparietal contact in which an enlarged lappet of the frontal extends medially to

extensively overlap the lateral region of the interfrontal (anterior) process of the parietal.

Comments: The incomplete right frontal, TMP 1996.005.0008, is considerably smaller than the holotype, but can be referred to *Albertavenator curriei* based on the presence of an enlarged lappet of the frontal that extends medially to extensively overlap the lateral region of the interfrontal (anterior) process of the parietal, an autapomorphy of *A. curriei* (see discussion below). An almost complete left dentary with several *in situ* teeth, TMP 1983.012.0011, described by Currie (1987a) is from the TMP bonebed HC 1 locality in Midland Provincial Park (LSD 11, Sec. 17, Twp. 29, Rge. 20, W 4th) and occurs slightly lower within the Horsethief Member, at the level of coal zones 7-8 (Eberth et al. 2013). While it might be tempting to assign TMP 1983.012.0011 to *A. curriei*, based on its generally consistent troodontid morphology, size, and stratigraphic occurrence, we refrain from doing so formally since its dental and jaw morphology cannot be distinguished from material collected from Dinosaur Provincial Park (Currie 1987a; see below). We discuss the implications of a potential referral of this specimen to *A. curriei* below.

Description.

Holotype. TMP 1993.105.0001 is an incomplete left frontal (Figure 2), lacking the postorbital ramus and a segment of the central orbital rim. The frontal preserves the sutural surfaces for the nasal anteriorly, the lacrimal anterolaterally, and postorbital posterolaterally, the parietal posteriorly, and the complementary frontal medially. In dorsal view, the frontal is triangular in outline as preserved, resembling a right-angled triangle that is longer than it is wide, with an almost straight medial margin that meets its counterpart medially. Based on the

posteriormost preserved portion of the orbital rim, it is clear that the frontal was “L-shaped” when complete, as in troodontids. This is in contrast to the generally ‘T-shaped’ frontals of dromaeosaurids (Evans et al. 2014; Makovicky and Norell 2004). The dorsal surface is dominated by a broad, parasagittally oriented groove that extends from the posterior end of the nasal suture towards the supratemporal ridge. This groove is often cited as a distinctive characteristic of troodontids (Evans et al. 2014; Makovicky and Norell 2004), and contrasts with the flat condition seen in adult dromaeosaurids (Norell and Makovicky 2004) and ornithomimids (Currie 1987b; Longrich 2008a), and the weakly concave frontals of therizinosaurs (Averianov 2016; Averianov and Sues 2016). Laterally, this groove defines a strongly upturned orbital rim. The rim appears to be elevated in TMP 1993.105.0001 to an even greater degree than other troodontid specimens, such as TMP 1993.036.0086 (Figure 4), although it is possible that this is accentuated by taphonomic compression. The ratio of the length of the frontal (measured from the midline parietal contact to the posterior end of the nasal contact) to its width (measured from the midline to the medial extent of the postorbital contact) is 1.22 in TMP 1993.105.0001, whereas it ranges from 1.4 to 1.6 in *Troodon* frontals from the Dinosaur Park Formation. This ratio is 1.7 in the troodontid frontal from the Kaiparowits formation (Zanno et al. 2013). The frontal tends to be relatively more elongate in Asian troodontids. This ratio is 1.56 in *Gobivenator* (Tsuihiji et al. 2014), and 1.75 in *Zanabazar junior* (Norell et al. 2009). The length of the frontal is reported to be approximately twice that of its width in *Linhevenator* (Xu et al. 2011).

Anteriorly, the sutural surface of the nasal contact is wide along the anterolateral margin of the frontal, indicating that the nasal overlapped the frontal considerably in this region. The posterior periphery of the nasal contact has a series of distinct ridges indicating strong

interdigitation with the nasal along the posterior edge of the suture, a feature that is not as pronounced in other troodontid frontals such as TMP 1986.049.0010 or TMP 1993.036.0086 (Figure 4). The lacrimal contact is located posterolaterally to the nasal contact, as in other specimens of *Troodon inequalis*. However, the lacrimal contact extends farther posteriorly than in other troodontid specimens examined, and does not meet the orbital rim. Rather, it intersects with a large foramen located along to the orbital rim, that we hypothesize is homologous to a large foramen that occurs posterior to the lacrimal contact and communicates obliquely with the orbit in all other troodontid frontals. This foramen, termed here as the primary supraciliary foramen, occurs 4.5 mm posterior to the lacrimal contact in CMN 12340, 8.4 mm TMP 1986.049.0010, and 5.5 mm posterior to this contact in TMP 1993.036.0086. In specimens from the Dinosaur Park Formation, the primary supraciliary foramen is variable in size within the sample, and can be asymmetrically developed (e.g., CMN 12340), but occurs within the irregular, rugose bone directly adjacent to the orbital margin, where it is typically associated with a small notch but does not communicate directly with the orbit in dorsal view. Although this region of bone is often perforated by small foramina, this large foramen is easily identifiable in most specimens, and we suggest it is homologous landmark that reflects the passage of neurovasculature. A large foramen in a similar location is present in UMNH.VP.16303, and in the holotype of *Zanabazar junior* (IGM 100/1) from the Nemegt Formation of Mongolia (Norell et al. 2009: Fig 24b, right side). However, in TMP 1993.105.0001 the primary supraciliary foramen is open anteriorly, presumably towards the lacrimal, and laterally in the direction of the orbital rim, indicating that this foramen was bound anteriorly by the lacrimal, whereas it is completely enclosed by the frontal where this feature can be identified in other troodontids. On the ventral surface of TMP 1993.105.0001, a transversely oriented groove extends medially from

the ventral aperture of the foramen towards the crista cranii, across the surface of the orbital cavity. A similar groove is preserved in CMN 12340 and TMP 1993.036.0086, but is not present TMP 1986.049.0010, where the primary supraciliary foramen is relatively smaller. As in other specimens examined, several small foramina located posteromedially to the primary supraciliary foramen pierce the dorsal surface of the frontal and communicate with the orbit ventrally.

Posteriorly, the supratemporal ridge traverses the frontal at approximately a right angle to the medial interfrontal suture. The well-demarcated ridge, which is bounded anteriorly by a fine groove, extends from the parietal contact at the midline to the broken edge at the base of the postorbital process. Posterior to the supratemporal ridge, the frontal forms a subvertical, slightly mediolaterally convex supratemporal fossa. Medially, the supratemporal ridge terminates at the anteromedial region of the rugose contact surface for the parietal. The contact surface for the parietal is located along the entire posterior margin of the frontal. The parietal contact also lies on the ventral surface of the frontal at its lateral extreme, and extends towards the dorsal surface towards the midline. Here a dorsal process is wedged between the posteromedial corners of the paired frontals. The frontoparietal contact in this region has an enlarged lappet of the frontal that extends medially to extensively overlap the lateral region of the anteromedial process of the parietal. This differs from the more finely striated, roughened parietal suture seen in this region in the sample of frontals from Dinosaur Provincial Park (e.g, TMP 1986.049.0010, TMP 1993.036.0086). Unfortunately, this region cannot be compared to most named Asian troodontids, which are represented by articulated skulls.

In ventral view, the forebrain fossae are bound laterally by the crista cranii, which projects ventrally to separate the orbit from the endocranial cavity. The olfactory bulb impression is large and ovoid, with the long axis oriented parasagittally. The olfactory tracts are long, and

extend from the posterior end of the bulb fossa to the anterior end of the globular cerebral fossa, which loosely mimics the triangular form of the frontal as a whole. The olfactory bulb fossa and tract are long and large compared to the much shorter olfactory region in dromaeosaurids and ornithomimids, but compare readily to troodontids (Currie 1987b; Evans et al. 2014; Longrich 2008a; Russell 1969; Sues 1978). The lacrimal contact extends onto the ventral surface of the frontal, where it is expressed as a tall, transversely oriented buttress at the anterior end of the crista cranii, as is characteristic of troodontids (Evans et al. 2014). Lateral to the olfactory tracts, the crista cranii is complete and takes the form of a low, broad ridge, as in other specimens of *Troodon inequalis*, but unlike the tall flange present in dromaeosaurids (Evans et al. 2014). The cerebral fossa occupies the posteromedial region of the ventral surface of the frontal and is bound by the parietal suture posteriorly, the interfrontal suture medially, and the ventrally broken crista cranii laterally. The crista cranii is complete anteriorly, but is broken ventraposteriorly. The orbital fossa is much larger than the impression of the cerebral depression, occupying the majority of the lateral portion of the ventral surface.

Referred specimen. TMP 1996.005.0008 (Figure 3) is a partial right frontal comprised of two associated fragments. The smaller fragment includes the olfactory bulb fossa ventrally, and parts of the contact surfaces for the nasal and lacrimal dorsally. The second, larger fragment is derived from the posterior end of the bone, and preserves the cerebral fossa, parietal contact, orbital rim, and a large portion of the crista cranii that is complete ventrally. Despite its fragmentary nature, this specimen can be attributed to Troodontidae based on the transverse orientation of the weakly developed supratemporal ridge demarcating the anterior extent of the supratemporal fossa on the frontal, the interfrontal suture interdigitation morphology that

corresponds to that in troodontids, and the anteroposteriorly elongate olfactory bulbs; all features that are not present in dromaeosaurid or ornithomimid frontals (Evans et al. 2014).

TMP 1996.005.0008 is approximately two-thirds the size of the larger TMP 1993.105.0001 (in terms of interorbital width). The dorsal surface of the posterior region of the frontal is relatively flat, but a shallow parasagittal groove and upturned orbital margin are apparent in the broken cross section on the anterior end of the large fragment, although these are weakly developed compared to TMP 1993.105.0001. Anteriorly, the nasal and lacrimal contact surfaces are thin and are weakly interdigitated along their posterior periphery. Posteriorly, a weakly developed supratemporal ridge extends transversely across the posterior end of the bone, anterodorsal to the largely complete parietal contact. Interestingly, an enlarged lappet of the frontal extends medially to extensively overlap the lateral region of the interfrontal (anterior) process of the parietal, as in TMP 1993.105.0001 but unlike specimens from the Dinosaur Park Formation. On the ventral surface, the contact between the roof of the cerebral impression and the wall of bone containing the laterosphenoid forms a marginally wider angle than in other troodontid specimens, and appears to lack a robust, interdigitating lacrimal buttress on the anterior end of the crista cranii, although it is possible this region is not quite preserved.

Morphometric Results.

Frontal. In geometric morphometric (GM) PC morphospace, TMP 1993.105.0001 falls outside of the range of variation seen in the Dinosaur Park Formation (DPF) *Troodon* frontals along PC1 (Figure 5A), while falling within or near the range of variation in DPF *Troodon* frontals along PC2, PC3, and PC4 (Figure 5A, B). The Kaiparowits Formation troodontid frontal

is similarly separated from DPF frontals along PC1, though it also separates from both TMP 1993.105.0001 and DPF frontals along PC2 (Figure 5A). In order to further assess the quantitative differences in morphology between TMP 1993.105.0001 and DPF *Troodon* frontals, and the effect of size or ontogenetic stage on the morphometric results, comparisons were made between a series of frontal linear measurements (Supplementary Figure 1). The suite of linear measurements (Appendix 1) necessary for these comparisons was present on nine of the examined frontals (TMP 1993.105.0001, seven DPF frontals, and the Kaiparowits Formation frontal UNMH.VP.16303) (Table 1, Appendix 3). A negative relationship was found to exist between GM PC1 and brain length in most frontals (particularly those from the Dinosaur Park Formation), though TMP 1993.105.0001 and UNMH.VP.16303 plotted more negatively than was seen in the overall trend (Figure 5C). Linear morphometric (LM) PCA also separated TMP 1993.105.0001 from DPF frontals, in this case along LM PC2 (which was primarily controlled by relative frontal length) (Figure 5D, Appendix 4). The Kaiparowits Formation frontal, UNMH.VP.16303, also plots separate from the DPF frontals, though opposite to that of TMP 1993.105.0001. In comparisons of brain length to frontal length (parietal contact to nasal contact), TMP 1993.105.0001 plots distantly from the trend seen in DPF troodontid frontals due to the relative shortness of the frontal to brain length (Figure 5E). When frontal width was compared (frontal width at medial extent of postorbital vs. frontal width at lacrimal contact), all frontals followed a very similar pattern.

Dentition. Results from the tooth morphometric analyses suggests that there is a distinction between the samples of isolated teeth recovered from the Horseshoe Canyon Formation and those found in the Dinosaur Park Formation (Figure. 6). In the dataset with mesial denticles (Figure 6J), only the first PC axis was significant. In the dataset without mesial

denticles (Figure 6K), the first two PC axes were significant, but only the second appears to separate specimens by formation. In both datasets, this distinction between formations is driven by relative denticle size (Appendix 4) with larger denticles being present in specimens from the Horseshoe Canyon Formation. In both the dataset with mesial denticles (Fig. 6; $p=8.771\text{e-}06$) and without mesial denticles (Fig. 6; $p=0.0002942$), the Dinosaur Park and Horseshoe Canyon teeth were found to be significantly different on the first and second axes respectively. However, it is important to note that there is also considerable overlap in both datasets. While specimens from each formation do occupy distinct areas of morphospace along PC2 of the dataset of teeth without mesial denticles (Figure. 6K), the majority of specimens, including the projected *in situ* teeth from both dentaries, occupy a zone of overlap. In the dataset of teeth with mesial denticles (Figure. 6J), substantial overlap occurs along PC1 such that all specimens from Dinosaur Park are within the range of variation of specimens from the Horseshoe Canyon Formation (including the projected *in situ* Horseshoe Canyon specimens); however, many of the Horseshoe Canyon specimens remain outside of the range of those from the Dinosaur Park. The range of Judith River teeth along PC1 of the dataset with mesial denticles is largely coincident with that seen for the Dinosaur Park specimens.

Discussion

With the exception of isolated teeth derived primarily from vertebrate microfossil sites (Larson et al. 2010; Larson et al. 2016; Larson and Currie 2013; Ryan et al. 1998; Torices et al. 2014), troodontid material is extremely rare in the Horseshoe Canyon Formation, despite over a century of intensive field collecting. TMP 1993.105.0001 has several distinctive features

commonly attributed to troodontids, including a longitudinal groove on the dorsal surface that is defined laterally by a raised orbital rim, a deep, transversely oriented lacrimal buttress of the crista cranii, and a distinct oval olfactory bulb impression offset from enlarged cerebral hemispheres by long olfactory tracts (Currie 1987b; Evans et al. 2014). Although TMP 1996.005.0008 is fragmentary, it also displays features that indicate it is from a troodontid, including the elongate oval olfactory bulb fossa, and the transversely oriented supratemporal ridge. Both specimens also fall well within the size range prescribed by troodontid frontals found in the Dinosaur Park Formation, with TMP 1993.105.0001 being approximately the same size as the largest specimens from the Dinosaur Park Formation.

To date, only three troodontid cranial bones have been recovered from the Horseshoe Canyon Formation: a dentary (Currie 1987a) and the two incomplete frontals described here (Eberth et al. 2013). Currie (1987a) described the dentary (TMP 1983.012.0011) and tentatively referred it to *Troodon formosus*. Reassessment of the dentary morphology of TMP 1983.012.0011 supports the conclusions of Currie (1987a), and revealed no significant differences between it and the specimens recovered from the Dinosaur Park Formation that would preclude identification to the same species. Eberth *et al.* (2013), following the assignment of the dentary to *T. formosus* by Currie (1987a), referred the frontals to this taxon.

More detailed comparisons provided here reveal that the foreshortened frontal (TMP 1993.105.0001) from the Horseshoe Canyon Formation is differentiable from the more elongate morphology of other known troodontids. It can be readily distinguished from the large sample of frontals known from the Dinosaur Park Formation that have been referred to *T. formosus* or *T. inequalis*, and can thus be recognized as a new taxon, *Albertavenator curriei*. The holotype frontal of *A. curriei* has a ratio of the frontal length (measured from the midline parietal contact

to the posterior end of the nasal contact) to its width (measured from the midline to the medial extent of the postorbital contact) of under 1.25. In *Troodon* frontals from Dinosaur Provincial Park, the frontals are more elongate, with ratios that range from 1.4 to 1.6 in *Troodon*.

Albertavenator curriei can also be distinguished from a troodontid frontal from the Kaiparowits Formation (Zanno et al. 2013), which has a length to width ratio of approximately 1.7.

Allometric analysis of these variables in Campanian troodontids from North America indicates that these proportional differences between *Albertavenator curriei* and other troodontids are independent of size, and we therefore interpret this difference to have phylogenetic and taxonomic significance. In geometric morphometric analyses (Figure 5A&B), *Albertavenator curriei* plots separately from DPF troodontids on PC1, and from the Kaiparowits troodontid frontal on PC2. Eigenvectors indicate that PC1 is related to a combination of the proportional length and width of the frontal, with proportionally shorter frontals, such as TMP 1993.105.0001, having more negative PC values (Appendix 4), and PC2 is primarily related to the relative position of the posterior of the frontal to that of the anterior of the frontal. It is on this latter PC axis that the taxon represented by the Kaiparowits Formation frontal most distinctly separates from the penecontemporaneous frontals in the Dinosaur Provincial Formation and the frontal of *Albertavenator curriei*. Changes in relative frontal shape noted on GM PC1 were found to have a generally ontogenetic component when plotted against brain length, with larger and presumably older specimens being proportionally wider and longer than smaller frontals (Figure 5C). Despite this pattern, TMP 1993.105.0001 and UNMH.VP.16303 plotted away from the DPF frontals with comparable brain lengths, indicating that the differences seen in TMP 1993.105.0001 are not the purely the result of ontogenetic effects. The differences in relative frontal length between *A. curriei* and DPF troodontids is further demonstrated by the comparisons of frontal and brain

length (Figure 5E), in which TMP 1993.105.0001 has considerably shorter frontal length when compared to DPF frontals of similar brain length.

While TMP 1993.105.0001 superficially appears wider and more robust than other DPF frontals, the width of the posterior region and the thickness of the frontal are closely comparable to large troodontid frontals from the Dinosaur Park Formation (e.g., TMP 1986.049.0010, TMP 1993.036.0086), indicating it is in fact relatively shorter (Figure 5, Table 1). The intersection of the posterior end of the lacrimal contact with the primary supraciliary foramen is a discrete character that is related to the proportionally shorter frontal in *A. curriei* than in other troodontids. *Albertavenator curriei* can be further differentiated from other taxa by a unique frontoparietal contact. Both known troodontid frontals from the Horseshoe Canyon Formation exhibit relatively large medially directed lappets that form an extensive lap joint with the anterior (interfrontal) process of the parietal, compared to the more weakly developed vertical striations that are present in this region in the sample from the Dinosaur Park Formation. We hypothesize that the differences between TMP 1993.105.0001 and 1996.005.0008, including the relatively weakly developed supratemporal ridge and the absence of a robust, interdigitating lacrimal buttress on the anterior end of the crista cranii, represent growth-related ontogenetic variation within the same taxon related to increased size and robusticity with age.

Comparisons with Asian troodontids also support the distinction of the Horseshoe Canyon troodontid as a new taxon. The frontal tends to be relatively more elongate in Asian troodontids than in TMP 1993.105.0001 and *Troodon inequalis*. The above-mentioned ratio is 1.56 in *Gobivenator* (Tsuihiji et al. 2014), and 1.75 in *Zanabazar junior* (Norell et al. 2009), and the length of the frontal is reported to be approximately twice that of its width in *Linhevenator* (Xu et al. 2011). The frontal of *Mei long* from the Yixian Formation of northeastern China has

been noted to be unusually broad posteriorly, and appears relatively short, but they are distinct from *A. curriei* in their convex, inflated morphology (Gao et al. 2012). *Albertavenator curriei* cannot be compared to *Byronosaurus* (Bever and Norell 2009; Makovicky et al. 2003), *Philovenator curriei* (Xu et al. 2012), *Sinornithoides mongoliensis* (Norell et al. 2009), *Sinovenator changii* (Xu et al. 2002), *Xixiasaurus* (Lü et al. 2010), or *Urbacodon* (Averianov and Sues 2007) due to lack of sufficiently preserved and illustrated comparable adult material.

The identification of a new species of troodontid in the Campanian-Maastrichtian of northern Laramidia is not unexpected, and corroborates predictions that troodontid diversity in the latest Cretaceous of North America is underestimated due to over-synonymization of fragmentary material (Zanno et al. 2011). Several researchers (Fiorillo 2008; Fiorillo et al. 2009; Larson and Currie 2013; Zanno et al. 2011) have noted the unusually wide geographic and stratigraphic distribution of small coelurosaurian theropod species in the Western Interior Basin, and that these ranges are largely defined by the assignment of isolated teeth to form taxa. In other groups, such as large ornithischians, differentiation of species relies on non-dentigerous skeletal elements, and these taxa have small geographic and stratigraphic ranges, and presumably exhibited high evolutionary rates and ecological specialization (Eberth et al. 2013; Gates et al. 2012; Mallon et al. 2012; Ryan and Evans 2005; Sampson and Loewen 2010). Zanno et al. (2011) recognized variation in the limited skeletal materials previously referred to *Troodon*, and hypothesized that the diversity of Late Cretaceous troodontids in North America is underestimated, a conclusion that was supported by a morphometric analysis of small theropod teeth by Larson and Currie (2013). This study confirms these predictions, and suggests that more detailed studies of collections from the Campanian of northern Laramidia may reveal additional, currently unrecognized, taxa.

Interestingly, tooth and jaw morphology from the single relatively complete dentary recovered from the Horseshoe Canyon Formation cannot be distinguished from dentaries from the Dinosaur Park Formation (Currie 1987a). Currie (1987a) found no significant morphological differences between TMP 1983.012.0011 and those dentaries recovered from the Dinosaur Park Formation. Larson and Currie (2013) showed that isolated troodontid teeth from the Horseshoe Canyon formation quantifiably differed from those in the both the Dinosaur Park and Judith River formations, suggesting that the two units potentially contain distinct taxa, but this differentiation was on a size-correlated PC1 axis. The size-corrected morphometric results presented here do agree with those of Larson and Currie (2013), confirming that troodontid teeth from the Horseshoe Canyon Formation can, on average, be quantitatively distinct from those recovered from the Dinosaur Park and the Judith River formations, where the holotype tooth of *Troodon formosus* was recovered. However, identification of a distinct taxon of troodontid from the Horseshoe Canyon Formation is weakly supported by our morphometric analysis of isolated troodontid teeth from the Late Cretaceous of North America.

In the morphometric analysis of the dentition, almost all of the specimens from the Judith River Formation fall within the range of variation of those from the Dinosaur Park Formation, suggesting that species from these two formations cannot be distinguished on the basis of teeth (consistent with the results in Larson and Currie, 2013). Notably, the Judith River Formation specimen with the lowest score on PC1 (indicating largest relative denticles) is the holotype specimen of *Troodon formosus* (ANSP 9259), a presumed premaxillary tooth (Currie et al. 1990) with large mesial denticles that is considered an outlier in this analysis relative to the other nine analyzed Judith River teeth. This specimen has a similar PC1 score to three teeth that also have large mesial denticles from the Dinosaur Park Formation (Fig. 6). Given that North American

troodontid mesial teeth (premaxillary, mesial maxillary, and mesial dentary teeth) are known to possess greatly enlarged mesial denticles (Currie 1987a; Longrich 2008b), it is probable that these specimens represent teeth in a more mesial position in comparison with other teeth in this dataset. A similar pattern may be present in the Horseshoe Canyon sample, as a few noted specimens likely pertaining to the premaxilla are also similarly found on the extreme negative end of PC1 (Fig. 6). Therefore, we predict that it is likely much of the apparent morphological overlap between teeth from the different formations will be reduced when positional variation can be more precisely defined.

When the full range of variation is considered, there is extensive overlap in the linear morphometrics of teeth from the Dinosaur Park and Horseshoe Canyon formations (Fig 6). If the dentary and teeth from the Horseshoe Canyon Formation prove to belong to a single troodontid species, *A. curriei*, overlap in tooth morphology between the Judith River, Dinosaur Park, and Horseshoe Canyon formations reinforce the notion that tooth morphotypes may exhibit stronger correspondence to variation along the tooth row than to species alpha diversity, and may encompass multiple closely-related taxa, as predicted by Zanno (2011), Fiorillio et al (2008), and Larson and Currie (2013). The presence of distinctive cranial morphotypes associated with broadly similar tooth assemblages argues that isolated troodontid teeth from the Campanian-Maastrichtian may not be diagnostic to the species level, and that *T. formosus* may be a nomen dubium. If this is true, then it necessitates a taxonomic revision of the large collection of troodontid material collected from the Dinosaur Park Formation, where it may be prudent to apply the name *Stenonychosaurus inequalis*, based on the holotype foot (CMN 8537) and referable skeleton (CMN 12340) described by Russell (1969). It also remains possible that more than one taxon is present in any given formational sample, as it is not unusual for Cretaceous

Asian dinosaur faunas to have multiple contemporaneous genera of troodontids (Fiorillo 2008; Fiorillo et al. 2009). It is therefore notable that the tooth sample from the Horseshoe Canyon Formation exhibits higher disparity than that of samples from the Judith River and Dinosaur Park formations. Due to these considerations, the diversity of Campanian-Maastrichtian troodontids from western North America will remain in flux until more complete skeletal material is found.

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Figure Captions

Figure 1. Map showing the localities where troodontid cranial material from the Horseshoe Canyon Formation has been collected. Modified from Eberth et al, 2013. A, map of Alberta with lithostratigraphic outcrops and field area indicated; B, collection localities of the primary specimens discussed in the text.

Figure 2. Interpretive illustrations and photographs of TMP 1993.105.0001, the holotype left frontal of *Albertavenator curriei* gen. et. sp. nov. A, specimen illustration in dorsal view; B, specimen illustration in ventral view; C, corresponding photograph of A in dorsal view; D, corresponding photograph of B in ventral view. Abbreviations: fc, frontal midline contact; lc, lacrimal contact with frontal; lsc, laterosphenoid contact with frontal; nc, nasal contact with frontal; pc, parietal contact with frontal; pl, parietal lappet; poc, postorbital contact with frontal; scf, supraciliary foramen. Scale bar equals 2 cm.

Figure 3. Referred right frontal of *Albertavenator curriei*, TMP 1996.005.0008, in A, ventral, B, dorsal, and C, posterior views. Abbreviations: pl, parietal lappet. Scale bar equals 1 cm.

Figure 4. Comparison of 3D frontal models in dorsal, lateral, ventral, medial, anterior, and posterior, respectively, of *Albertavenator curriei* (TMP 1993.105.0001: a, b, c, d, e, f) and *Troodon inequalis* (TMP 1993.036.0086: g, h, i, j, k, l; TMP 1986.049.0010: m, n, o, p, q, r).

Figure 5. Results of troodontid frontal bone morphometric analyses. A, geometric morphometric (GM) principal component analysis (PCA) axes 1 and 2. B, GM PCA axes 3 and 4. C, comparison of GM PC1 data and brain length for sampled specimens. D, linear morphometric (LM) PCA axes 1 and 2. E, comparison between brain length and frontal length to nasal for sampled specimens. F, comparison of frontal width at medial extent of postorbital to frontal width at lacrimal contact for sampled specimens.

Figure 6. Comparison of troodontid jaws and teeth. A-E, dentary of TMP 1983.012.0011 in lateral (A), dorsal (B), and medial (C) views, along with images of the posterior (D) and anterior (E) teeth. F-I, dentary of ROM 1445 lateral (F), dorsal (G), and medial (H) views, along with image of the posterior teeth (I). J-K, Principal component analysis (PCA) of isolated troodontid teeth from the Horseshoe Canyon (HCF), Dinosaur Park (DPF), and Judith River formations, with teeth recovered in situ (*) projected into the plots. 95% convex hulls for each formation were calculated along each axis that significantly differentiated the HCF and DPF teeth. Unfilled symbols represent specimens that are likely premaxillary teeth given the position of their carinae.

Filled symbols have not been checked for likely position. Boxplots illustrating quartiles also shown for the first two principal components. J, Dataset of teeth with mesial denticles; HCF and DPF teeth significantly different ($p=8.771e-06$) along PC1, the only significant axis. K, Dataset of teeth with no mesial denticles (distal dentary teeth); HCF and DPF teeth significantly different ($p= 0.0002942$) along PC2, the second significant axis.

Tables

Table 1: Linear measurements of troodontid frontals used in morphometric analyses. *T. inequalis* refers to specimens collected from the Dinosaur Park Formation.

Specimen number	Taxon	Brain length (mm)	Brain width (mm)	Frontal length from parietal contact to lacrimal contact (mm)	Frontal length from parietal contact to posterior nasal contact (mm)	Frontal length from parietal contact to supraciliary foramen (mm)	Frontal width at medialmost extension of postorbital (mm)	Frontal width at lacrimal contact (mm)	Frontal width at postorbital margin (mm)	Frontal thickness at midline from high point of cranial cavity (mm)	Ratio of frontal length (nasal) to frontal width (medial postorb.)
AMNH FARB 6174	<i>T. inequalis</i>	61.47	22.67	47.13	56.43	40.47	40.71	-	51.72	6.9	1.39
CMN 12340	<i>T. inequalis</i>	60.84	20.58	44.93	53.34	39.3	38.78	24.14	53.57	4.8	1.38
TMP 1979.008.0001	<i>T. inequalis</i>	58.42	23.3	45.01	53.75	37.03	36.05	21.53	46.62	-	1.49
TMP 1986.049.0010	<i>T. inequalis</i>	62.38	23.31	47.73	55.26	38.03	38.15	22.05	52.32	7.1	1.45
TMP 1986.078.0040	<i>T. inequalis</i>	-	24.2	48.74	60.33	38.18	40.88	22.4	49.3	-	1.48
TMP 1993.036.0086	<i>T. inequalis</i>	62.54	25.26	43.93	53.88	36.82	38.76	26.22	53.91	7.2	1.39
TMP 1998.093.0001	<i>T. inequalis</i>	55.1	19.1	46.8	50.1	40.74	31.49	13.11	39.41	3.2	1.59
UALVP 52611	<i>T. inequalis</i>	60.56	22.75	46.88	55.73	40.91	38.25	21.77	51.26	-	1.46
TMP 1982.019.0023	<i>T. inequalis</i>	-	-	44.9	48.49	34.95	28.537	20.01	44.15	-	1.70
TMP 1993.105.01	<i>A. curriei</i>	59.1	24.53	44.1	46.8	42.94	38.51	25.3	-	7.1	1.22
UNMH.VP.16303	Troodontidae indet.	65.22	22.98	48.18	54.89	38.73	36.13	18.44	53.04	-	1.52

Appendices

Appendix 1. Schematic diagram of a troodontid frontal showing geometric morphometric landmarks and linear measurement indices used in this study.

Appendix 2: Landmark coordinate data for specimens used in geometric morphometric analyses.

Appendix 3: Cranial linear measurements (from Table 1) and geometric morphometric PC scores formatted for use in R code for bivariate comparisons

Appendix 4: Eigenvectors/loadings from principal components analyses of a) cranial geometric morphometric data, b) cranial linear morphometric data, c) isolated tooth linear morphometric data, d) in-situ tooth linear morphometric data

Appendix 5: R code for frontal bone morphometric analyses.

Appendix 6: Measurements of isolated troodontid teeth used in the morphometric analyses.

Appendix 7: In-situ tooth measurements from troodontid jaws with teeth.

Appendix 8: R code for morphometric analyses of tooth data

a **b**

a

b

1 cm

c

Horseshoe Canyon Formation

Dinosaur Park Formation

j Troodontid teeth with mesial denticles

k Troodontid teeth with no mesial denticles