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Troodontids (Theropoda) from the Dinosaur Park Formation, Alberta, with a description of a unique new taxon: Implications for deinonychosaur diversity in North America

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ABSTRACT

Troodontids are known from Asia and North America, with the most complete specimens from the Jurassic of China and the Cretaceous of Mongolia. North American troodontids are poorly known, and specimens that have been described are isolated elements or partial skeletons with limited material. A new troodontid from the upper Dinosaur Park Formation (upper Campanian), is based on partial skulls, several vertebrae, ribs, gastralia, chevrons, a sacrum, partial pelvis, and partial fore and hind limbs. It is the largest troodontid known with an estimated height of 180 cm and length of 350 cm. Like other troodontids, it possesses an elongated ambiens process and has a horizontal ventral margin of the postacetabular process. It differs from all other derived troodontids in that the slightly retroverted pubis has a shaft that curves anteroventrally. Some specimens from the Dinosaur Park Formation previously assigned to *Troodon* are reassigned to the new taxon, including multiple partial crania, an associated dentary and metatarsus, and a partial skeleton. Previously undescribed elements from the lower part of the Dinosaur Park Formation are assigned to the resurrected *Stenonychosaurus inequalis*. Distinct stratigraphic separation of *Stenonychosaurus inequalis* and the new taxon indicates a replacement in troodontid fauna, similar to the turnover of large ornithischians in the same formation. The new taxon is phylogenetically more closely related to Mongolian taxa, indicating the replacement of *Stenonychosaurus* may have been from an earlier Asian form immigrating into North America.

RÉSUMÉ

Les troodontidés connus proviennent d'Asie et d'Amérique du Nord, les spécimens les plus complets du Jurassique de Chine et du Crétacé de Mongolie. Les troodontidés nord-américains sont peu connus, et les spécimens décrits consistent d'éléments isolés ou de squelettes partiels au matériel limité. Un nouveau troodontidé de la zone supérieure de la formation de Dinosaur Park (Campanien tardif) est basé sur des multiples crânes partiels, plusieurs vertèbres, des côtes, un gastralia, des chevrons, un sacrum, un pelvis partiel, et des membres antérieurs et postérieurs partiels. C'est le plus grand troodontidé connu, estimé à 180 cm de haut et 350 cm de long. Comme les autres troodontidés, il possède un processus ambiens allongé et une marge ventrale horizontale du processus post-acétabulaire. Il diffère des autres troodontidés dérivés par son pubis légèrement rétroversé qui a une diaphyse se recourbant antéroventralement. Certains spécimens de la formation de Dinosaur Park auparavant attribués à *Troodon*, incluant plusieurs crânes partiels, un os dentaire et métatarse associés, ainsi qu'un squelette partiel, sont réassignés au nouveau taxon. Les éléments non décrits précédemment de la zone inférieure de Dinosaur Park sont assignés à *Stenonychosaurus inequalis*. La séparation stratigraphique distincte de *Stenonychosaurus inequalis* et du nouveau taxon indique un remplacement de la faune troodontidée, similaire au renouvellement des grands ornithischiens de la même formation. Le nouveau taxon est phylogénétiquement plus étroitement apparenté à la taxa mongolienne, ce qui indique la possibilité que le remplacement de *Stenonychosaurus* soit dû à l'immigration en Amérique du Nord d'une forme asiatique plus ancienne.

INTRODUCTION

Although the Dinosaur Provincial Park (DPP) region has been a major focus of dinosaur research for well over a hundred years, depositional environments lead to a preservational bias towards larger animals, or common taxa (Brown et al., 2013). Large bonebeds of *Centrosaurus apertus* (Eberth and Getty, 2005) dominate the park, and articulated hadrosaurs are some of the most common specimens known from the Dinosaur Park Formation (DPF). Due to the preservational bias, to date only a handful of relatively complete small dinosaur specimens have been collected, including; a ‘baby’ *Chasmosaurus belli* (Currie et al., 2016), *Stegoceras validum*, *Struthiomimus altus*, and several *Ornithomimus edmontonicus* specimens (Currie, 2005). Because of this bias, the understanding of small theropods is quite limited. Until recently, only partial skeletons for both *Dromaeosaurus albertensis* (AMNH 5356) and *Saurornitholestes langstoni* (TMP 1974.010.0005) had been recovered.

Mallon et al. (2012) investigated the megaherbivore stratigraphic distribution throughout the DPF. Results indicated two major statistically significant megaherbivore zones, with the DPF being split roughly in half. The lower portion (MAZ-1) is characterized by the presence of *Centrosaurus* and *Corythosaurus*, and the upper portion (MAZ-2) is characterized by *Prosaurolophus* and *Styracosaurus*. Although this study explored the biostratigraphic positions of the megaherbivores in detail, it did not look into the stratigraphic positions of any theropods.

Troodontids are arguably one of the least understood groups of dinosaurs anywhere in the world, especially considering *Troodon formosus* was published more than 1.5 centuries ago (Leidy, 1856) as one of the first three dinosaurs ever described from North America. Since publication of the original description of *Troodon*, multiple taxa have been named in North America and Asia (D.A. Russell and Dong, 1993, Xu and Norell, 2004, Zanno et al., 2011, Tsuihiji et al., 2014). The lack of complete skeletal material from North America, however, prevents a clear understanding of phylogenetic relationships within the clade. Currently the most complete troodontid specimens from North America are embryonic skeletons found within eggs from the Two Medicine Formation of western Montana (Varricchio *et al*., 2002). One partial skeleton of the Upper Cretaceous troodontid, *Talos sampsoni* from the Kaiparowits Formation of Utah has also been described. Although the most of the skull was not found, a frontal was described (Zanno *et al*., 2011).

Troodontids from the DPF are represented primarily by isolated elements (Gilmore, 1932; Sternberg, 1932; L.S. Russell, 1948; Currie, 1987), partial cranial material (D.A. Russell, 1969; Currie and Zhou, 1993) and an associated skeleton (D.A. Russell, 1969). Gilmore (1932) described a dentary (CMN 8540) with a high number of alveoli as a large lizard -- *Polydontosaurus grandis*. The specimen was collected within the Steveville area (Fig.1), reportedly about 37 m below the top of the DPF (Fig. 2; Table 1), potentially placing it within MAZ-2 of the formation (Eberth, 2005). Unfortunately, the accuracy of this measurement cannot be verified. In the same year, C. M. Sternberg (1932) described a complete pes (CMN 8539), also from the Steveville area (Fig. 1) about 53 m below the top of the Dinosaur Park Formation (Fig. 2; Table 1), placing it within the lower half (MAZ-1) of the formation (Eberth, 2005). Loris Russell (1948) described the first North American troodontid dentary containing teeth (ROM 1445). Unfortunately, locality data only places it within the Dinosaur Provincial Park area, and there is no stratigraphic information. The first partial skeleton described from North America consisted of a partial skull, vertebrae, ribs, chevrons, gastralia, and bones from the forelimb and hind limb (CMN 12340), making it the most complete troodontid skeleton recovered from Canada (D.A. Russell, 1969). The specimen did not include any pelvic elements, however.

Similarities observed in the metatarsus of CMN 8539 and CMN 12340 prompted the specimen to be assigned to *Stenonychosaurus inequalis*. The specimen was recovered roughly 3.1 km north northeast of Dinosaur Provincial Park (Fig. 1), 39 m above the Oldman Formation (Fig. 2; Table 1). This elevation places the specimen within the upper half (MAZ-2) of the Dinosaur Park Formation (Eberth, 2005). Currie (1985) assigned a partial skull (TMP 82.016.0023) from DPP to *Stenonychosaurus inequalis* (Fig.1); it was collected 31 m above the Oldman Formation (Fig. 2; Table 1) from the upper half (MAZ-2) of the DPF (Eberth, 2005). Two years later, Currie (1987) described a partial dentary with six teeth from the Horseshoe Canyon Formation from the Drumheller (Alberta) region and synonymized *Stenonychosaurus* with *Troodon*. The last paper to address Canadian troodontid material was the description of a partial braincase recovered from ~12 m (MAZ-1) above the Oldman Formation (Fig. 2; Table 1) in DPP (Fig. 1) (Currie and Zhou, 1993).

Material referred to *Troodon* has been described from New Mexico (Williamson and Brusatte, 2014) north to Alaska (Fiorillo et al., 2009). Named North American troodontids currently include *Geminiraptor suarezarum* (Senter et al., 2010), *Troodon formosus* (Leidy, 1856; Varricchio et al., 2002), and *Talos sampsoni* (Zanno et al., 2011). *Gobivenator mongoliensis* (Tsuihiji et al., 2014), *Mei long* (Xu and Norell, 2004), *Saurornithoides mongoliensis* (Osborn, 1924), *Sinovenator changii* (Xu et al., 2002), *Sinusinasus magnodens* (Xu and Wang, 2004), and *Zanabazar junior* (Norell et al., 2009) are the major forms described from Asia. *Anchiornis huxleyi* (Hu et al., 2009) has been interpreted as a troodontid, however, recent work provides evidence that it is more closely related to avialans than deinonychosaurians (Pei et al., 2017).

In June 2014, a partial small theropod pelvis (UALVP 55804) was recovered 42 m above the contact with the Oldman Formation (Fig.2, Table 1) in Dinosaur Provincial Park (Fig. 1), placing the specimen within the upper part of the Dinosaur Park Formation (MAZ-2). The specimen is from a relatively large troodontid individual, approximately 50% larger than *Talos sampsoni* (Zanno et al., 2011). It was recovered from a sandstone point-bar deposit containing small rip-up clasts of mud and silt. Although the sacrum was in contact with the ilia and pubis, the ischia were not recovered. The uniqueness of the pelvis prompted an in-depth review of previously collected troodontid material from the DPF, revealing the presence of a previously unknown species. The new taxon is supported by both isolated and associated elements recovered from the Upper DPF (MAZ-2), and is diagnostically distinguishable from the smaller *Stenonychosaurus inequalis* found in the lower part of the DPF (MAZ-1). Identifying the presence of two troodontids within the DPF prompts a reappraisal of the validity of *Stenonychosaurus inequalis* (MAZ-1) as well.

MATERIALS AND METHODS

Preparation of the new specimen was conducted at the University of Alberta Laboratory for Vertebrate Palaeontology in the Department of Biological Sciences building. Hand operated pneumatic tools, and needles in pin vices were used to remove matrix from the specimen. Detailed work around the bone was conducted with the aid of a microscope. PaleoBOND^{TM} Penetrant Stabilizer, and Vinac^{TM} crystals dissolved in acetone were used as consolidants for skeletal material.

Photographic images of UALVP 55804 were captured using a Canon 7D with a Tamron 24-70 mm lens set to 24 mm, ISO 200 *f*4.5, and exposure of 1/250 second. Other specimen images were captured using a Canon 7D mark II using the same lens and similar settings. Photos were processed using Adobe© Photoshop© CS6 Extended and were stitched together for large final images of each specimen. These were then imported into Adobe© Illustrator© CS6 where line drawings were created by tracing the original image with the aid of a Wacom© Intuos© 5 Touch (Large) drawing tablet. Stipple drawings were produced in Adobe© Photoshop© CS6 Extended using the drawing tablet.

All measurements that were done using digital calipers accurate to 1/100th of a millimeter, and are reported to 1/10th of a millimeter.

Phylogenetic analysis was performed using the character list and accompanying matrix published by Gao et al. (2012). Matrix coding for *Gobivenator* were incorporated from Tsuihji et al. (2014). Matrix coding for *Urbacodon* were incorporated from Averianov and Sues (2007). Character coding for the new taxa was incorporated using Mesquite (Maddison and Maddison, 2008). Three new characters (characters 364, 365, and 366) were added. The character matrix was then exported to TNT (Tree analysis using New Technology) (Goloboff et al., 2013) for analysis. TBR (Tree Bisection Reconnection) swapping algorithm was used, completing 999999 random addition sequences with 1000 trees per replicate, and retaining 60 trees with the best score of 1357. A 50% majority rules tree was calculated from the retained trees. Bremer support values were calculated from the 60 calculated shortest trees. Bootstrap values were calculated from 5000 replicates (Fig. 3). A strict consensus tree was produced from the 60 calculated shortest trees (Appendix 1). To ensure that the assignment of other specimens was not skewing results, CMN 12340 and TMP 82.019.0023 were removed from the matrix and UALVP 55804 was run through TNT (Appendix 2). To ensure that UALVP 55804 was not pulling CMN 12340 and TMP 82.019.0023 into an incorrect clade, UALVP 55804 was removed from the matrix.

TNT was then run containing only characters for CMN 12340 and TMP 82.019.0023 (Appendix 3). The resulting phylogenetic tree for Theropoda is provided in Appendix 4, the data matrix for the phylogenetic analysis is provided in Appendix 5, and the character matrix is provided in Appendix 6. Trees were drawn using Adobe© Illustrator© CS6.

Institutional Abbreviations

CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; MPC, Mongolian Institute of Geology and Paleontology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; MOR, Museum of the Rockies, Bozeman, Montana, USA; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UALVP, University of Alberta Laboratory for Vertebrate Palaeontology, University of Alberta, Edmonton, Alberta, Canada.

Specimens Studied

All specimens described herein were collected from the Dinosaur Park Formation from within or around Dinosaur Provincial Park, Alberta, unless otherwise stated.

RESULTS

SYSTEMATIC PALAEONTOLOGY

Theropoda Marsh, 1881

Maniraptora Gauthier, 1986

Troodontidae Gilmore, 1924 sensu Turner et al., 2012

Troodontinae, clade nov.

Definition

The most inclusive clade containing *Gobivenator mongoliensis*, and *Zanabazar junior*.

Diagnosis

Troodontinae differs from all other more basal troodontids by possessing an elongated ambiens process that is present on the anterior margin of the iliopubic symphysis.

Latenivenatrix mcmasterae gen. et sp. nov.

Etymology

The generic name derives from 'latens' (Latin for latent and hiding) and 'venatrix' (feminine form in Latin for hunter). 'Latent' refers to the taxon having been in multiple collections for nearly 100 years but unrecognized until now. 'Hiding' a similar meaning to 'latent', but also referring to a predatory animal hiding in cover until a suitable time to attack its prey. 'Hunter' refers to it being carnivorous. The specific epithet honours the late mother of the first author, Lynne (McMaster) van der Reest.

Holotype

CMN 12340, a partial skeleton including: paired frontals and parietals, right postorbital, basioccipital, basisphenoid, partial dorsal vertebra, three partial caudal vertebrae, three chevrons, four ribs, seven gastralia, complete left and partial right ulna, proximal left radius, left carpalia (fused carpals), partial manus, femoral shaft, both partial astragalocalcanea, and both partial pedes, and other unidentified fragments (D.A. Russell, 1969) (Fig. 4). See original description for more detailed description.

Locality and Horizon

3.1 km NNE of the north-eastern corner of Dinosaur Provincial Park, Alberta (Fig. 1); upper Dinosaur Park Formation, Upper Campanian, Upper Cretaceous (Eberth, 2005).

Referred Specimens

The following specimens are herein referred to the new taxon based on morphological similarities and/or accurate stratigraphic position within the Dinosaur Park Formation. They are referenced here specifically due to their significance and completeness in their respective regions of the skeleton.

UALVP 55804, an articulated sacrum, partial left ilium and pubic shaft, and a complete right ilium and partial pubis. Erosion had damaged the left ilium and pubis, and distal ends of both pubes.

TMP 1982.019.0023, a partial skull including: left lacrimal, frontals, parietals, postorbitals, squamosals, parasphenoid-basisphenoid, orbitosphenoids, laterosphenoids, prootics, supraoccipital, exoccipitalopisthotics, and basioccipital (Currie, 1985).

TMP 1992.036.575, 90% complete right dentary, a complete left metatarsal II, distal half of metatarsal III, and complete metatarsals IV and V.

Diagnosis

A troodontid dinosaur within Troodontinae that is distinguished from other derived troodontines by possessing a triangular frontal with a single deep groove in the frontonasal contact surface, and a concave anterior surface of metatarsal III. It has the following three autapomorphies: 17° retroverted pubis, an anteriorly curving pubic shaft, and a large muscle scar on the lateral surface of the pubic shaft slightly proximal to the pubic boot.

DESCRIPTION AND COMPARISON

For detailed descriptions of the cranium, manus, and pes refer to D.A. Russell (1969) and Currie (1985). Herein, characters distinguishing *Latenivenatrix mcmasterae* from *Stenonychosaurus inequalis* are the focus. All specimens identifiable to *Latenivenatrix mcmasterae* originate from MAZ-2, suggesting that the taxon is limited to the upper half of the Dinosaur Park Formation. Referred specimens lacking overlapping skeletal material are attributed to *Latenivenatrix mcmasterae* based on tight stratigraphic correlation.

Frontal

A frontal (AMNH 6174) and partial skeleton (CMN 12340) described by D.A. Russell (1969) were originally assigned to "*Stenonychosaurus inequalis"* based on hind limb material matching that of the type specimen described by Sternberg (1932). Observations of specimens (TMP 1979.008.001, TMP 1980.016.1478, TMP 1982.019.023, and TMP 1986.036.004) and illustrations previously published (D.A. Russell, 1969; Currie, 1985) provide clear diagnostic characters of *Latenivenatrix mcmasterae* frontals. The frontals of *Latenivenatrix mcmasterae* are triangular and distinguishable from the "L" shaped frontals of *Stenonychosaurus inequalis*. The orbital margin of the latter curves slightly medially in dorsal view (Fig. 5, 6). A more triangular frontal is also present in *Saurornithoides mongoliensis* (Norell et al., 2009). In both AMNH 6174 and CMN 12340, a small bone (palpebral? or prefrontal?) has not yet fused to the anterior orbital margin of the frontal, creating the appearance of an abrupt notch to be present along the frontal margin at the front of the orbit. Close attention to the surface indicates that if the palpebral were present, the frontals would be triangular in shape. The nasofrontal suture in *Latenivenatrix mcmasterae* is formed by a single deep grove that is triangular in cross section, plus three short narrow grooves close to the medial, interfrontal suture (Fig. 7). The nasofrontal contact surface is unknown in *Gobivenator mongoliensis* because the nasals are in anatomical position (Tsuihiji et al., 2014). It is also unknown in *Saurornithoides mongoliensis* due to breakage (Norell et al., 2009). The main articular groove is long and angles at approximately 60 degrees from the medial frontal suture to the most posterior portion of the nasofrontal suture. There is little surface topology on the nasofrontal suture, but the presence of the deep articular groove may have helped stiffen the joint with the aid of the smaller, intricate, medial grooves.

Latenivenatrix mcmasterae possesses a transversely oriented ridge that defines the anterior margin of the supratemporal fossa. It originates from the frontal suture and terminates at the frontopostorbital suture. A transverse ridge is also present in other derived troodontids such as *Gobivenator, Saurornithoides,* and the Two Medicine troodontid (Norell et al., 2009; Tsuihiji et al., 2014). A shallow grove formed by a tall orbital rim and the raised mid frontal is present. TMP 1980.016.1478 is the largest set of frontals measuring approximately 116 mm wide. Although a significant portion of this specimen is missing, based on width, it is estimated the length of the frontals would approach 140 mm in length.

Parietals

Several partial and one complete pair of parietals have been recovered and described in detail for *Latenivenatrix mcmasterae* (D.A. Russell, 1969; Currie, 1985). Complete parietals (AMNH 6174, TMP 1979.008.001, TMP 1982.019.023) show the anterior ends narrow towards the frontoparietal suture (Fig 5, 6). This contrasts the anterior broadening present in the parietals of *Stenonychosaurus inequalis*. The sagittal and nuchal crests are tall and thin as seen in *Stenonychosaurus inequalis* and *Gobivenator mongoliensis* (Tsuihiji et al., 2014). However, the lateral margins of the nuchal crest do not expand as far laterally like those of *Stenonychosaurus inequalis*. The narrow parietals and nuchal crest in *Latenivenatrix mcmasterae* therefore make the back of the skull appear narrow.

Dentary

A right dentary (TMP 1992.036.575) (Fig. 8) was recovered with other postcranial elements (metatarsals) from MAZ-2 (Fig. 2; Table 1), and is like that described by D.A. Russell (1969). The dentary is 130.3 mm long but is missing the posteroventral process: if it was present, the total length would have been about 160 mm. In dorsal view, the anterior end curves strongly medially. The entire tooth row is present and possesses 32 alveoli. When the dentary symphysis is oriented vertically, the anterior alveoli are directed dorsolabially, and the posterior alveoli dorsally, causing the tooth row to appear twisted. This tooth orientation is also observed in the Horseshoe Canyon Formation troodontid (Fig. 8), *Urbacodon itemirensis* (Averianov and Sues, 2007) and *Xixiasaurus henanensis* (Junchang et al., 2010). The entire dentary is quite robust, with the mediolaterally thickest point being mid height. A small foramen is present on the lateral face slightly anterodorsal to a small ventral process at the most anterior end of the dentary. On the medial side of this same process, a larger foramen is present at the front of the Meckellian groove. Foramina such as these are also reported in the Horseshoe Canyon troodontid (Fig. 8), *Urbacodon itemirensis* (Averianov and Sues, 2007) and *Xixiasaurus henanensis* (Junchang et al., 2010). As in other specimens (Currie, 1987), interdental plates are no longer present. A second troodontidae indet. dentary (TMP 1967.014.0039) from the DPF has no stratigraphic data, although the size and morphology resembles that of TMP 1992.036.575 (Fig. 8).

Among theropods described from the Dinosaur Park Formation, no pelvic material has ever been described for deinonychosaurs. This limits comparisons of *Latenivenatrix mcmasterae*. As a result, an exclusive comparison is necessary. *Daspletosaurus torosus* and *Gorgosaurus libratus*, the two tyrannosaurs in the DPF, each possess a large hooked preacetabular process (Holtz, 2004) that is not found on *Latenivenatrix mcmasterae*. The ornithomimids from the formation include five taxa, *Dromiceiomimus samueli*, *Rativates evadens*, *Struthiomimus altus*, *Ornithomimus edmontonicus*, and *Qiupalong* sp. (McFeeters et al., 2017) possess laterally enlarged supracetabular crests (Makovicky et al., 2004), unlike *Latenivenatrix mcmasterae*. Oviraptorosaurs vary significantly in iliac and pubic shapes (Osmólska et al., 2004), although none possess a large anterior process at the ilio-pubic symphysis such as is found in *Latenivenatrix mcmasterae*. By eliminating all theropod groups except deinonychosaurs a more focused comparison is possible.

Sacrum

The total anteroposterior length of the sacrum measures 207.4 mm with little deformation and consists of six coossified vertebrae (Fig. 9). Six is also the sacral number reported in each of *Gobivenator mongoliensis* (Tsuihiji et al., 2014), *Saurornithoides mongoliensis*, Two Medicine troodontid, and *Zanabazar junior* (Norell et al., 2009). Five coossified sacral vertebrae are known for the dromaeosaurids *Deinonychus antirrhopus* (Ostrom, 1976), *Saurornitholestes langstoni* (Fig. 9) (TMP 1967.020.0036, TMP 1992.036.0129, and TMP 1992.050.0021), and *Velociraptor mongoliensis* (MPC-D 100/985, Norell and Makovicky, 1997), as well as the basal Troodontidae members *Mei long* and *Sinovenator changii* (Norell et al., 2009). In lateral view, the ventral surface of the sacrum in *Latenivenatrix mcmasterae* remains horizontal throughout its length. This is in contrast to *Saurornitholestes* (TMP 1992.36.129), in which the sacrum is slightly arched dorsally. The sacral centra of UALVP 55804 have been slightly compressed mediolaterally, although the thicker bone where centra have fused prevented significant crushing in these regions.

The anterior articular surface of the sacrum in *Latenivenatrix mcmasterae* is moderately concave and is vertically elliptical in anterior view, measuring 41.7 mm dorsoventrally and 33.7

mm mediolaterally. The most ventral point of the articular surface extends 8.8 mm below the midpoint of the first centrum. The posterior articular surface is also vertically elliptical, similar to the anterior articular surface, although slight erosional damage prevents accurate measurements (Fig. 9). *Saurornitholestes langstoni* (TMP 1980.016.1790 and TMP 1992.036.0129), in contrast, possesses a horizontally trapezoidal posterior articular surface (Fig. 9). In *Latenivenatrix mcmasterae,* the prezygapophyses of the first sacral vertebra measure 18.1 mm in length, originate from the base of the pedicle, and angle approximately 45 degrees anterodorsally. The lateral edges of the prezygapophyses are oriented anteriorly and are approximately horizontal. The articular surfaces of the prezygapophyses are angled approximately 45 degrees medially. Due to crushing, the postzygapophyses have suffered significant distortion, preventing accurate measurements.

The sacral neural spines are thin laminae measuring 1 mm in mediolateral thickness along the dorsal margin. Four separate neural plates are present; two above the two dorsosacral vertebrae, the anteroposteriorly elongate and coossified middle spines that extend above sacral vertebrae three, four, and five (the three true sacral vertebrae), and the last one associated with sacral six (the caudosacral vertebra). Similar fused laminae above multiple sacrals are observed in *Velociraptor mongoliensis* (MPC-D 100/985, Norell and Makovicky, 1997), and appear to have been present in *Saurornitholestes langstoni* (TMP 1967.020.0036, TMP 1980.016.1790, TMP 1992.036.129, TMP 1992.050.0021). However, unlike *Latenivenatrix mcmasterae*, dromaeosaurids have laminae that extend from sacral vertebrae one through four, with the fifth neural spine unfused. A shallow fossa is present ventral to the transverse process and sacral rib. A second, deeper fossa is located on the midline dorsal to the fused postzygapophyses. Lateromedial crushing in UALVP 55804 prevents accurate interpretation and measurement of most sacral ribs. The most posterior sacral vertebra, however, possesses a sacral rib oriented posterolaterally measuring approximately 50.5 mm in mediolateral width. With the sixth sacral centrum measuring 13.3 mm, the total lateral width for the last sacral vertebra (centrum plus sacral ribs) is estimated to be 115 mm. Each last sacral rib is nearly four times wider than the associated centrum in *Latenivenatrix mcmasterae*. In *Saurornitholestes langstoni* (TMP 1992.036.0129), the sacral rib is shorter than the mediolateral width of the centrum for the posterior sacral vertebra (Fig. 9). The lateromedially longer posterior sacral ribs are associated with the ilia diverging posterolaterally from one another. This divergence in ilia is also reported in *Mei long* (Gao et al., 2012), although to a relatively greater degree.

Unlike *Saurornitholestes langstoni* (TMP 1967.020.0036, TMP 1980.016.1790, 1992.036.0129), *Velociraptor mongoliensis* (MPC-D 100/985, Norell and Makovicky, 1997), and *Zanabazar junior* (Norell et al., 2009), *Latenivenatrix mcmasterae* possesses a shallow sulcus on the ventral surface of the sacrum (Fig. 9). It is restricted to centra three through five, terminating at the intercentral fusion of centra five and six. The intercentral surface between sacrals five and six is narrower than between two and three, three and four, and four and five. This is also reported in *Zanabazar junior* (Norell et al., 2009).

Ilium

The right ilium of *Latenivenatrix mcmasterae* is nearly complete -- missing only a portion of the supracetabular crest and fragment of the anterodorsal corner (Fig. 10). The anteroposterior length measures 302.4 mm. A muscle scar, presumably for the origin of the M. iliotibialis (IT) 2 & 3, runs the length of the iliac crest. It originates 55.1 mm from the anterior margin of the preacetabular process and terminates 67.7 mm from the posterior margin of the postacetabular process. A small trauma scar is present where the IT 2 & 3 scar margin begins anteriorly as a depression in the dorsolateral surface of the iliac crest. This depression is interpreted as a trauma scar because it is not present on the left ilium. Posteriorly the IT 2 & 3 scar extends ventrally onto the lateral surface of the postacetabular process, forming a sharp rugose ridge extending 4.3 mm laterally. Throughout the length of the IT 2 & 3 origin, a small ridge on the dorsal margin slightly overhangs the lateral surface of the iliac blade. Although a similar IT scar is present in *Saurornitholestes langstoni* (MOR 660, UALVP 55800) and *Velociraptor mongoliensis* (MPC-D 100/985, Norell and Makovicky, 1997), it terminates at the posterior tip of the postacetabular process. The iliac crest of *Latenivenatrix mcmasterae* is from 8.3– 9.6 mm thick. The dorsal margin of the crest has a weakly convex profile in lateral view. Posteriorly, the crest merges with the brevis ridge 20.4 mm prior to the posterior margin of the ilium, preventing the iliac crest from converging on the ventral margin of the postacetabular process. This feature is also present in *Gobivenator mongoliensis* (Tsuihiji et al., 2014). In contrast, dromaeosaurids such as *Adasaurus mongoliensis* (Norell and Makovicky, 2004), *Bambiraptor feinbergorum* (Burnham et al., 2000), *Hesperonychus elizabethae* (UALVP 48778), *Saurornitholestes langstoni* (MOR 660, UALVP 55800) and *Velociraptor mongoliensis* (MPC-D 100/985, Norell and Makovicky, 1997) have postacetabular processes that narrow to acute ends. It should be noted that the avialan *Anchiornis huxleyi* has a similar posterior terminus of the ilium to that of dromaeosaurs (Xu et al., 2008).

The preacetabular process measures 137.6 mm in length from the centre of the acetabulum, although reconstructing a small missing fragment of the anterodorsal edge would extend the length to ~143 mm. If this corner was complete, it would be gently rounded, similar to the anteroventral corner. A shallow, dorsoventrally elongate notch (measuring 34.6 mm vertically) is present on the anterior margin of the preacteabular process, and is approximately

6.4 mm deep anteroposteriorly (Fig. 10). The anteroventral corner is rounded, and possesses a small muscle scar, presumably for the origin of IT 1, 5.4 mm ventral to the anterior notch. It terminates at the ventral edge. Unfortunately, no complete, derived troodontid ilia have been described for comparison to *Latenivenatrix mcmasterae*. Dromaeosaurids that have been described preserving the preacetabular process indicate that there is significant variation in the anterior margin. In *Saurornitholestes langstoni* (MOR 660, UALVP 55800) the anterodorsal edge extends well beyond the anteroventral edge. *Adasaurus mongoliensis* has a slight anteriorly overhung dorsal margin, and a characteristic deeply notched anterior margin of the preacetabular process (Turner et al., 2012). *Rahonavis ostromi* has a smoothly curved anterior margin of the preacetabular process (Turner et al., 2012). *Unenlagia comahuensis* has an anterior margin that has become nearly horizontal as the iliac crest dips anteroventrally (Turner et al., 2012). It is unknown if such variation would be present in troodontids. The ventral margin of the preacetabular process in *Latenivenatrix mcmasterae* is thin anteriorly, progressing posteriorly into the cuppedicus ridge. The cuppedicus ridge merges posteriorly and ventrally into the anterior margin of the pubic peduncle. The ventral margin of the preacetabular process and the anterior margin of the pubic peduncle form part of the arch of a near perfect circle in lateral view (Fig. 10). This is not seen in any dromaeosaurids, and it is unknown if it is present in other derived troodontids.

The postacetabular process is preserved on the right ilium and measures 164.6mm from the centre of the acetabulum (Fig. 10). The ventral margin of the postacetabular process in *Latenivenatrix mcmasterae* remains horizontal the entire length and possesses a small muscle scar approximately half way to the posterior tip. A horizontal ventral surface is also found in the troodontids *Gobivenator mongoliensis* (Tsuihiji et al., 2014) and *Sinovenator changii* (Xu et al., 2002). In contrast, the ventral surfaces of the postacetabular processes of dromaeosaurids typically dip posteroventrally such as in *Hesperonychus elizabethae* (Longrich and Currie, 2009), *Mahakala omnogovae* (Turner et al., 2012), *Saurornitholestes langstoni* (MOR 660, UALVP 55804) and *Velociraptor mongoliensis* (MPC-D 100/985, Norell and Makovicky, 1997). The posterior edge of the postacetabular process in *Latenivenatrix mcmasterae* measures 34.3 mm dorsoventrally and is nearly vertical (Fig. 10), like that of *Gobivenator mongoliensis* (Tsuihiji et al., 2014). This contrasts with the postacetabular process of a dromaeosaurid, which tapers posteriorly to an acute point (Norell and Makovicky, 2004). Anteroventrally, the postacetabular process extends ventrally into the antitrochanter, which is located laterally on the ischial peduncle (Fig. 10).

The medial half of the acetabular wall has been crushed laterally, resulting in deformity of the acetabulum (Fig. 10). Although the supracetabular crest is partially damaged, it is still evident the antitrochanter is formed by an expansion of the posterior portion of the crest. The antitrochanter overlies the articular surface of the ischial peduncle and is oriented at 45^{o} from vertical, which is similar to *Saurornitholestes langstoni* (MOR 660). The ischial peduncle measures 34.4 mm dorsoventrally, 28.6 mm anteroposteriorly, and 32.9 mm mediolaterally. The articular surface on the ischial peduncle is horizontal in lateral view. The lateral surface of the ischial peduncle is longer ventrally than the medial surface, resulting in the articular surface being hidden in lateral view. The anterior surface of the acetabulum on the pubic peduncle measures approximately 29.5 mm mediolaterally. The pubic peduncle is anteriorly elongate (Fig. 10) to form the dorsal 30% of a thin anterior process on which the ambiens muscle originates. This process measures 33.0 mm in length anteroposteriorly, measured from the anterior face of the pubic shaft. This enlarged ambiens process is also seen in many derived troodontids, including *Gobivenator mongoliensis* (Tsuihiji, 2014), *Saurornithoides mongoliensis* (Norell et al., 2009), and the Two Medicine troodontid (MOR 553S 8.3.9.387). As the dorsal margin of the ambiens process begins to expand anteriorly, the posterior portion of the pubic peduncle begins to expand posteriorly, creating 7.7 mm of the ventral margin of the acetabulum. The medial surface of the pubic peduncle is slightly concave, and extends posteromedially. The ventral margin expands mediolaterally at the symphysis, and appears to be partially fused with the pubis.

The left ilium is incomplete, missing the postacetabular process, including the posterior portion of the supracetabular crest. The recovered portion of the left ilium measures 239.5 mm anteroposteriorly, 131.4 mm dorsolaterally from the pubic peduncle to the iliac crest, and 78.4 mm from the ventral surface of the acetabulum to the iliac crest. The iliac crest is slightly convex in lateral view, with uniform topography. The iliac crest possesses a small muscle scar nearly the entire length corresponding to the origin of the IT 2 & 3. It originates approximately 26 mm posterior to the anterior margin of the preacetabular process. The termination of the IT 2 & 3 muscle scar cannot be determined for the left ilium due to the eroded surface of the specimen. Anteriorly, this muscle scar extends ventrally 13.4 mm on the lateral surface of the preacetabular process from the dorsal surface of the iliac crest, creating a slight rugosity. Posteriorly, the IT 2 & 3 muscle scar terminates in a small rugosity on the dorsolateral surface of the postacetabular process, creating a distinct ridge extending laterally 3.1 mm. The iliac crest measures a uniform thickness of approximately 7.7 – 8.5 mm. The anterior margin of the preacetabular process is mediolaterally thin, measuring 2.2 mm thick. The edge suffered damage at the dorsal and ventral corners. Both the anterior and ventral margins are concave in lateral view, with the ventral margin being near circular in shape. Although the left pubic peduncle is incomplete, the remaining portion measures 33.0 mm ventrally from the narrowest point. The pubic peduncle forms the anterior margin of the acetabulum. The anterior margin of the peduncle is formed by the posteroventrally descending lateral face of the preacetabular process as it converges with the cuppedicus ridge. The pubic peduncle is narrowest at approximately mid acetabulum and measures 21.1 mm anteroposteriorly. The supracetabular crest is relatively complete anteriorly from the antitrochanter. Although the crest is poorly developed, it is most pronounced over the dorsal surface of the acetabulum. The lateral surface of the entire ilium in concave in anterior view. There is a small foramen at the midpoint between the iliac crest and the middle of the supracetabular crest.

Pubis

The right pubis is incomplete, represented by the proximal half to two thirds of the length, which extends 197.4 mm dorsoventrally (Fig. 10). The most striking feature of the pubis of *Latenivenatrix mcmasterae* is the seventeen degrees of retroversion. This angle is measured along the centre of the proximal pubic shaft in relationship to the fused contact surface between the pubis and pubic peduncle of the ilium. Retroversion of the pubis is characteristic within Dromaeosauridae (Norell and Makovicky, 2004). However, this state has also been observed in the basal troodontid, *Sinovenator changii* (Xu et al., 2002). Interestingly, the pubic shaft curves anteriorly as it extends distally (Fig. 10). No other troodontid is known to possess this feature, nor is this character known to be present in any dromaeosaurid (Norell and Makovicky, 2004). However, it is present in the oviraptorosaur *Ingenia yanshini* (Osmolska et al., 2004), but to a much greater degree. Viewed anteriorly, the shaft curves medially towards the other pubic shaft. Because the distal half is missing, the connection between the aprons cannot be seen. In cross section, the proximal end of the pubic shaft is compressed mediolaterally, with the lateral side flattened and the medial side slightly convex. The lateral face preserves small muscle scars visible as elongate striations running posterodorsally to anteroventrally. Medially, the pubic shaft includes the base of the pubic apron as a rounded ridge. Distally, 197.5 mm from the iliac suture, the pubic apron begins to expand, and becomes posteromedially oriented at approximately 45˚. This indicates the pubic apron extended posteriorly beyond the pubic shaft.

The ischial peduncle of the pubis measures 11.0 mm anteroposteriorly from the posterior margin of the pubic shaft. In posterior view, the articular surface is an elongate triangle, measuring 32.4 mm dorsoventrally with the dorsal end and measuring 18.1 mm mediolaterally. The elongate ambiens process is partially formed by the pubic peduncle of the ilium, continues onto the pubis to a full anteroposterior length of 59.1 mm. In dorsal view, the process curves laterally, but is not as pronounced as in the Two Medicine troodontid (MOR 553S 8.3.9.387). Proximally, the pubis expands mediolaterally at the iliac peduncle to match the size of the peduncle of the ilium.

The left pubis consists of only a partial pubic shaft, representing the portion just below the ischial peduncle and extending to just proximal of the pubic boot. Unfortunately, the apron is missing. The partial pubic shaft reflects the same features seen on the right shaft. However, the medial ridge that forms the base of the apron is much sharper than the curved surface seen on the left shaft. The additional length to the left pubic shaft provides enough information to suggest that the distal half was oriented vertically. A large and moderately pronounced muscle scar is located on the lateral surface at the distal end of the recovered portion of pubic shaft (Fig 11). This muscle scar has never been reported for any other troodontid (D.A. Russell and Dong, 1993; Xu and Norell, 2004; Zanno et al., 2011; Tsuihiji et al., 2014). No other theropods, save microraptorines such as *Hesperonychus elizabethi* (Longrich and Currie, 2009), are known to possess a muscle scar is this region. Although the shape and size of the pubic boot is unknown, it appears the boot begins at the distal break point due to a slight posterior expansion.

A composite image of both right and left pubes was produced to further illustrate the degree of retroversion and pubic curvature with an estimated outline for the pubic boot and ischium (Fig. 12).

Metatarsals

TMP 1992.036.575 is a large set of metatarsals (II-V) (Fig. 13) recovered from bonebed 75 in Dinosaur Provincial Park (found with a dentary and a partial tibia) (Fig. 2; Table 1). Proximally, metatarsals II and IV are in direct contact, excluding metatarsal III from the ankle joint surface, forming an arctometatarsalian metatarsus as in most other troodontids (Kurzanov and Osmólska, 1991; D.A. Russell and Zhi-Ming, 1993; Xu et al., 2012; Tsuihiji et al., 2014). Metatarsal II is slender through the entire length of the shaft (11.9 mm mediolaterally, and 18.2 mm anteroposteriorly), and expands proximally for articulation with the ankle. The non-ginglymoid distal condyle of metatarsal II is angled laterally approximately 30 degrees. A sharp ridge is present on the anterior surface slightly proximal to the condyles where it contacts metatarsal III.

Although metatarsal III is missing the middle portion, its length can be estimated as 258.8 mm. The proximal end is thin (1 mm anterodorsally), but wide (8.5 mm mediolaterally). Distally, the shaft is progressively wider and measures 29.4 mm mediolaterally at the ginglymoid condyle. A shallow semi-circular fossa for ligament attachments is directly proximal to the condyles on the anterior surface, as in *Gobivenator mongoliensis*. This contrasts with other specimens of metatarsal III in which a proximally elongate fossa is present. At the laterally broadest point, the anterior surface is slightly concave (Fig. 14). Concave anterior surfaces of metatarsal III are also present in *Gobivenator mongoliensis* (Tsuihiji, et al. 2014), MPC-D 100/140 (Tsuihiji et al., 2016), and *Philovenator curriei* (Xu et al., 2012).

Metatarsal IV is both the longest and most robust element, and measures 266.2 mm long, 28.5 mm anteroposteriorly, and 24.9 mm mediolaterally. The proximal end of Metatarsal IV forms approximately 60 percent of the articular surface of the ankle. The proximal surface possesses a small posterolateral process associated with contacting the distal tarsals. Distally, the condyle is slightly deflected laterally. A prominent ridge extends the length of the anterior surface, to help form a shallow groove distally, just proximal to the semi-ginglymoid distal articulation (Fig. 13).

Metatarsal V, which is no more than a splint, contacts the posterolateral process on the proximal articular surface of metatarsal IV, and measures 74.1 mm in total length (Fig. 13).

STENONYCHOSAURUS INEQUALIS

SYSTEMATIC PALEONTOLOGY

Theropoda Marsh, 1881

Maniraptora Gauthier, 1986

Troodontidae Gilmore, 1924 sensu Turner et al., 2012

Troodontinae, clade nov.

Stenonychosaurus inequalis Sternberg, 1932

Holotype

A partial skeleton consisting of six caudal vertebrae, left metacarpal I, distal end of metacarpal II?, three partial manual phalanges, distal end of left tibia and astragalus, and left pes (Sternberg, 1932; D.A. Russell, 1969) (Fig. 15).

Locality and Horizon

Lower Dinosaur Park Formation, N.W. ¼ Sec. 21, T. 21, R. 12, W 4th meridian “Railway Grade” west side of Red Deer River. Approximately 53 m below base of Bearpaw Formation (Fig. 1, 2).

Referred Material

UALVP 52611. 90% complete frontoparietal complex with the right frontonasal contact surface. Lower part of Dinosaur Park Formation, “Happy Jack’s West”, Dinosaur Provincial Park, Alberta (Fig. 1, 2, 5, 6).

TMP 1986.036.0457. A partial braincase consisting of the supraoccipital, exoccipitals, basioccipitals, partial basisphenoid – parasphenoid, opisthotics, laterosphenoids, and prootics. Lower Dinosaur Park Formation, Dinosaur Provincial Park core, Alberta (Currie and Zhao, 1993) (Fig, 1, 2).

Diagnosis

A troodontid within Troodontinae that is distinguished from other troodontids by possessing a convex anterior surface metatarsal III, and an “L” shaped frontal with a flat shallowly anteroposteriorly rippled nasofrontal contact.

DESCRIPTION AND COMPARISON

All specimens identifiable to *Stenonychosaurus inequalis* originate from MAZ-1, suggesting that the taxon is limited to the lower half of the Dinosaur Park Formation. Referred specimens lacking overlapping skeletal material are attributed to *Stenonychosaurus inequalis* based on morphological similarities and tight stratigraphic correlation.

Frontals

All frontals of *Stenonychosaurus inequalis* originally illustrated by D.A. Russell (1969) and Currie (1985) are now referred to *Latenivenatrix mcmasterae*. Although not illustrated, Currie (1985) observed and mentioned UALVP 5282 while describing the sagittal suture of the frontals. Because this was the only specimen known at the time from MAZ-1 (Fig. 2; Table 1), it was not determined to be different than other frontals from the DPF. UALVP 5282 is a nearly complete right frontal, missing only the nasal suture (Fig. 5, 6). The posterior margin of the orbit rim is strongly curved laterally, to produce a slight “L” shape to the frontal bone when seen in dorsal view. Since UALVP 5282 was originally mentioned (Currie, 1985), three more confirmed specimens possessing an “L” shape have been recovered, including UALVP 52611, a nearly complete set of frontals and parietals (Fig. 5, 6) from MAZ-1 (Fig. 2; Table 1). UALVP 52611 has the sutures for the nasal and lacrimal of the right side. The nasal suture consists of a single surface that is relatively flat, with shallow, smooth undulations (Fig. 7). A single thin midline ridge on the dorsal surface of the paired frontals separates the nasals medially to produce a “v” shaped fork in the paired nasals posteriorly. The smooth and shallow undulations of the nasal suture suggest some sliding may have been possible between the two bones. The orbit rim is elevated to a similar level as the most medial portion of the frontal, and there is a long shallow depression through the mid length of each frontal as in *Gobivenator mongoliensis* (Tsuihiji et al., 2014), *Latenivenatrix mcmasterae*, and *Saurornithoides mongoliensis* (Norell et al., 2009). Posteriorly, as in *Latenivenatrix mcmasterae* and other derived troodontids (Norell et al., 2009; Tsuihiji et al., 2014), a transversely oriented ridge is present just anterior to the frontoparietal suture, defining the supratemporal fossa. The postorbital suture in UALVP 52611 is visible in dorsal view.

TMP 1986.078.0040, a single left frontal, and TMP 1988.050.0088, a partial pair of frontals and parietals, both show the same "L" shaped morphology (Fig. 5, 6).

Parietals

The parietals of UALVP 52611 are complete, whereas those of TMP 1988.050.0088 are fragmentary (Fig. 5, 6). Both specimens, however, do preserve the anterior portions, revealing that the parietals of *Stenonychosaurus inequalis* expand laterally along the frontoparietal suture. Slightly posterior to the frontoparietal suture, a shallow ridge extends laterally from the sagittal crest, terminating as it flattens out. The sagittal crest is tall and narrow, and joins the nuchal crest as in other troodontids (Currie, 1985; Tsuihiji et al., 2014). The nuchal crest is tall and thin, and extends nearly as far laterally as the frontal. Ventrally, the parietals extend on either side into a small protrusion in the same plane as the nuchal crest.

Dentary

A partial left dentary (TMP 1982.019.0151; Fig. 8) collected from approximately 2.6 metres below the DPF in the Oldman Formation (Table. 1), is similar to *Latenivenatrix mcmasterae* (TMP 92.036.0575) and the Horseshoe Canyon troodontid (TMP 83.012.0011) in possessing a deep Meckelian groove, and lingual and labial distal foramina above a small ventrally oriented process, and by the lack of interdental plates. Unlike *Latenivenatrix mcmasterae* and the Horseshoe Canyon troodontid, TMP 82.019.0151 is straight through its entire length, only deviating medially at the dentary symphysis.

Metatarsals

Sternberg (1932) described the holotype (CMN 8539) as a left pes including a complete metatarsus, although it had been severely eroded when recovered (D.A. Russell, 1969). Due to the damage, the specimen had been encased in plaster in the field and never fully prepared.

Fortunately, the specimen has been prepared enough to make a diagnosis. Enough of the anterior surface of metatarsal III is exposed to indicate a small subtriangular ligament fossa directly proximal to the distal condyles, whereas the same fossa in *Latenivenatrix mcmasterae* is subcircular. The remaining anterior face of metatarsal III is slightly convex at the laterally broadest point, instead of concave as in *Latenivenatrix mcmasterae* (Fig. 14). The only other confirmed metatarsal for *Stenonychosaurus inequalis* from the DPF is the distal portion of a single metatarsal III (TMP 1998.068.0090) (Fig. 14), and presents the same condition observed in the holotype (CMN 8539). A subtriangular fossa and a slightly convex anterior face of metatarsal III are also observed in *Talos sampsoni* and the Two Medicine troodontid specimens (Zanno et al., 2011) from North America. It is reported for *Urbacodon sp.* (Averianov and Sues, 2016), although it is not certain that the specimens truly represent this taxon.

DISCUSSION

The pelvis (UALVP 55804) of *Latenivenatrix mcmasterae* shares several characters with other troodontids. However, because of the lack of complete pelves throughout Troodontidae, it is difficult to map synapomorphic characters. The most distinguishable synapomorphic feature that unites *Latenivenatrix mcmasterae* with other derived troodontids including *Gobivenator mongoliensis, Saurornithoides mongoliensis,* the Two Medicine troodontid, and *Zanabazar junior* is the elongate ambiens process of the iliopubic symphysis. An elongate ambiens process suggests that the ambiens muscle in derived troodontids was modified for their specialized cursorial locomotion. The new subfamily, Troodontinae, is proposed to refer to taxa within Troodontidae that possess elongated ambiens processes. When this character is mapped phylogenetically, it becomes synapomorphic at the node, uniting *Gobivenator mongoliensis* and

Zanabazar junior (Fig. 16). However, because of incomplete pelvic data, this feature is ambiguous for the clade uniting *Mei long* and other troodontids, and may have evolved earlier in Troodontidae than its currently recognized node. This character therefore is reliable for identifying derived troodontids from other deinonychosaurs, although more complete data is required to clarify which node the character arose. *Latenivenatrix mcmasterae* also possesses a nearly vertical posterior margin of the postacetabular process, similar to the gently curved margin observed in *Gobivenator mongoliensis* (Tsuihiji, 2014). In dromaeosaurids, the ilia taper posteriorly to acute points (Norell and Makovicky, 2004). This character may help identify partial troodontid pelvic material. This is also true for the horizontal ventral margin of the postacetabular process. Three autapomorphies distinguish *Latenivenatrix mcmasterae* from other taxa in Troodontinae. First, character 175 is the slight pubic retroversion (~17^{o}, Fig. 10, 12). Pubic retroversion is observed in Dromaeosauridae (Norell and Makovicky, 2004), although it is typically rotated more posteriorly. The second autapomorphy, character 178, is the anteriorly curving pubic shaft (Fig. 10, 11, 12). Although slight retroversion is reported in the basal Troodontidae member *Sinovenator changii* (~15^{o}, Xu et al., 2002), this taxon lies outside Troodontinae, preserving the autapomorphic state in *Latenivenatrix mcmasterae*. The third autapomorphy is the presence of a proportionately large, moderately pronounced muscle scar on the lateral surface of the pubic shaft slightly proximal to the pubic boot. The only other group of theropods to have a pronounced muscle scar in this region are microraptorines such as *Hesperonychus elizabethae* (Longrich and Currie, 2009).

All known Asian troodontids for which the character can be observed, except *Saurornithoides mongoliensis*, each possess a concave anterior surface of metatarsal III at its laterally broadest point, like that found in *Latenivenatrix mcmasterae*. Neither *Talos sampsoni* nor the Two Medicine troodontid possess this character, suggesting a concave metatarsal III evolved after *Talos* phylogenetically, and was secondarily lost in the clade containing *Saurornithoides, Troodon,* and *Zanabazar*. This character may be useful in tracking troodontids with Asian affinities within North America.

Based on all available stratigraphic data and a thorough re-evaluation of previously described and undescribed specimens, it is evident two troodontid taxa are present in the Dinosaur Park Formation. The two taxa are stratigraphically separated into the same levels seen in megaherbivores (Mallon *et al*., 2012). Similarities between frontals and metatarsals of *Stenonychosaurus inequalis* from the Dinosaur Park Formation and those of the Two Medicine troodontid suggest that the two taxa may in fact be the same species. Further investigation into the Two Medicine Formation troodontids is required to confirm the assignment of these specimens to *Stenonychosaurus inequalis*.

The Dinosaur Park Formation has produced significant deinonychosaur material including *Dromaeosaurus albertensis* (Matthew and Brown, 1922), *Hesperonychus elizabethae* (Longrich and Currie, 2009), *Saurornitholestes langstoni* (Sues, 1978), and *Stenonychosaurus inequalis* (Currie and Zhao, 1993). *Dromaeosaurus albertensis* is only represented by one partial skeleton that lacks the pelvic girdle. The possibility that UALVP 55804 represents this taxon was eliminated by the presence of the elongate ambiens process at the pubic peduncle. Although pelvic material for the Two Medicine troodontid has never been published, a pubis (MOR 553S 8.3.9.387) resembles those of *Gobivenator mongoliensis* (Tsuihiji et al., 2014), *Saurornithoides mongoliensis* (Norell et al., 2009), and *Talos sampsoni* (Zanno et al., 2011) where the shaft is straight and circular in cross section, and the anterior ambiens process on the pubis curves sharply laterally. After observations of other taxa found in the Dinosaur Park Formation and performing the phylogenetic analysis, it was determined that *Latenivenatrix mcmasterae* is a new taxon within Troodontidae. The sizes of several specimens (TMP 1980.016.1748, TMP 1992.036.0575, and UALVP 55804) suggest *Latenivenatrix mcmasterae* is currently the largest known troodontid based on skeletal material, although the largest known teeth originate from Alaska (Fiorillo and Gangloff, 2000). The largest frontal specimen from the same stratigraphic level (TMP 1980.016.1748) (116 mm laterally) provides an estimated skull length of 45 cm. The head is estimated to have been held 180-200 cm off the ground, and a total body length of 300-350 cm based on comparisons with *Gobivenator* (approximately 160 cm in length).

The possibility exists that *Latenivenatrix mcmasterae* represents the previously named taxon *Polydontosaurus grandis*. Locality information given by Gilmore (1932) for the dentary of *Polydontosaurus* places it on the west side of the Red Deer River in the "Railway Cut" badlands. CMN 8540 was reportedly recovered approximately 4.8 km (3 miles) southwest of the mouth of Berry Creek, however, this distance would place the specimen in the grasslands southwest of the Railway Cut. Additionally, the specimen was reported to have come from approximately 37 m below the top of the Dinosaur Park Formation, only a few metres above the middle of the formation. The closest location at which this level is exposed to the area Gilmore (1932) reports is 1.6 km away. Other confounding factors in obtaining a proper stratigraphic position for CMN 8540 are variation in formation thickness (Eberth, 2005), the reliability in the method of which C. M. Sternberg used to estimate the provenance of the specimen, and differences in what may have been considered the top of the formation at the time of collection. Furthermore, troodontid dentary morphology is not highly variable and as such cannot be reliably used to distinguish between taxa (MOR 563, TMP 1983.012.0011, TMP 1992.036.0575; Norell et al., 2009). Because it is impossible to discover the true horizon from which CMN 8540 originates, and the lack of diagnostic characters in troodontid dentaries, *Polydontosaurus grandis* is considered a *nomen dubium*

Dromaeosaurid diversity during the late Campanian in Laramidia also suggests troodontid diversity may likely be higher. *Bambiraptor feinbergi* (Two Medicine Formation, Burnham at al., 2000), *Dromaeosaurus albertensis* (Dinosaur Park Formation, Matthew and Brown, 1922) and *Saurornitholestes langstoni* (Dinosaur Park Formation, Sues, 1978) lived coeval to one another, suggesting that dromaeosaurids may have existed in restricted ecosystems. Late Cretaceous troodontid diversity in Laramidia is currently debated, and is likely much higher than currently acknowledged (Zanno et al., 2011). Results reported herein support a higher diversity, and suggest that troodontids may also have similar diversity as dromeaosaurids.

Zanno et al. (2011) and others have suggested *Troodon formosus* should be considered a *nomen dubium*. Additionally, Larson and Curie (2013) performed a multivariate analysis of troodontid teeth from the late Cretaceous of western North America and found no statistical differences between teeth within the Dinosaur Park Formation, indicating that *Latenivenatrix mcmasterae* and *Stenonychosaurus inequalis* cannot be distinguished using teeth. The same research (Larson and Currie, 2013) also produced no statistical significance between troodontid teeth from the Dinosaur Park Formation and the Judith River Formation, from which the holotype of *Troodon formosus* originated, indicating that teeth are not diagnostic between taxa. According to the International Code of Zoological Nomenclature Article 75.5, if a species holotype cannot be distinguished from other taxa, it is considered a *nomen dubium*. Based on issues using teeth to identify troodontids in North America, Article 75.5 applies to *Troodon formosus* because the holotype is an isolated tooth. Although, the validity of *Troodon formosus* may be contentious, future discoveries may provide the osteological information required to sort out true relationships in North American troodontids. For any specimens that are positively identified as *Troodon formosus*, however, they must originate from the Judith River Formation in the region from where the holotype was recovered. For this reason, *Stenonychosaurus inequalis* is resurrected and considered a valid genus and species herein. At the time a new specimen from the type locality is described, specimens from different formations and times can then properly be assigned to *Troodon formosus*.

For Dinosaur Park Formation troodontids, *Stenonychosaurus inequalis* is only present in MAZ-1, spanning approximately 76.4 – 75.9 mya, whereas *Latenivenatrix mcmasterae* is only present in MAZ-2. It is hypothesized that *Latenivenatrix mcmasterae* replaced *Stenonychosaurus inequalis* at or around the MAZ-1/MAZ-2 boundary (29 metres above the Oldman Formation). This suggests *Latenivenatrix mcmasterae* is present in the region between at least 75.9 – 75.3 mya. Two possible explanations for troodontid replacement are proposed; 1) ecological shift during transgressive events with *Latenivenatrix mcmasterae* and *Stenonychosaurus inequalis* following their preferred environments, or 2) direct competitive exclusion between troodontid taxa with *Latenivenatrix mcmasterae* out-competing *Stenonychosaurus inequalis*.

All identified specimens of *Latenivenatrix mcmasterae* were recovered between two and fourteen metres of stratigraphic section within the MAZ-2 (Fig. 2, Table 1). Stratigraphic and ichnological studies of the upper portion of MAZ-2 provide evidence of a transgressive shoreline related to the Bearpaw Sea (Eberth, 2005) influencing ecosystems. Mallon et al. (2012) discuss the megaherbivore ranges within the Dinosaur Park Formation, focusing on ankylosaurs, ceratopsians, and hadrosaurs. The shift in herbivore composition suggests an ecological change and therefore it is possible that the carnivores also went through a shift. Evidence of a faunal shift within troodontids provides support for this possible explanation.

Closely-related taxa of other clades have been found in both North America and Asia including Caenagnathidae (Funston and Currie, 2016), Pachycephalosauridae (Evans et al., 2013), and Tyrannosauridae (Lü et al., 2014). The identification of a sister taxon to the Mongolian taxa *Philovenator curriei* and *Linhevenator tani* in North America is not unexpected. The presence of an Asian lineage of troodontid in the DPF during the upper Campanian provides evidence for a third troodontid species in North America that is a sister taxon to an Asian species. These three species are *Latenivenatrix mcmasterae, Talos sampsoni* (Zano et al., 2011), and *Troodon formosus* (Leidy, 1856) (Fig. 3). *Latenivenatrix mcmasterae* represents a more basal troodontid replacing the derived *Stenonychosaurus inequalis* in the Dinosaur Park Formation. This may have been possible given the much larger size of *Latenivenatrix mcmasterae*.

The discovery of *Latenivenatrix mcmasterae* provides better understanding of small theropods in the Dinosaur Park Formation and ultimately evidence of greater diversity than previously thought for Troodotidae during the late Cretaceous in North America. Phylogenetic analysis indicates *Latenivenatrix mcmasterae* is the sister taxon to *Philovenator curriei* and *Linhevenator tani*, suggesting an Asian origin for the new taxon. The identification of this new taxon in the Dinosaur Park Formation provides evidence that theropods may have undergone major faunal changes like those observed in megaherbivores.

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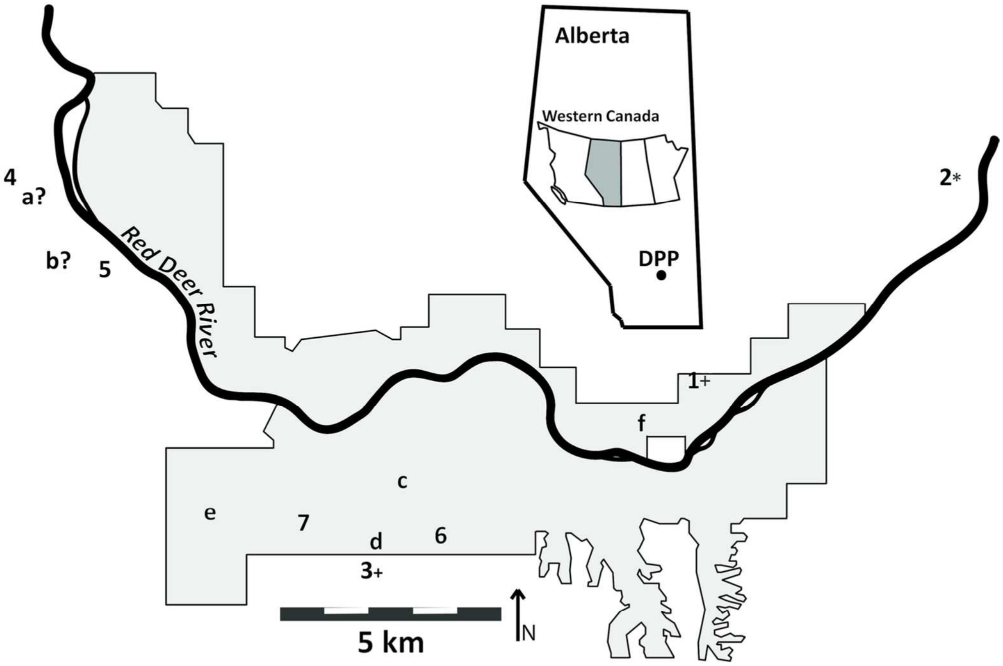


Figure 1. Locality map of troodontid specimens within and around Dinosaur Provincial Park of Latenivenatrix mcmasterae (numbers) and Stenonychosaurus inequalis (letters). ‘*’ represents locality where the holotype of the former was found. ‘+’ represents localities for primary referred specimens of the same species. Stenonychosaurus inequalis; a) CMN 8540, dentary. b) CMN 8539, pes. c) TMP 1986.036.0457, braincase. d) TMP 1986.078.0040, frontal. e) UALVP 5282, frontal. f) UALVP 52611, frontals and parietals. Latenivenatrix mcmasterae; 1) UALVP 55804, pelvis. 2) CMN 12340, partial skeleton (Russell, 1969). 3) TMP 1982.019.0023, partial skull (Currie, 1985). 4) TMP 1979.008.0001, frontals and parietals. 5) TMP 1980.016.1478, frontal. 6) TMP 1992.036.0575, metatarsus and dentary. 7) TMP 1997.133.0008, metatarsal III.

130x93mm (300 x 300 DPI)

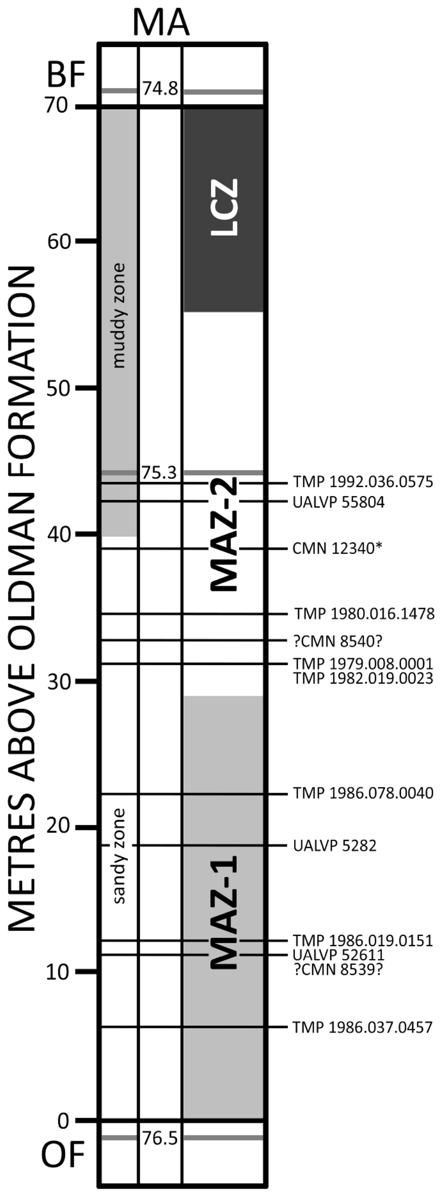


Figure 2. Stratigraphic cross-section of the Dinosaur Park Formation with known troodontid specimen elevations marked. Specimens with no elevation data could not be placed and therefore not marked.

236x653mm (300 x 300 DPI)

Figure 4. Profile view of composite skeletal map for Latenivenatrix mcmasterae based on four specimens. In the case of overlapping specimen elements (i.e. cranial material), most complete specimens were used.

64x23mm (300 x 300 DPI)

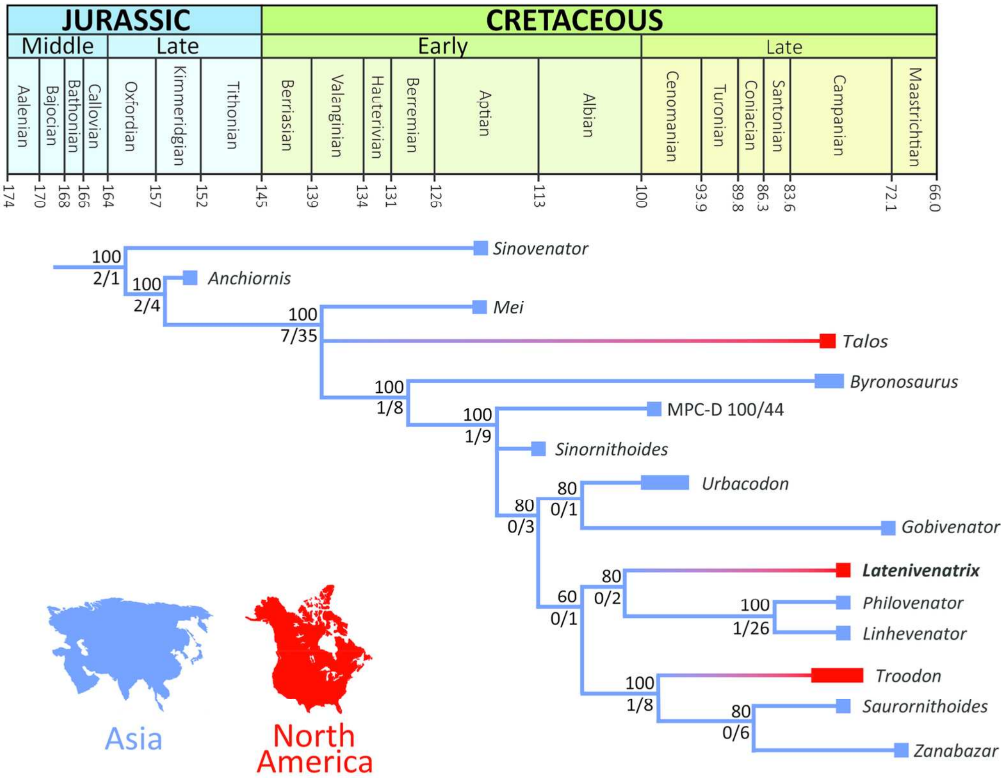


Figure 3. Time calibrated portion of Majority Rules (60%) tree as reconstructed for Troodontidae. Produced from the most parsimonious 60 trees (999999 replications with 454185609141 rearrangements) resulting from the data sets of Tsuihji, et al. (2014), Gao, et al. (2012), and Averianov and Sues (2007). Reconstructed with addition of Latenivenatrix mcmasterae. Note, Anchiornis is reconstructed as a basal troodontid, however it is no longer considered a part of this clade (Pei et al., 2017). Numbers above nodes are 50% Majority Rules values (in %). Numbers below nodes represent the Bremer support value/Bootstrap Value (calculated from 5000 replications).

143x113mm (300 x 300 DPI)

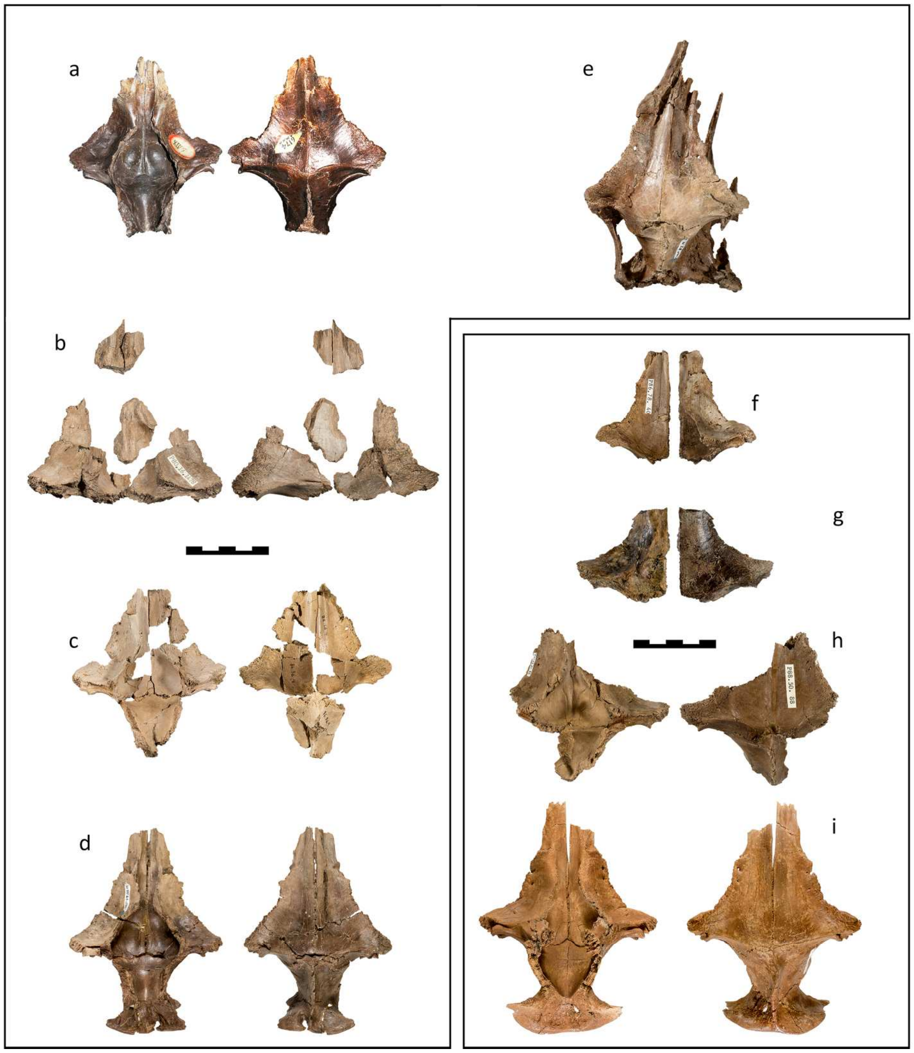


Figure 5. Troodontid cranial material from the Dinosaur Park Formation. a-e, Latenivenatrix mcmasterae specimens with triangular frontals possessing a deeply grooved nasofrontal suture surface. Parietals are narrow anteriorly. f-j, Stenonychosaurus inequalis specimens with "L" shaped frontals possessing smoother nasofrontal suture surface. Parietals broaden anteriorly. a) UALVP 55285 (left – dorsal, right – ventral). b) TMP 1982.019.0023 (dorsal view) c) TMP 1980.016.1748 (left – dorsal, right – ventral). d) TMP 1986.036.0004 (left – dorsal, right – ventral). e) TMP 1979.008.0001 (left – dorsal, right – ventral). f) TMP 1986.070.0040 (left – dorsal, right – ventral). g) UALVP 5282 (left – ventral, right – dorsal). h) TMP 1991.036.0690 (left – ventral, right – dorsal). i) TMP 1988.50.0088 (left – ventral, right – dorsal). j) UALVP 52611 (left – ventral, right – dorsal). Scale = 5 cm.

192x203mm (300 x 300 DPI)

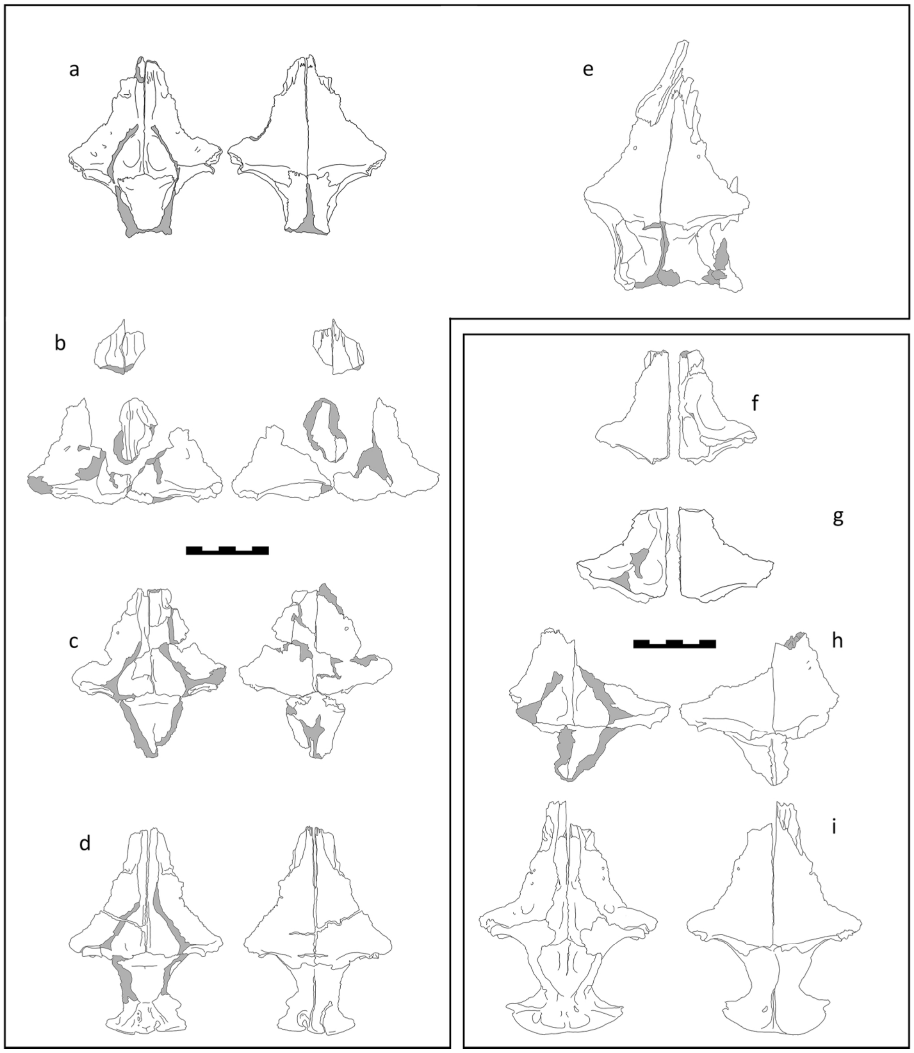


Figure 6. Line drawings of Dinosaur Park Formation troodontid cranial material. a-e, Latenivenatrix mcmasterae specimens with triangular frontals possessing a deeply grooved nasofrontal suture surface. Parietals are narrow anteriorly. f-j, Stenonychosaurus inequalis specimens with "L" shaped frontals possessing smoother nasofrontal suture surface. Parietals broaden anteriorly. a) UALVP 55285 (left – dorsal, right – ventral). b) TMP 1982.019.0023 (dorsal view) c) TMP 1980.016.1748 (left – dorsal, right – ventral). d) TMP 1986.036.0004 (left – dorsal, right – ventral). e) TMP 1979.008.0001 (left – dorsal, right – ventral). f) TMP 1986.070.0040 (left – dorsal, right – ventral). g) UALVP 5282 (left – ventral, right – dorsal). h) TMP 1991.036.0690 (left – ventral, right – dorsal). i) TMP 1988.50.0088 (left – ventral, right – dorsal). j) UALVP 52611 (left – ventral, right – dorsal). Scale = 5 cm.

192x203mm (300 x 300 DPI)

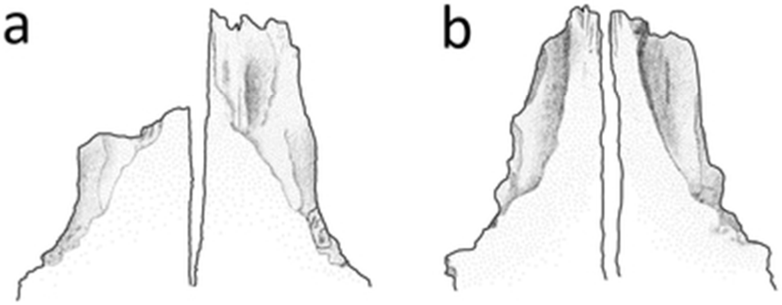


Figure 7. Nasofrontal suture patterns of (a) Stenonychosaurus inequalis (TMP 1979.008.0001), and (b) Latenivenatrix mcmasterae (UALVP 52611).

38x14mm (300 x 300 DPI)

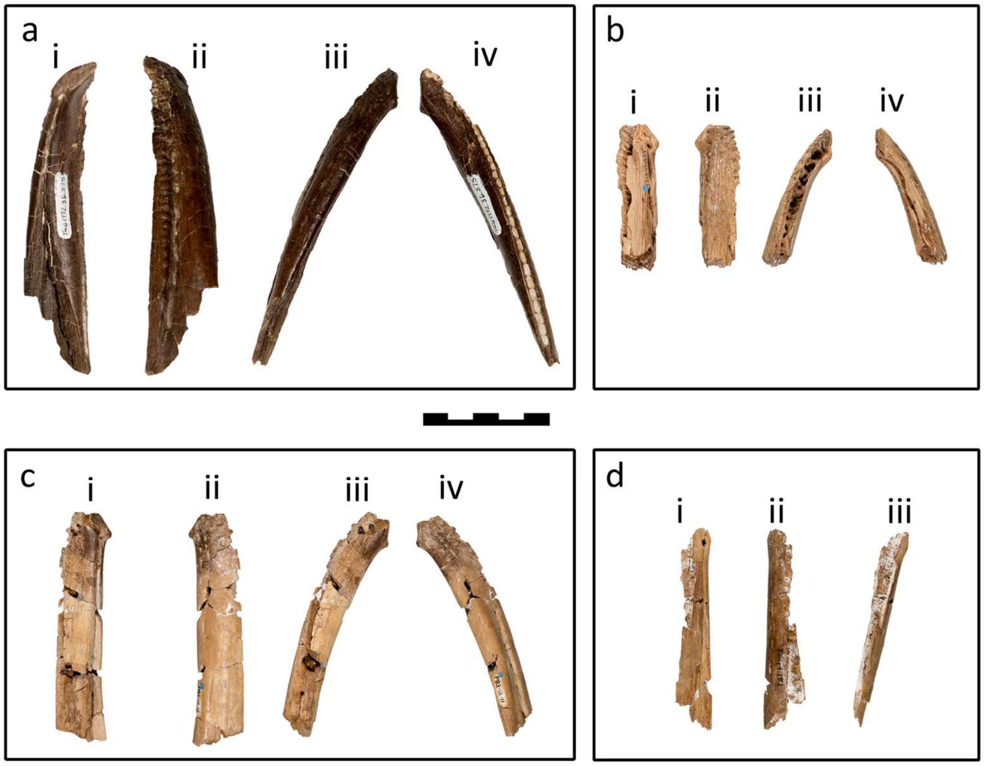


Figure 8. Troodontid dentaries from Alberta, Canada. a) right dentary of Latenivenatrix mcmasterae (TMP 1992.036.0575) (i, lingual; ii, labial; iii, ventral; iv, dorsal). b) left dentary of Troodontidae indet. from the Dinosaur Park Formation (TMP 1967.014.0039) (i, lingual; ii, labial; iii, dorsal; iv, ventral). c) left dentary of "Troodon formosus" (Currie, 1987) from the Horseshoe Canyon Formation (Campanian-Maastritchian), Drumheller, Alberta (TMP 1983.012.0011) (i, lingual; ii, labial; iii, dorsal; iv, ventral). d) left dentary of cf. Stenonychosaurus inequalis from Oldman/Dinosaur Park Formation boundary (TMP 1982.019.0151) (i, lingual; ii, labial; iii, dorsal).

139x107mm (300 x 300 DPI)

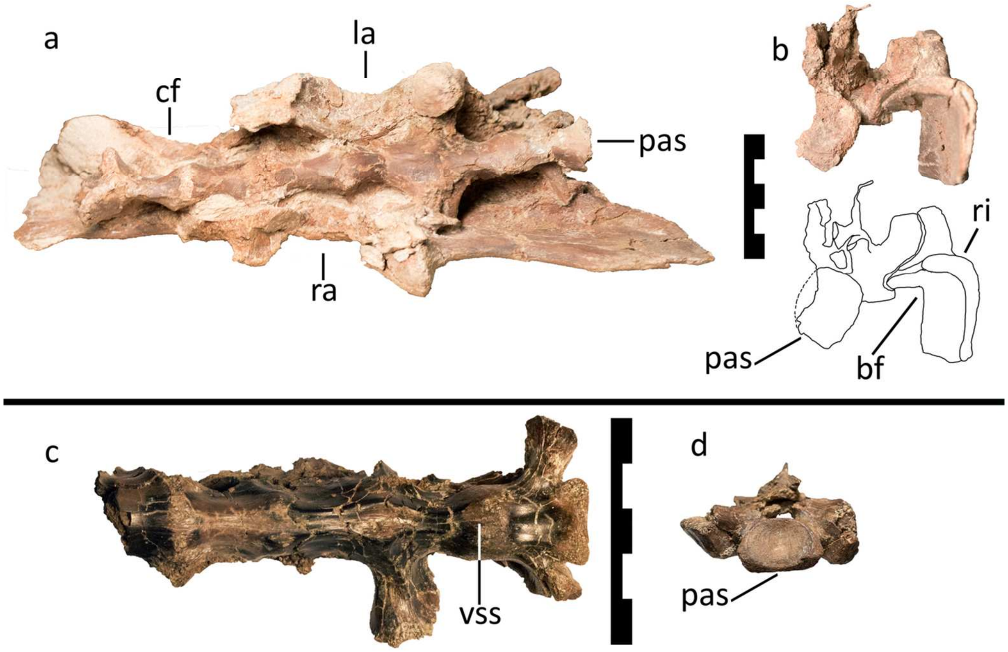


Figure 9. A) Ventral view of Latenivenatrix mcmasterae (UALVP 55804) sacrum and ilia (anterior to left). B) Posterior view of Latenivenatrix mcmasterae (UALVP 55804) sacrum and right ilium. C) Ventral view of Saurornitholestes langstoni (TMP 1992.036.0129) sacrum (anterior to left). D) Posterior view of Saurornitholestes langstoni (TMP 1992.036.0129) sacrum. Scale bar, 5 cm. bf, brevis fossa; cf, cuppedicus fossa; la, left acetabulum; pas, posterior articular surface; ra, right acetabulum; ri, right ilium; vss, ventral sulcus of the sacrum.

124x85mm (300 x 300 DPI)

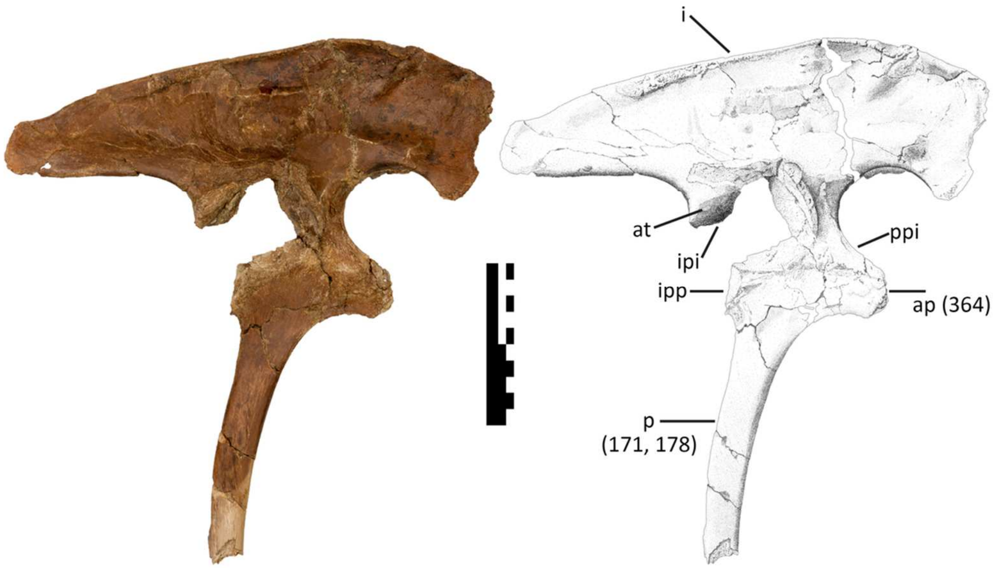


Figure 10. Photo and stipple drawing of the right ilium and fused pubis of Latenivenatrix mcmasterae (UALVP 55804) in lateral view. Scale bar, 10 cm. ap, ambiens process; at, antitrochanter; i, ilium; ipi, ischiadic peduncle of the ilium; ipp, ischiadic peduncle of the pubis; p, pubis; ppi, pubic peduncle of the ilium. Numbers in brackets indicated characters of note that pertain to those features. Character 364 is a new character.

103x59mm (300 x 300 DPI)

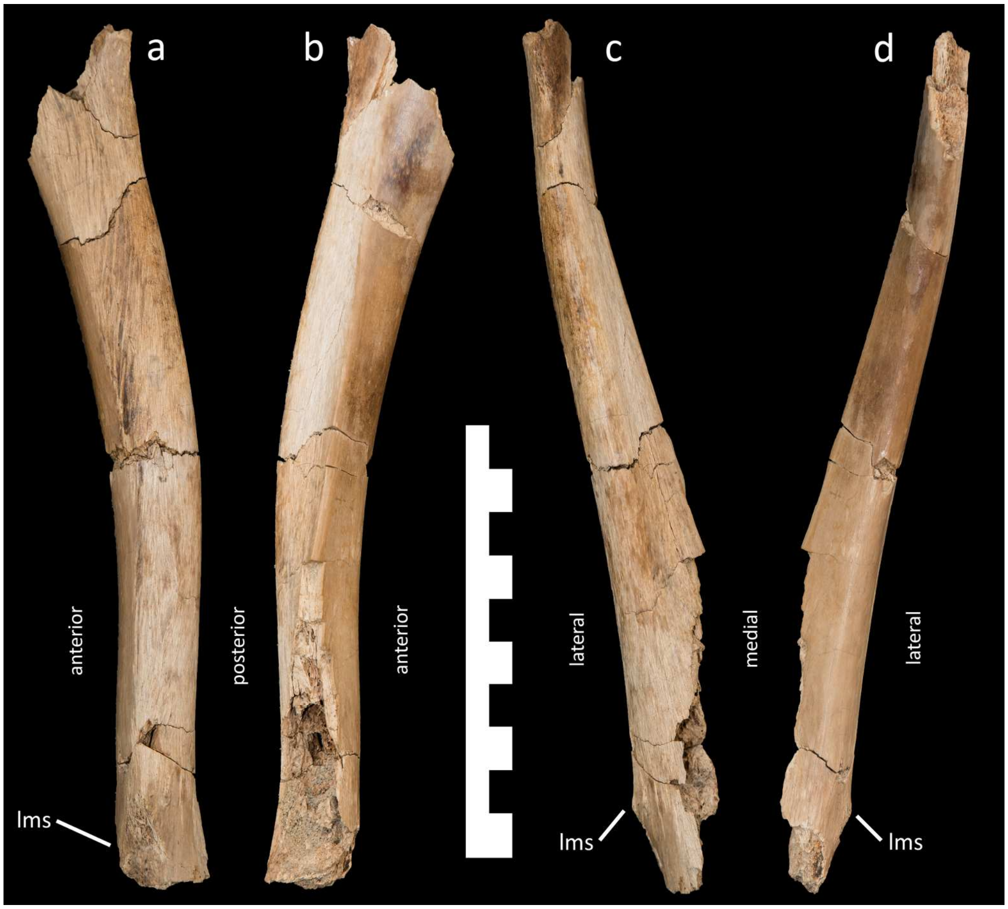


Figure 11. Left pubic shaft of Latenivenatrix mcmasterae (UALVP 55804) showing vertical ventral half with large pronounced muscle scar above brakeage point. a) Lateral. b) Medial. c) Anterior. d) Posterior. Scale, 10 cm.

179x161mm (300 x 300 DPI)

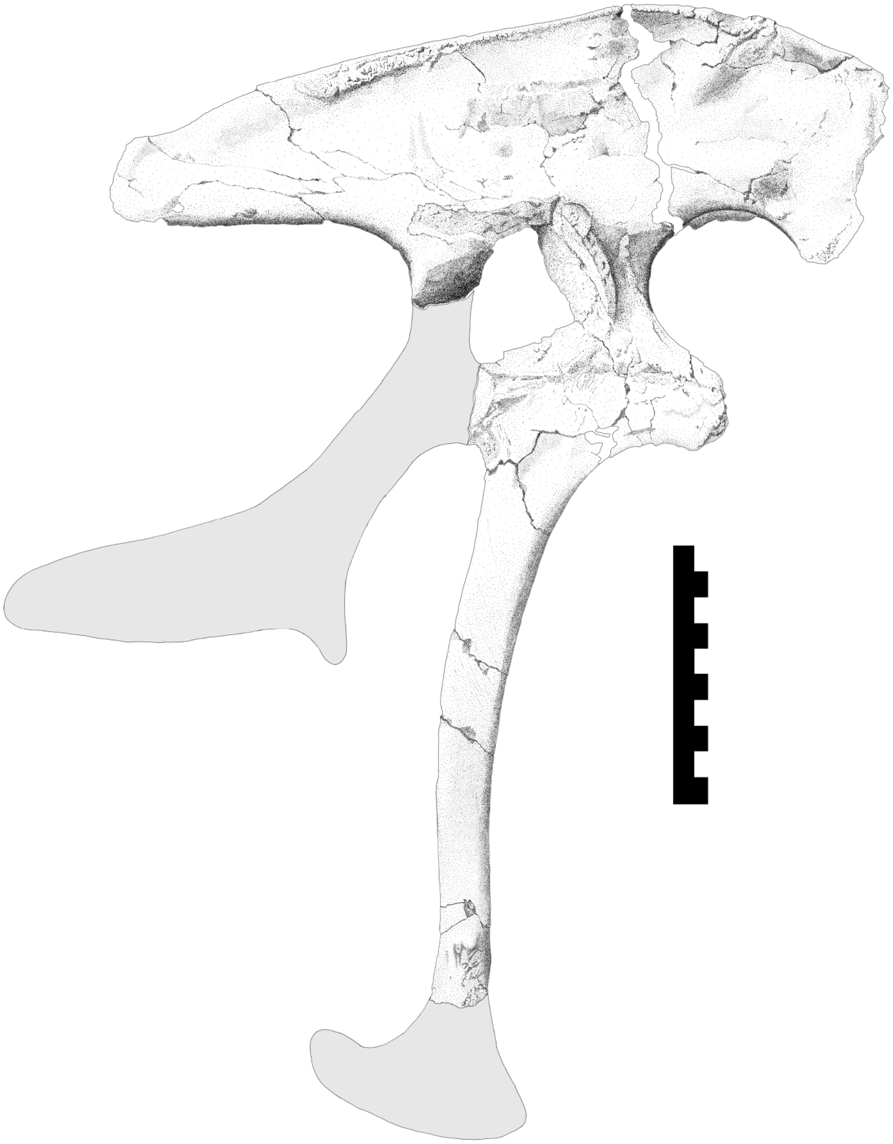


Figure 12. Reconstruction of the pelvis (UALVP 55804) of Latenivenatrix mcmasterae with all known pubic material combined. Grey regions are estimated shapes for the pubic boot and ischium. Scale = 10 cm.

237x312mm (300 x 300 DPI)

Figure 13. Latenivenatrix mcmasterae right metatarsus (TMP 1992.36.575). a) Anterior. b) Posterior. c) Medial. d) Lateral. e) Proximal. f) Distal. MT, Metatarsal. Scale bar, 5 cm.

223x273mm (300 x 300 DPI)

Figure 14. Anterior view of metatarsal III and cross section shape (anterior up) of distal shaft (black line). This cross sectional shape is the newly added character 366. Latenivenatrix mcmasterae, a) TMP 1992.036.0575, b) TMP 1997.133.0008. Stenonychosaurus inequalis, c) TMP 1998.068.0090. Latenivenatrix mcmasterae possesses a concave anterior surface, while Stenonychosaurus inequalis possesses a slightly convex anterior surface.

236x520mm (300 x 300 DPI)

Figure 15. Profile view of composite skeletal map for Stenonychosaurus inequalis based on three specimens.

64x23mm (300 x 300 DPI)

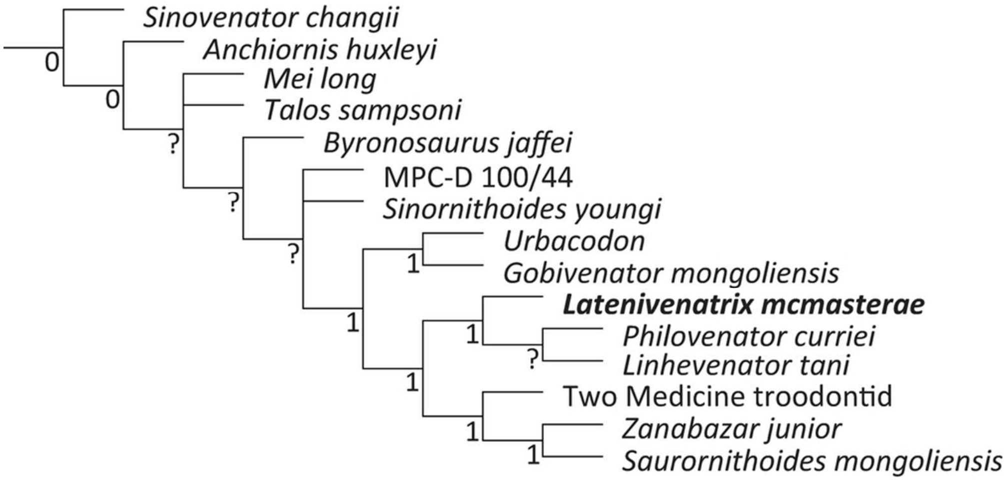
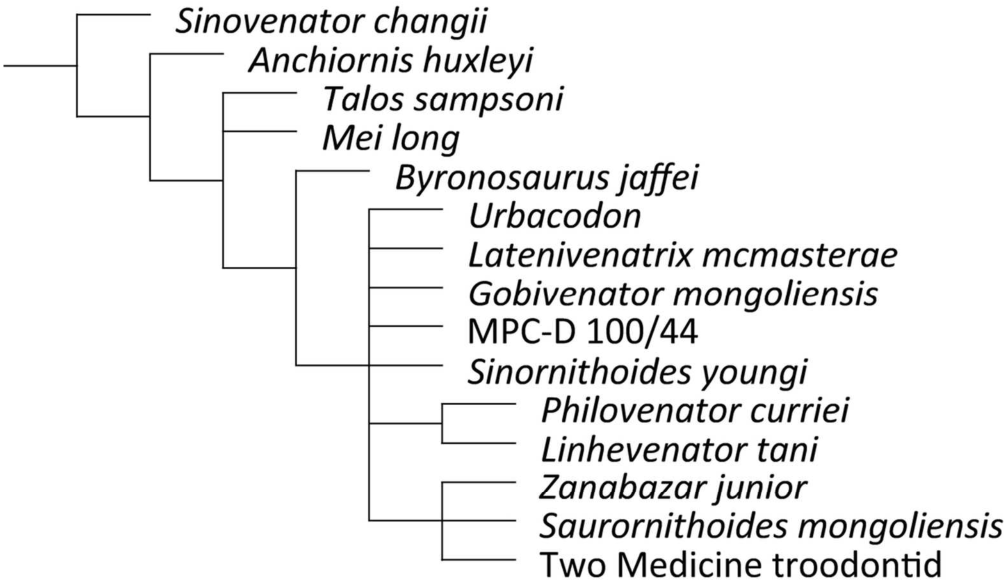


Figure 16. Portion of Majority Rules (50%) tree as reconstructed for Troodontidae. Reconstructed with addition of Latenivenatrix mcmasterae. Character state map for character 364 (elongated ambiens process); 0 = absent, 1 = present, ? = unknown state at node. Produced from the most parsimonious 60 trees resulting from the data set of Tsuihji, et al. (2014), Gao et al. (2012), and Averianov and Sues (2007).

85x40mm (300 x 300 DPI)

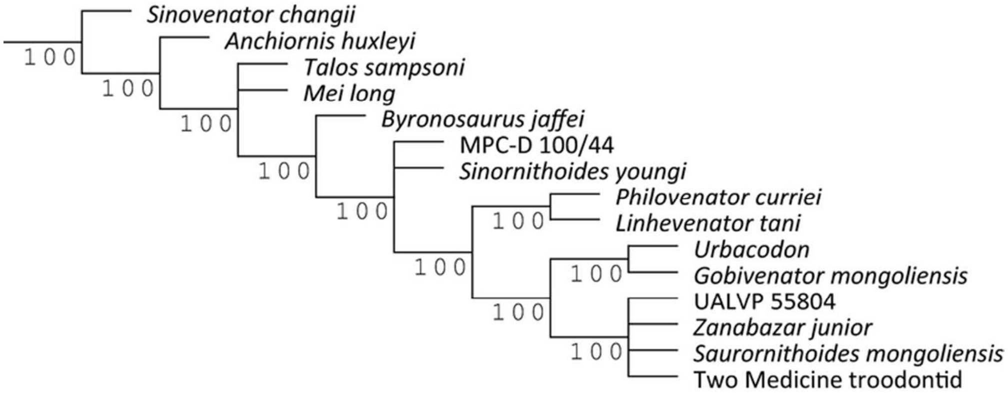
Table 1. Known elevations of identifiable troodontid specimens from the Dinosaur Park Formation and their placement within either MAZ-1 or MAZ-2. OMF = Oldman Formation.

Specimen	Morph Type	Elevation	m Above OMF	m in MHZ 1	m in MHZ 2	OMF Top Elev
Frontals						
CMN 12340	Triangle	699	39		10	660
TMP 1979.008.0001	Triangle	678.109	31.109		2.109	647
TMP 1980.016.1478	Triangle	682	34		5	648
TMP 1982.019.0023	Triangle	706.05	31.05		2.05	675
TMP 1986.078.0040	L Shape	689	22	22		667
UALVP 5282	L Shaped	680	19	19		661
UALVP 52611	L Shape	671	11	11		660
TMP 1986.036.0004	?Triangle?	??				
TMP 1988.050.0088	L Shaped	??				
TMP 1991.036.0690	?L Shape?	??				
UALVP 55285	?Triangle?	??				
Braincases						
TMP 1982.019.0023		706.05	31.05		2.05	675
TMP 1986.036.0457		669.374	12.174	12.174		657.2
Dentaries						
TMP 1982.019.0151		652.4	-2.6	-2.6		655
TMP 1992.036.0575		704	43		14	661
Metatarsals						
TMP 1992.036.0575	Concave	704	43		14	661
TMP 1997.133.0008	Concave	??				
TMP 1998.068.0090	Convex	688.1	26.1	26.1		662
Pelvic Elements						
UALVP 55804		671	42		13	650



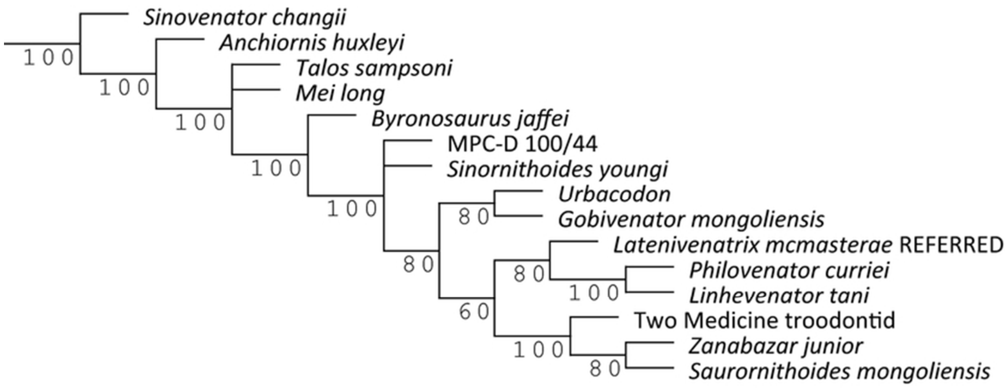
APPENDIX 1. Troodontidae portion of the strict consensus tree produced from the most parsimonious 60 trees resulting from the data set of Gao, et al. (2012), Tsuihji, et al. (2014), and Averianov and Sues (2007), incorporating Latenivenatrix mcmasterae. Tree length 1357.

105x62mm (300 x 300 DPI)



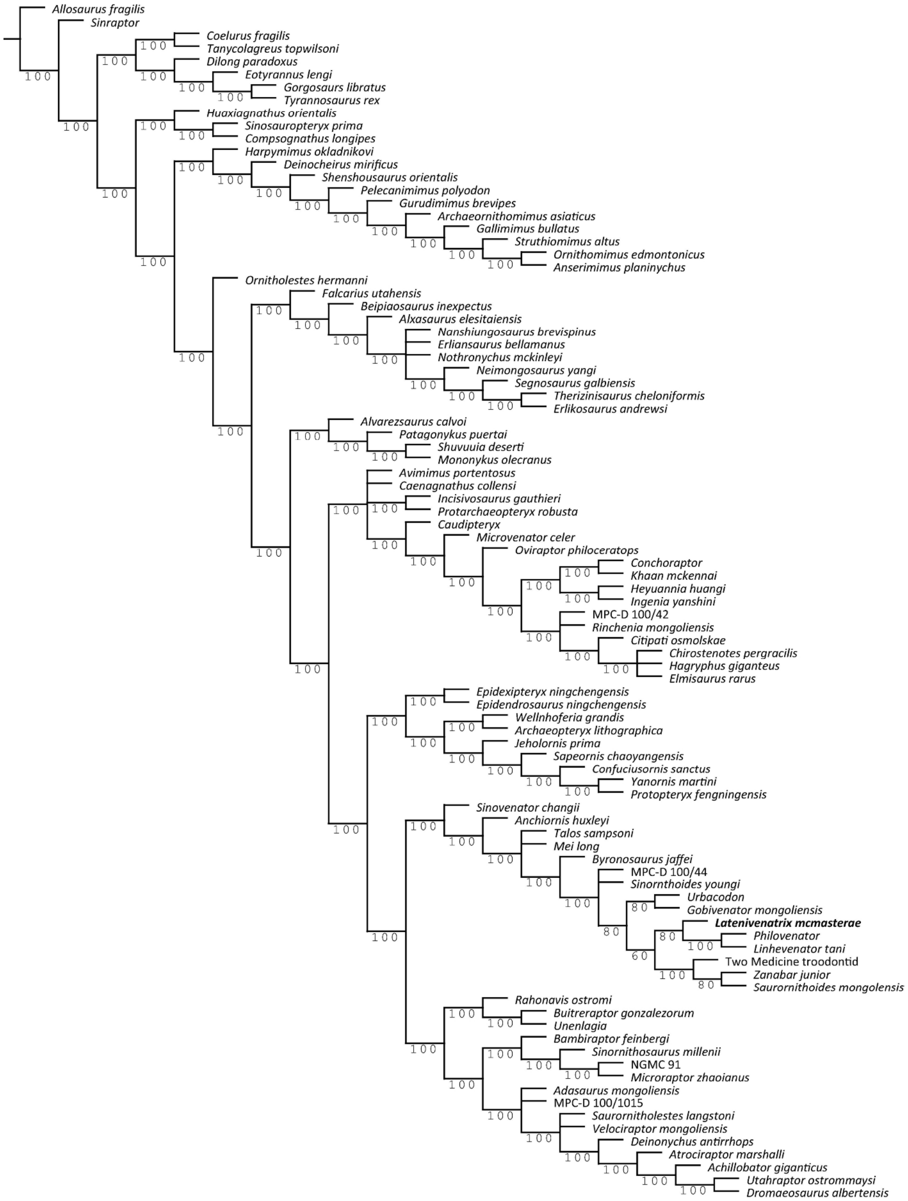
APPENDIX 2. Troodontidae portion of 50% Majority Rules coded for UALVP 55804 only.

71x28mm (300 x 300 DPI)



APPENDIX 3. Troodontidae portion of 50% Majority Rules coded for the Latenivenatrix mcmasterae paratypes (CMN 12340 and TMP 82.019.023).

70x27mm (300 x 300 DPI)



APPENDIX 4. 50% Majority Rules tree produced using from the most parsimonious 60 trees resulting from the data set of Gao, et al. (2012), Tsuihji, et al. (2014), and Averianov and Sues (2007), incorporating Latenivenatrix mcmasterae. Tree length 1357.

226x301mm (300 x 300 DPI)

APPENDIX 5. Character list. Characters 1-363 are from Gao, et al., characters 364, 365, and 366 are new characters (italicized).

APPENDIX 5

1. Vaned feathers on forelimb symmetric (0) or asymmetric (1). The barbs on opposite sides of the rachis differ in length; in extant birds, the barbs on the leading edge of flight feathers are shorter than those on the trailing edge.
2. Orbit round in lateral or dorsolateral view (0) or dorsoventrally elongate (1). It is unclear that the eye occupied the entire orbit of those taxa in which it is keyhole shaped.
3. Anterior process of postorbital projects into orbit (0) or does not project into orbit (1).
4. Postorbital in lateral view with subhorizontal anterior (frontal) process (0) or frontal process diagonal (anterior tip of process higher than base of process) (1). [Formerly: postorbital in lateral view with straight anterior (frontal) process (0) or frontal process curves anterodorsally and dorsal border of temporal bar is dorsally concave (1)]
5. Postorbital bar parallels quadrate, lower temporal fenestra rectangular in shape (0) or jugal and postorbital approach or contact quadratojugal to constrict lower temporal fenestra (1).
6. Otosphenoidal crest vertical on basisphenoid and prootic, and does not border an enlarged pneumatic recess (0) or well developed, crescent shaped, thin crest forms anterior edge of enlarged pneumatic recess (1). This structure forms the anterior, and most distinct, border of the "lateral depression" of the middle ear region (see Currie, 1985; Currie and Zhao, 1992) of troodontids and some extant avians.
7. Crista interfenestralis confluent with lateral surface of prootic and opisthotic (0) or distinctly depressed within middle ear opening (1).
8. Subotic recess (pneumatic fossa ventral to fenestra ovalis) absent (0) or present (1)
9. Basisphenoid recess present between basisphenoid and basioccipital (0) or entirely within basisphenoid (1) or absent (2).
10. Posterior opening of basisphenoid recess single (0) or divided into two small, circular foramina by a thin bar of bone (1).
11. Base of cultriform process not highly pneumatized (0) or base of cultriform process (parasphenoid rostrum) expanded and pneumatic (parasphenoid bulla) (1).
12. Basipterygoid processes ventral or anteroventrally projecting (0) or lateroventrally projecting (1).
13. Basipterygoid processes well developed, extending as a distinct process from the base of the basisphenoid (0) or processes abbreviated or absent (1).
14. Basipterygoid processes solid (0) or processes hollow (1).
15. Basipterygoid recesses on dorsolateral surfaces of basipterygoid processes absent (0) or present (1).
16. Depression for pneumatic recess on prootic absent (0) or present as dorsally open fossa on prootic/opisthotic (1) or present as deep, posterolaterally directed concavity (2). The dorsal tympanic recess referred to here is the depression anterodorsal to the middle ear on the opisthotic, not the recess dorsal to the crista interfenestralis within the middle ear as seen in Archaeopteryx lithographica, Shuuvuia deserti and Aves.
17. Accessory tympanic recess dorsal to crista interfenestralis absent (0) small pocket present (1) or extensive with indirect pneumatization (2). According to Witmer (1990), this structure may be an extension from the caudal tympanic recess, although it has been interpreted as the main part of the caudal tympanic recess by some authors (e.g., Walker, 1985).
18. Caudal (posterior) tympanic recess absent (0) present as opening on anterior surface of paroccipital process (1) or extends into opisthotic posterodorsal to fenestra ovalis, confluent with this fenestra (2).
19. Exits of C. N. X-XII flush with surface of exoccipital (0) or cranial nerve exits located together in a bowl-like basisphenoid depression (1).

20. Maxillary process of premaxilla contacts nasal to form posterior border of nares (0) or maxillary process reduced so that maxilla participates broadly in external naris (1) or maxillary process of premaxilla extends posteriorly to separate maxilla from nasal posterior to nares (2).
21. Internarial bar rounded (0) or flat (1).
22. Crenulate margin on buccal edge of premaxilla absent (0) or present (1).
23. Caudal margin of naris farther rostral than (0), or nearly reaching or overlapping (1), the rostral border of the antorbital fossa (Chiappe et al. 1998).
24. Premaxillary symphysis acute, V-shaped (0) or rounded, U-shaped (1).
25. Secondary palate short (0) or long, with extensive palatal shelves on maxilla (1). [Reworded according to Makovicky et al. 2005. Formerly: secondary palate formed by premaxilla only (0) or by premaxilla maxilla and vomer (1)]
26. Palatal shelf of maxilla flat (0) or with midline ventral ‘tooth-like’ projection (1)
27. Pronounced, round accessory antorbital fenestra absent (0) or present (1). A small fenestra, variously termed the accessory antorbital fenestra or maxillary fenestra, penetrates the medial wall of the antorbital fossa anterior to the antorbital fenestra in a variety of coelurosaurs and other theropods.
28. Accessory antorbital fossa situated at rostral border of antorbital fossa (0) or situated posterior to rostral border of fossa (1).
29. Tertiary antorbital fenestra (fenestra promaxillaris) absent (0) or present (1).
30. Antorbital fossa without distinct rim ventrally and anteriorly (0) or with distinct rim composed of a thin wall of bone (1). A rim is most strongly developed in the therizinosauroid Erlikosaurus andrewsi (Clark et al., 1994) but is nearly absent in ornithomimosaurs.
31. Narial region apneumatic or poorly pneumatized (0) or with extensive pneumatic fossae, especially along posterodorsal rim of fossa (1).
32. Jugal and postorbital contribute equally to postorbital bar (0) or ascending process of jugal reduced and descending process of postorbital ventrally elongate (1).
33. Jugal quadratojugal process tall beneath lower temporal fenestra, twice or more as tall dorsoventrally as it is wide transversely (0) or rod-like (1) or concealed by quadratojugal (2). [Formerly: lacked italicised additions.] State 2 added in reference to the condition exhibited by most ornithomimosaurs.
34. Jugal pneumatic recess in posteroventral corner of antorbital fossa present (0) or absent (1).
35. Medial jugal foramen present on medial surface ventral to postorbital bar (0) or absent (1).
36. Quadratojugal without horizontal process posterior to ascending process (reversed “L” shape) (0) or with process (i.e., inverted ‘T’ or ‘Y’ shape) (1).
37. Jugal and quadratojugal separate (0) or quadratojugal and jugal fused and not distinguishable from one another (1).
38. Supraorbital crests on lacrimal in adult individuals absent (0) or dorsal crest above orbit (1) or lateral expansion anterior and dorsal to orbit (2).
39. Enlarged foramen or foramina opening laterally at the angle of the lacrimal, absent (0) or present (1).
40. Lacrimal posterodorsal [Formerly: ‘anterodorsal’, probably a typographical error] process absent (inverted ‘L’ shaped) (0) or lacrimal ‘T’ shaped in lateral view (1) or anterodorsal process much longer than posterior process (2) or posterodorsal process subvertical (3). [Formerly without character state 3] State 3 added in reference to the condition in oviraptorids.
41. Prefrontal large, dorsal exposure similar to that of lacrimal (0) or greatly reduced in exposure (1) or without exposure (2). [Formerly: prefrontal large, dorsal exposure similar to that of lacrimal (0) or greatly reduced in size (1) or absent (2).] State 2 reworded to recognize the finding that a prefrontal that appears to be absent is present but unexposed in some taxa.
42. Frontals narrow anteriorly as a wedge between nasals (0) or end abruptly anteriorly, suture with nasal transversely orientated (1) or suture with nasals W-shaped (2). [Formerly without character state 2]
43. Anterior emargination of supratemporal fossa on frontal straight or slightly curved (0) or strongly sinusoidal and reaching onto postorbital process (1)(Currie 1995).
44. Frontal postorbital process (dorsal view): smooth transition from orbital margin (0) or sharply demarcated from orbital margin (1), (Currie 1995).
45. Frontal edge smooth in region of lacrimal suture (0) or edge notched (1) (Currie 1995).

46. Dorsal surface of parietals flat, lateral ridge borders supratemporal fenestra (0) or parietals dorsally convex with very low sagittal crest along midline (1) or dorsally convex with well developed sagittal crest (2).
47. Parietals separate (0) or fused (1).
48. Descending process of squamosal parallels quadrate shaft (0) or nearly perpendicular to quadrate shaft (1).
49. Descending process of squamosal contacts quadratojugal (0) or does not contact quadratojugal (1).
50. Posterolateral shelf on squamosal overhanging quadrate head absent (0) or present (1).
51. Dorsal process of quadrate single headed (0) or with two distinct heads, a lateral one contacting the squamosal and a medial head contacting the braincase (1).
52. Quadrate vertical (0) or strongly inclined anteroventrally so that distal end lies far forward of proximal end (1).
53. Quadrate solid (0) or hollow, with depression on posterior surface (1).
54. Lateral border of quadrate shaft straight (0) or with lateral tab that touches squamosal and quadratojugal above an enlarged quadrate foramen (1)
55. Foramen magnum subcircular, slightly wider than tall (0) or oval, taller than wide (1). See Makovicky and Sues (1998).
56. Occipital condyle without constricted neck (0) or subspherical with constricted neck (1).
57. Paroccipital process elongate and slender, with dorsal and ventral edges nearly parallel (0) or process short, deep with convex distal end (1).
58. Paroccipital process straight, projects laterally or posterolaterally (0) or distal end curves ventrally, pendant (1).
59. Paroccipital process with straight dorsal edge (0) or with dorsal edge twisted rostrolaterally at distal end (1) (Currie 1995).
60. Ectopterygoid with constricted opening into fossa (0) or with open ventral fossa in the main body of the element (1).
61. Dorsal recess on ectopterygoid absent (0) or present (1).
62. Flange of pterygoid well developed (0) or reduced in size or absent (1).
63. Palatine and ectopterygoid separated by pterygoid (0) or contact (1) (Currie 1995).
64. Palatine tetraradiate, with jugal process (0) or palatine triradiate, jugal process absent (1).
65. Suborbital fenestra similar in length to orbit (0) or about half or less than half orbital length (1) or absent (2).[Formerly: reduced in size (less than one quarter orbital length) or absent (1)]
66. Symphyseal region of dentary broad and straight, paralleling lateral margin (0) or medially recurved slightly (1) or strongly recurved medially (2).
67. Dentary symphyseal region in line with main part of buccal edge (0) or abruptly downturned at rostral end (1) or dentary ramus gradually, weakly downturned through its length (2). [Formerly without italicised additions] Reworded to recognise the difference between the abruptly downturned dentary tips of certain oviraptorosaurs and the gradual downturn in the entire dentary ramus of taxa such as Coelurus and therizinosauroids.
68. Mandible without coronoid prominence (0) or with coronoid prominence (1).
69. Posterior end of dentary without posterodorsal process dorsal to mandibular fenestra (0) or with dorsal process above anterior end of mandibular fenestra (1) or with elongate, strongly arched dorsal process extending over most of fenestra (2). [Formerly without italicized addition]
70. Labial face of dentary flat (0) or with lateral ridge and inset tooth row (1).
71. Dentary subtriangular in lateral view (0) or with subparallel dorsal and ventral edges (1) (Currie 1995).
72. Nutrient foramina on external surface of dentary superficial (0) or lie within deep groove (1).
73. External mandibular fenestra oval (0) or subdivided by a spinous rostral process of the surangular (1).
74. Internal mandibular fenestra small and slit-like (0) or large and rounded (1) (Currie 1995).
75. Foramen in lateral surface of surangular rostral to mandibular articulation, absent (0) or present (1).
76. Splenial not widely exposed on lateral surface of mandible (0) or exposed as a broad triangle between dentary and angular on lateral surface of mandible (1).
77. Coronoid ossification large (0) or only a thin splint (1) or absent (2).

78. Articular without elongate, slender medial, posteromedial, or mediodorsal process from retroarticular process (0) or with process (1).
79. Retroarticular process short, stout (0) or elongate and slender (1).
80. Mandibular articulation surface as long as distal end of quadrate (0) or twice or more as long as quadrate surface, allowing anteroposterior movement of mandible (1).
81. Premaxilla toothed (0) or edentulous (1).
82. Second premaxillary tooth approximately equivalent in size to other premaxillary teeth (0) or second tooth markedly larger than third and fourth premaxillary teeth (1) or first premaxillary tooth huge, other premaxillary teeth tiny (2) or first premaxillary tooth larger than the others but all premaxillary teeth tiny (3).[Formerly without character states 2 and 3] State 2 added in reference to the condition in Protarchaeopteryx and Incisivosaurus (Senter et al. 2004). State 3 added in reference to the condition in Caudipteryx.
83. Maxilla toothed (0) or edentulous (1).
84. Maxillary and dentary teeth serrated (0) or some without serrations anteriorly (except at base in S. mongoliensis) (1) or all without serrations (2).
85. Dentary and maxillary teeth large, less than 25 in dentary (0) or large number of small teeth (25 or more in dentary) (1) or small number of dentary teeth (≤11) (2) or dentary without teeth (3). [Formerly: dentary and maxillary teeth large, less than 25 in dentary (0) or moderate number of small teeth (25–30 in dentary) (1) or teeth relatively small and numerous (more than 30 in dentary) (2).] State 2 added to recognise the extreme reduction in dentary tooth count in some ornithomimosaurs.
86. Serration denticles large (0) or small (1). Farlow et al. (1991) quantify this difference.
87. Serrations simple, denticles convex (0) or distal and often mesial edges of teeth with large, hooked denticles that point toward the tip of the crown (1).
88. Teeth constricted between root and crown (0) or root and crown confluent (1).
89. Dentary teeth evenly spaced (0) or anterior dentary teeth smaller, more numerous, and more closely appressed than those in middle of tooth row (1).
90. Dentaries lack distinct interdental plates (0) or with interdental plates medially between teeth (1). Currie (1995) suggests the interdental plates of dromaeosaurids are present but fused to the medial surface of the dentary, but in the absence of convincing evidence for this fusion we did not recognize this distinction.
91. In cross section, premaxillary tooth crowns sub-oval to sub-circular (0) or asymmetrical (D-shaped in cross section) with flat lingual surface (1) or first premaxillary tooth with flat lingual surface, other premaxillary teeth without flat lingual surfaces (2). [Formerly without state 2] State 2 added in reference to the condition in Protarchaeopteryx and Incisivosaurus.
92. Number of cervical vertebrae: 10 (0) or 12 or more (1).
93. Axial epipophyses absent or poorly developed, not extending past posterior rim of postzygopophyses (0) or large and posteriorly directed, extend beyond postzygapophyses (1).
94. Axial neural spine flared transversely (0) or compressed mediolaterally (1).
95. Epipophyses of cervical vertebrae placed distally on postzygapophyses, above postzygopophyseal facets (0) or placed proximally, proximal to postzygapophyseal facets (1).
96. Anterior cervical centra level with or shorter than posterior extent of neural arch (0) or centra extending beyond posterior limit of neural arch (1).
97. Carotid process on posterior cervical vertebrae absent (0) or present (1).
98. Anterior cervical centra subcircular or square in anterior view (0) or distinctly wider than high, kidney shaped (1).
99. Cervical neural spines anteroposteriorly long and dorsoventrally tall (0) or anteroposteriorly short, dorsoventrally low and centred on neural arch, giving arch an ‘X’ shape in dorsal view (1) or anteroposteriorly short and dorsoventrally tall (2) or anteroposteriorly long and dorsoventrally short (3). [Formerly without italicised additions] Changes introduced in recognition of a wider variety of cervical neural spine shapes than was recognised by the previous wording.
100. Cervical centra with one pair of pneumatic openings (0) or with two pairs of pneumatic openings (1).
101. Cervical and anterior trunk vertebrae amphiplatyan (0) or opisthocoelous (1).
102. Anterior trunk vertebrae without prominent hypapophyses (0) or with large hypapophyses (1).

103. Parapophyses of posterior trunk vertebrae flush with neural arch (0) or distinctly projected on pedicels (1).
104. Hyposphene -hypantrum articulations in trunk vertebrae absent (0) or present (1).
105. Zygapophyses of trunk vertebrae abutting one another above neural canal, opposite hyposphenes meet to form lamina (0), or zygapohyses placed lateral to neural canal and separated by groove for interspinuous ligaments, hyposphens separated (1).
106. Middle and posterior dorsal vertebrae not pneumatic (0) or pneumatic (1). [Formerly: cervical vertebrae but not dorsal vertebrae pneumatic (0) or all presacral vertebrae pneumatic (1).] This character was reworded so as to be able to score the conditions of taxa in which dorsal vertebrae are known but cervicals are not.
107. Transverse processes of anterior dorsal vertebrae long and thin (0) or short, wide, and only slightly inclined (1).
108. Neural spines of dorsal vertebrae not expanded distally (0) or expanded to form 'spine table' (1).
109. Scars for interspinous ligaments terminate at apex of neural spine in dorsal vertebrae (0) or terminate below apex of neural spine (1).
110. Number of sacral vertebrae: 5 (0) or 6 (1) or 7 or more (2). [Formerly: character state 2 was '8 or more']
111. Sacral vertebrae with unfused zygapophyses (0) or with fused zygapophyses forming a sinuous ridge in dorsal view (1).
112. Ventral surface of posterior sacral centra gently rounded, convex (0) or ventrally flattened, sometimes with shallow sulcus (1) or centrum strongly constricted transversely, ventral surface keeled (2). Note that in Alvarezsaurus calvoi it is only the fifth sacral that is keeled, unlike other alvarezsaurids (Novas, 1997).
113. Pleurocoels absent on sacral vertebrae (0) or present on anterior sacrals only (1) or present on all sacrals (2). A pleurocoel may be present on the first sacral in Alxasaurus elesitaiensis, although this area is badly crushed (Russell and Dong, 1993b). .
114. Last sacral centrum with flat posterior articulation surface (0) or convex articulation surface (1).
115. Caudal vertebrae with distinct transition point (0) or without transition point (1). [Formerly: caudal vertebrae with distinct transition point, from shorter centra with long transverse processes proximally to longer centra with small or no transverse processes distally (0) or vertebrae homogeneous in shape, without transition point (1)] Vertebrae are not homogeneous in any theropod tails, but there is a distinct difference between the tails of those with the transition point and those without it. Russell (1972) coined the term 'transition point' for the point of abrupt change in vertebral morphology in the coelurosaurian tail, defining it as the point in the tail 'between the last vertebra bearing transverse processes and the first with distinctly elongate prezygapophyses' (p. 376).However, inmany coelurosaurian tails, the abrupt change occurs without prezygapophyseal elongation. Therefore, here, the transition point is considered the point of abrupt change in vertebral morphology in the tail, at which sudden reduction in the lengths of neural spines and transverse processes occurs, with or without concomitant prezygapophyseal elongation and/or change in haemal arch morphology from dorsoventrally long to dorsoventrally short and shaped like an inverted 'T'.
116. Transition point in caudal series begins distal to the 10th caudal (0) or between 7th and 10th caudal vertebra (1) or proximal to the 7th caudal vertebra (2). [reworded according to Makovicky et al. 2005. Formerly: transition point in caudal series begins distal to the 10th caudal (0) or at or proximal to the 10th caudal vertebra (1)]
117. Anterior caudal centra tall, oval in cross section (0) or with box-like centra in caudals I-V (1) or anterior caudal centra laterally compressed with ventral keel (2).
118. Neural spines of caudal vertebrae simple, undivided (0) or separated into anterior and posterior alae throughout much of caudal sequence (1).
119. Neural spines on distal caudals form a low ridge (0) or spine absent (1) or midline sulcus in center of neural arch (2).
120. Prezygapophyses of distal caudal vertebrae between 1/3 and whole centrum length (0) or with extremely long extensions of the prezygapophyses (up to 10 vertebral segments long in some taxa) (1) or strongly reduced as in Archaeopteryx lithographica (2).

121. More than 30 caudal vertebrae (0) or 21–30 caudal vertebrae (1) or < 10 caudal vertebrae, followed by pygostyle (2) or 11–20 vertebrae (3). [Formerly: more than 40 caudal vertebrae (0) or 25–40 caudal vertebrae (1) or no more than 25 caudal vertebrae (2)] State 1 altered due to the difficulty in determining caudal counts greater than 40 in most fossils due to the prevalence of missing tail tips. State 2 added in reference to the condition in ornithothoracine birds. State 3 added in reference to the condition in Wellnhoferia.
122. Proximal end of chevrons of proximal caudals short anteroposteriorly, shaft proximodistally elongate (0) or proximal end elongate anteroposteriorly, flattened and plate-like (1). [Formerly 'cylindrical' instead of 'proximodistally elongate'] Wording changed because chevrons are laterally compressed, rather than cylindrical, in theropods generally.
123. Distal caudal chevrons are simple (0) or anteriorly bifurcate (1) or bifurcate at both ends (2).
124. Shaft of cervical ribs slender and longer than vertebra to which they articulate (0) or broad and shorter than vertebra (1).
125. Ossified uncinate processes absent (0) or present (1).
126. Ossified ventral rib segments absent (0) or present (1).
127. Lateral gastral segment shorter than medial one in each arch (0) or distal segment longer than proximal segment (1).
128. Ossified sternal plates separate in adults (0) or fused (1).
129. Sternum without distinct lateral xiphoid process posterior to costal margin (0) or with lateral xiphoid process (1).
130. Anterior edge of sternum grooved for reception of coracoids (0) or sternum without grooves (1).
131. Articular facet of coracoid on sternum (conditions may be determined by the articular facet on coracoid in taxa without ossified sternum): anterolateral or more lateral than anterior (0); almost anterior (1) (Xu et al. 1999).
132. Hypocleidium on furcula absent (0) or present (1). The hypocleidium is a process extending from the ventral midline of the furcula, and is attached to the sternum by a ligament in extant birds.
133. Acromion margin of scapula continuous with blade (0) or anterior edge laterally everted (1).
134. Anterior surface of coracoid ventral to glenoid fossa unexpanded (0) or anterior edge of coracoid expanded, forms triangular subglenoid fossa bounded laterally by coracoid tuber (1).
135. Scapula and coracoid separate (0) or fused into scapulacoracoid (1).
136. Coracoid in lateral view subcircular, with shallow ventral blade (0) or subquadrangular with extensive ventral blade (1) or shallow ventral blade with elongate posteroventral process (2) or subtriangular (proximal end constricted, distal end wide) (3). [Formerly without character state 3] State 3 added in reference to the condition in certain birds and dromaeosaurids.
137. Scapula and coracoid form a continuous arc in posterior and anterior views (0) or coracoid inflected medially, scapulocoracoid 'L' shaped in lateral view (1).
138. Glenoid fossa without (0) or with extension of glenoid floor onto external surface of scapula (the surface opposite the costal surface) (1). [Formerly: glenoid fossa faces posteriorly or posterolaterally (0) or laterally (1).] The direction in which the glenoid faces is influenced by both glenoid morphology and scapular position. Here, the wording was changed to remove ambiguity by making it explicit that the character refers to glenoid morphology and not to scapular position.
139. Scapula longer than humerus (0) or humerus longer than scapula (1).
140. Deltopectoral crest large and distinct, proximal end of humerus quadrangular in anterior view (0) or deltopectoral crest less pronounced, forming an arc rather than being quadrangular (1) or deltopectoral crest very weakly developed, proximal end of humerus with rounded edges (2) or deltopectoral crest extremely long (3) or proximal end of humerus extremely broad, triangular in anterior view (4).
141. Anterior surface of deltopectoral crest smooth (0) or with distinct groove or ridge near lateral edge along distal end of crest (1).
142. Olecranon process weakly developed (0) or distinct and large but not hypertrophied (1) or hypertrophied (2). [Formerly without italicised additions] Wording and extra state added in recognition of the difference between a weak olecranon process (as in oviraptorosaurs and dromaeosaurids), a strong but not hypertrophied olecranon process (as in Allosaurus and ornithomimosaurs) and a hypertrophied olecranon process (as in Mononykus).

143. Distal articular surface of ulna flat (0) or convex, semilunate surface (1).
144. Proximal surface of ulna a single continuous articular facet (0) or divided into two distinct fossae separated by a median ridge (1).
145. Lateral proximal carpal (ulnare?) quadrangular (0) or triangular in proximal view (1). The homology of the carpal elements of coelurosaurs is unclear (see, e.g., Padian and Chiappe, 1998) but the large, triangular lateral element of some taxa most likely corresponds to the lateral proximal carpal of basal tetanurans.
146. Two distal carpals in contact with metacarpals, one covering the base of metacarpal I (and perhaps contacting metacarpal II) the other covering the base of metacarpal II (distal carpals 1 and 2 unfused) (0) or a single distal carpal capping metacarpals I and II (distal carpals 1 and 2 fused) (1). [Formerly without italicized additions]
147. Distal carpals not fused to metacarpals (0) or fused to metacarpals, forming carpometacarpus (1).
148. Distal carpals 1+2 well developed, covering all of proximal ends of metacarpals I and II (0) or small, cover about half of base of metacarpals I and II (1) or cover bases of allmetacarpals (2). [Formerly: 'semilunate carpal' instead of 'distal carpals 1+2'] The conditions in Allosaurus and therizinosauroids make it clear that the 'semilunate carpal' of birds and deinonychosaurs is fused distal carpals 1+2. The wording was changed here so as not to necessarily imply semilunate shape for this pair of carpals.
149. Metacarpal I half or less than half the length of metacarpal II, and longer proximodistally than wide transversely (0) or subequal in length to metacarpal II (1) or very short and wider transversely than long proximodistally (2).
150. Third manual digit present, phalanges present (0) or reduced to no more than metacarpal splint (1).
151. Flexor tubercles of manual unguals proximal (0) or displaced distally from articular end (1) or proximodistally elongated with proximal end close to articular facet (2). [Formerly: manual unguals strongly curved, with large flexor tubercles (0) or weakly curved with weak flexor tubercles displaced distally from articular end (1) or straight with weak flexor tubercles displaced distally from articular end (2)] Wording changed to separate ungual curvature, flexor tubercle size and flexor tubercle position into three different characters (ungual curvature is addressed here by characters 298 and 299, while flexor tubercle size is addressed by character 348).
152. Unguals on all digits generally similar in size (0) or digit I bearing large ungual and unguals of other digits distinctly smaller (1).
153. Proximodorsal 'lip' on first manual ungual – a transverse ridge immediately dorsal to the articulating surface – absent (0) or present (1). [Formerly without 'first'] Wording changed to separate the conditions on different unguals into different characters (characters 153 and 300).
154. Ventral edge of anterior ala of ilium straight or gently curved (0) or ventral edge hooked anteriorly (1) or very strongly hooked (2).
155. Preacetabular part of ilium roughly as long as postacetabular part of ilium (0) or preacetabular portion of ilium markedly longer (more than 2/3 of total ilium length) than postacetabular part (1).
156. Anterior end of ilium gently rounded or straight (0) or anterior end strongly curved (1) or pointed at anterodorsal corner (2).
157. Supraacetabular crest on ilium as a separate process from antitrochanter, forms "hood" over femoral head present (0) reduced, not forming hood (1) or absent (2).
158. Postacetabular ala of ilium in lateral view squared (0) or acuminate (1).
159. Postacetabular blades of ilia in dorsal view parallel (0) or diverge posteriorly (1).
160. Tuber along dorsal edge of ilium, dorsal or slightly posterior to acetabulum absent (0) or present (1).
161. Brevis fossa shelf-like (0) or deeply concave with lateral overhang (1).
162. Antitrochanter posterior to acetabulum absent or poorly developed (0) or prominent (1).
163. Ridge bordering cuppedicus fossa extends far posteriorly and is confluent or almost confluent with acetabular rim (0) or ridge terminates rostral to acetabulum or curves ventrally onto anterior end of pubic peduncle (1). [Reworded according to Makovicky et al. 2005, but with states reversed. Formerly: cuppedicus fossa formed as antiliac shelf anterior to acetabulum, extends posteriorly to above anterior end of acetabulum (0) or posterior end of fossa on anterior end of pubic peduncle, anterior to acetabulum (1)]

164. Cuppedicus fossa deep, ventrally concave (0) or fossa shallow or flat, with no lateral overhang (1) or absent (2).
165. Posterior edge of ischium without (0) or with prominent proximodorsal prong (1). [Formerly: posterior edge of ischium straight (0) or with median posterior process (1)]Wording changed to eliminate potential confusion between the posterodorsal process at the midshaft of Archaeopteryx and some dromaeosaurids with the proximodorsal ischial prong of some birds.
166. Shaft of ischium straight in lateral view (0) or ventrodistal end curved anteriorly (1) or curved dorsally (posterodorsally concave) (2) (Marya´nska et al. 2002). [Formerly: ischium straight (0) or ventrodistally curved anteriorly (1) or twisted at midshaft and with flexure of obturator process toward midline so that distal end is horizontal (2) or with laterally concave curvature in anterior view (3)] State 2 added in reference to the condition in oviraptorosaurs.
167. Obturator process of ischium absent (0) or proximal in position (1) or distally displaced (2). [Formerly: obturator process of ischium absent (0) or proximal in position (1) or located near middle of ischiadic shaft (2) or located at distal end of ischium (3)] Placement of the obturator process at the middle or distal end of the ischium depends on whether or not the process is displaced (character 167) and whether or not the ischium is reduced in length (character 171).
168. Obturator process does not contact pubis (0) or contacts pubis (1).
169. Length of pubic boot≤30% length of pubis (0) or≥40% (1). [Formerly: obturator notch present (0) or notch or foramen absent (1)] The former character was uninformative. If it referred to the pubic obturator notch, only one taxon in this data matrix (Sinraptor) exhibited state 1, because only Sinraptor retains the pubic portion of the puboischiadic plate and therefore lacks an obturator notch. If it referred to the ischial obturator notch (notch between obturator process and pubic peduncle), then all taxa with an obturator process exhibited state 0 and state 1 was redundant with respect to state 0 of character 167 (ischial obturator process absent). Therefore, this character was replaced by an informative pelvic character.
170. Semicircular scar on posterior part of the proximal end of the ischium, absent (0) or present (1).
171. Ischium more than 70% (0) or 70% or less of pubis length (1). [Formerly: ‘two thirds’ instead of ‘70%’]
172. Distal ends of ischia form symphysis (0) or approach one another but do not form symphysis (1) or widely separated (2). .
173. Ischial boot (expanded distal end) present (0) or absent (1).
174. Tubercle on anterior edge of ischium absent (0) or present (1).
175. Pubis propubic (0) or pubis vertical (1) or pubis moderately posteriorly oriented (2) or pubis fully posteriorly oriented (opisthopubic) (3). The oviraptorid condition, in which the proximal end of the pubis is vertical and the distal end curves anteriorly, is considered to be state 1.
176. Pubic boot projects anteriorly and posteriorly (0) or with little or no anterior process (1) or no anteroposterior projections (2).
177. Shelf on pubic shaft proximal to symphysis (‘pubic apron’) extends medially from middle of cylindrical pubic shaft (0) or shelf extends medially from anterior edge of anteroposteriorly flattened shaft (1).
178. Pubic shaft straight (0) or distal end curves anteriorly, anterior surface of shaft concave in lateral view (1) or anterior surface of shaft convex in lateral view (2). [Formerly without character state 2; similar character state present in character list of Makovicky et al. 2005]
179. Pubic apron about half of pubic shaft length (0) or less than 1/3 of shaft length (1).
180. Femoral head without fovea capitalis (for attachment of capital ligament) (0) or circular fovea present in center of medial surface of head (1).
181. Lesser and greater trochanters unfused (0) or fused (1). [Formerly: lesser trochanter separated from greater trochanter by deep cleft (0) or trochanters separated by small groove (1) or completely fused (or absent) to form crista trochanteris (2)] The former states 1 and 2 both represent fusion of the greater and lesser trochanters. In some cases, fusion is incomplete apically, leaving a ‘small groove’ (former state 1). The degree of apical incompleteness of fusion varies continuously, with no real cut-off between cases in which the groove is distinct, those in which it is present, but just barely, and those in which fusion is complete enough to obliterate most or all of the groove. For this reason, itwas

decided to combine former states 1 and 2 into one state, rather than commit to an artificial cut-off between degrees of fusion between greater and lesser trochanters.

182. Lesser trochanter of femur alariform (0) or cylindrical in cross section (1).
183. Posterior trochanter absent or represented only by rugose area (0) or posterior trochanter distinctly raised from shaft, mound-like (1). Cited by Gauthier (1986) as synapomorphy of Coelurosauria (his character 64), but he termed it the greater trochanter, which he equated with the posterior trochanter. Ostrom (1969a, 1990) identifies the posterior and greater trochanter as separate structures, and we follow his terminology.
184. Fourth trochanter on femur present (0) or absent (1).
185. Accessory trochanteric crest distal to lesser trochanter absent (0) or present (1). This character was identified as an autapomorphy of Microvenator celer (Makovicky and Sues, 1998), but it is more widespread.
186. Anterior surface of femur proximal to medial distal condyle without longitudinal crest (0) or crest present extending proximally from medial condyle on anterior surface of shaft (1).
187. Popliteal fossa on distal end of femur open distally (0) or closed off distally by contact betweeen distal condyles (1).
188. Fibula reaches proximal tarsals (0) or short, tapering distally, and not in contact with proximal tarsals (1).
189. Medial surface of proximal end of fibula concave along long axis (0) or flat (1).
190. Deep oval fossa on medial surface of fibula near proximal end absent (0) or present (1).
191. Distal end of tibia and astragalus without distinct condyles (0) or with distinct condyles separated by prominent tendinal groove on anterior surface (1).
192. Medial cnemial crest absent (0) or present on proximal end of tibia (1).
193. Ascending process of the astragalus tall and broad, covering most of anterior surface of distal end of tibia (0) or process short and slender, covering only lateral half of anterior surface of tibia (1) or ascending process tall with medial notch that restricts it to lateral side of anterior face of distal tibia (2).
194. Ascending process of astragalus confluent with condylar portion (0) or separated by transverse groove or fossa across base (1).
195. Astragalus and calcaneum separate from tibia (0) or fused to each other and to the tibia in late ontogeny (1).
196. Distal tarsals separate, not fused to metatarsals (0) or form metatarsal cap with intercondylar prominence that fuses to metatarsal early in postnatal ontogeny (1).
197. Metatarsals not co-ossified (0) or co-ossification of metatarsals begins proximally (1) or distally (2).
198. Distal end of metatarsal II smooth, not ginglymoid (0) or with developed ginglymus (1).
199. Distal end of metatarsal III smooth, not ginglymoid (0) or with developed ginglymus (1).
200. In anterior view, metatarsal III not pinched (0) or pinched proximally (1) or pinched both proximally and through midshaft (2). [Formerly: shaft of metatarsal III prominently visible between metatarsals II and IV in anterior view (0) or metatarsal III pinched between metatarsals II and IV, the latter two contacting one another proximally in front of III (1) or metatarsal III does not reach proximal end of metatarsus (2)] The former 'character' is a combination of two characters: pinching of metatarsal III and contact between metatarsals II and IV. Here, the latter character has been separated out as character 358.
201. Ungual of pedal digit II similar in size to that of III (0) or pedal ungual II about 50% larger than pedal ungual III (1). [Formerly: ungual and penultimate phalanx of pedal digit II similar to those of III (0) or penultimate phalanx highly modified for extreme hyper-extension, ungual more strongly curved and about 50% larger than that of III (1)] Character reworded to separate the condition of the ungual from the condition of the penultimate phalanx (character 323).
202. Metatarsal I articulates at middle of metatarsal II (0) or metatarsal I attaches to distal quarter of metatarsal II (1) or metatarsal I articulates with metatarsal II near its proximal end (2) or metatarsal I absent (3). [Formerly: metatarsal I articulates in the middle of the medial surface of metatarsal II (0) or metatarsal I attaches to posterior surface of distal quarter of metatarsal II (1) or metatarsal I articulates to medial surface of metatarsal II near its proximal end (2) or metatarsal I absent (3)]

203. Metatarsal I attenuates proximally (0) or proximal end of metatarsal I similar to that of metatarsals II–IV (1). [Formerly: metatarsal I attenuates proximally, without proximal articulating surface (0) or proximal end of metatarsal I similar to that of metatarsals II–IV (1)] Phrase removed to accommodate the condition in Neimongosaurus, in which metatarsal I attenuates proximally and retains a proximal articulating surface (Zhang et al. 2001).
204. Shaft of MT IV round or thicker dorsoventrally than wide in cross section (0) or shaft of MT IV mediolaterally widened and flat in cross section (1).
205. Foot symmetrical (0) or asymmetrical with slender MTII and very robust MT IV (1).
206. Neural spines on posterior dorsal vertebrae in lateral view rectangular or square (0) or anteroposteriorly expanded distally, fanshaped (1).
207. Shaft diameter of phalanx I-1 less (0) or greater (1) than shaft diameter of radius.
208. Angular exposed almost to end of mandible in lateral view, reaches or almost reaches articular (0) or excluded from posterior end angular suture turns ventrally and meets ventral border of mandible rostral to glenoid (1).
209. Laterally inclined flange along dorsal edge of surangular for articulation with lateral process of lateral quadrate condyle absent (0) or present (1).
210. Distal articular ends of metacarpals I + II ginglymoid (0) or rounded, smooth (1).
211. Radius and ulna well separated (0) or with distinct adherence or syndesmosis distally (1).
212. Kink and downward deflection in dentary buccal margin at rostral end of dentary: absent (0) or present (1). [Formerly: jaws occlude for their full length (0) or diverge rostrally due to kink and downward deflection in dentary buccal margin (1)]
213. Quadrate head covered by squamosal in lateral view (0) or quadrate cotyle of squamosal open laterally exposing quadrate head (1).
214. Brevis fossa poorly developed adjacent to ischial peduncle and without lateral overhang, medial edge of brevis fossa visible in lateral view (0), or fossa well developed along full length of postacetabular blade, lateral overhang extends along full length of fossa, medial edge completely covered in lateral view (1).
215. Vertical ridge on lesser trochanter present (0) or absent (1).
216. Supratemporal fenestra bounded laterally and posteriorly by the squamosal (0) or supratemporal fenestra extended as a fossa on to the dorsal surface of the squamosal (1).
217. Dentary fully toothed (0) or only with teeth rostrally (1) or edentulous (2).
218. Posterior edge of coracoid not or shallowly indented below glenoid (0), or posterior edge of coracoid deely notched just ventral to glenoid, glenoid lip everted (1).
219. Retroarticular process points caudally (0) or curves gently dorsocaudally (1) (Kobayashi, 2001).
220. Flange on supraglenoid buttress on scapula (see Nicholls and Russell, 1985) absent (0) or present (1).
221. Depression (possibly pneumatic) on ventral surface of postorbital process of laterosphenoid absent (0) or present (1).
222. Basal tubera set far apart, level with or beyond lateral edge of occipital condyle and/or foramen magnum (may connected by a web of bone or separated by a large notch) (0) or tubera small, directly below condyle and foramen magnum, and separated by a narrow notch (1).
223. Basioccipital without pneumatization on occipital surface (0) or with subcondylar recess (1).
224. Ventral surface of dentary straight or nearly straight (0) or descends strongly posteriorly (1).
225. Distal humerus with small or no medial epicondyle (0) or with large medial epicondyle, medial condyle centered on distal end (1).
226. Distal humeral condyles on distal end (0) or on anterior surface (1).
227. Ilium and ischium articulation flat or slightly concavo-convex (0) or ilium with process projecting into socket in ischium (1).
228. Roots of dentary and maxillary teeth mediolaterally compressed (0) or circular in cross-section (1).
229. Preacetabular portion of ilium parasagital (0) moderately laterally flaring (1) strongly laterally flaring (2).
230. Maxillary and dentary teeth labiolingually flattened and recurved, with crowns in middle of tooth row more than twice as high as the basal mesiolateral width (0) or lanceolate and subsymmetrical (1) or conical (2) or labiolingually flattened and recurved, with crowns in middle of tooth row less than

twice as high as the basal mesiolateral width (fore–aft basal length) (3) [Formerly without italicised additions] State 2 added in reference to the condition in birds and basal ornithomimosaurs. State 3 added in reference to the unique shape of the teeth of some troodontids.

231. Dentary teeth do not (0) or do increase in size anteriorly, becoming more conical in shape (1). [Formerly: dentary teeth homodont (0) or increasing in size anteriorly, becoming more conical in shape (1). Character reworded to refer only to tooth size (homodonty refers also to tooth shape).
232. Length of skull more than 90% femoral length (0) or less than 80% (1).
233. Height of skull (minus mandible) at middle of naris more than half the height of skull at middle of orbit (0) or less than half (1).
234. Dorsal margin of naris below level of dorsal margin of orbit (0) or above (1) (modified from Marya´nska et al. 2002).
235. Snout does not (0) or does taper to an anterior point (1).
236. Area of antorbital fenestra greater than that of orbit (0) or less than that of orbit (1).
237. Body of premaxilla dorsoventrally deep (0) or dorsoventrally shallow (1).
238. Antorbital fossa anteriorly bounded by maxilla (0) or by premaxilla (1) (Marya´nska et al. 2002).
239. Maxillary antorbital fossa: small, from 10% to less than 40% of the rostrocaudal length of the antorbital cavity (0), large, greater than 40% of the rostrocaudal length of the antorbital cavity (1) (Holtz et al. 2004).
240. Maxillary fenestra large and round (0), a large, craniocaudally elongate oblong (1), a small, craniocaudally elongate slit, not dorsally displaced (2), or a small, dorsally displaced opening (3).
241. Nasal fusion: absent, nasals separate (0) or present, nasals fused together (1).
242. Nasal surface: smooth (0) or rugose (1).
243. Suborbital process of jugal short and dorsoventrally stout (0) or elongate and dorsoventrally narrow (1).
244. Nasals at least as long as frontals (0) or shorter than frontals (1).
245. Anterior upturning of nasals absent (0) or present (1).
246. Jugo-maxillary bar at ventral end of antorbital fenestra dorsoventrally deep (0) or dorsoventrally narrow (1).
247. Anteroventral corner of premaxilla does not (0) or does form an acute, ventrally orientated point in lateral view (1).
248. Length of preorbital region of cranium>height at anterior edge of preorbital bar (exclusive of midline sagittal ridge, if any) (0) or≤height at anterior edge of preorbital bar (1).
249. Frontals without supraorbital rim (0) or with supraorbital rim (1).
250. Parietals shorter than frontals (0) or longer (1).
251. Length of ventral border of infratemporal fenestra comparable to that of orbit (0) or much shorter (1).
252. Foramen magnum smaller than or subequal to size of occipital condyle (0) or larger than occipital condyle (1).
253. Dentary not bowed (0) or bowed (concave dorsally) (1).
254. Meckelian groove of dentary deep (0) or shallow (1) (Currie & Varricchio 2004).
255. Dentary without posteroventral process extending to posterior end of external mandibular fenestra (0) or with such a process (1) (Marya´nska et al. 2002).
256. Horizontal shelf on the lateral surface of the surangular, rostral and ventral to the mandibular condyle: absent or faint ridge (0), prominent and extending laterally (1) (Holtz et al. 2004).
257. Premaxillary teeth subequal in size to (0) or much smaller than (1) the maxillary teeth (Holtz et al. 2004).
258. Approximately the same number of denticles per 5 mm on mesial keels of teeth as on distal keels (0) or markedly more denticles per 5 mm on mesial keels (1).
259. Maxillary teeth subperpendicular to ventral margin of maxilla (0) or strongly inclined (1) (Currie&Varricchio 2004).
260. Dentary tooth implantation: in sockets (0), in paradental groove (1) (Holtz et al. 2004).
261. Dentary dentition continues cranially to tip of dentary (0) or terminates before reaching dentary tip (1).

262. Length of mid-cervical centra approximately the same as dorsal centra (0) or markedly longer than dorsal centra (1).
263. Cervical prezygapophyses unflexed (0) or flexed (1) (Holtz et al. 2004).
264. Dorsal centra≥1.2×taller than long (0) or height≤length (1).
265. Posterior dorsal neural spines≥1.5×taller than long (0) or height<1.5×length (1).
266. Postzygapophyses of middle and posterior dorsal vertebrae do not extend posterior to centrum (0) or do (1).
267. Anteriormost haemal arches≥1.5×longer than associated centra (0) or<1.5×as long as centra (1).
268. Angle between furcular arms>80◦ (0) or<60◦ (1).
269. Acromion process contacts coracoid (0), or reduced and does not contact coracoid (1).
270. Acromion process does not match any of the following descriptions: (0) rectangular with its dorsal edge forming a 90◦ angle with the dorsal edge of the scapular blade (1) or a quarter-circle in shape (2) or triangular, with apex pointing away from and subparallel to scapular blade (3).
271. Scapulocoracoid dorsal margin: pronounced notch between the acromion process and the coracoid (0) or margin smooth (1) (Holtz et al. 2004).
272. Wide distal expansion of scapula absent (0) or present (1).
273. Acrocoracoid process absent (0) or present (1).
274. Humeral length is half femoral length or less (0) or shorter than femur but more than half femoral length (1) or longer than femur (2).
275. Length of humeral shaft between deltopectoral crest and distal condyles<4.5×shaft diameter (0) or>4.5×shaft diameter (1).
276. Ulna not bowed away from humerus (0), or bowed away from humerus (1) (Gauthier 1986).
277. Length of radius<1/3 femoral length (0) or between 1/3 and 2/3 femoral length (1) or between 2/3 and 1×femoral length (2) or>femoral length (3).
278. Radial diameter>0.5×ulnar diameter (0) or≤0.5× (1).
279. Distal carpals 1+2 flattish (0) or semilunate in shape (1).
280. Length of manual digit II (including metacarpal) less than 1.25×femoral length (0) or≥1.25×femoral length (1).
281. Distal end of metacarpal I medially (0) or laterally rotated (1) (P´erez-Moreno et al. 1994).
282. Medial side of metacarpal II: expanded proximally (0), not expanded (1) (Holtz et al. 2004).
283. Metacarpal III>0.8×length of metacarpal II (0) or<0.8×(1).
284. Manual phalanx I-1 longer than metacarpal II (0) or shorter (1) (P´erez-Moreno et al. 1994).
285. Length of metacarpal II<length of metacarpal I + phalanx I-1 (0) or≥(1).
286. Metacarpals II and III are not (0) or are appressed for their entire lengths (1).
287. Proximal end of metacarpal III is not (0) or is mainly palmar to that of metacarpal II (1) (Holtz et al. 2004).
288. Length of manual phalanx II-2<1.2×length of phalanx II-1 (0) or>1.2×(1).
289. Medial ligament pits of manual phalanges deep (0) or shallow (1) (Clark et al. 2004).
290. Posterior flange on manual phalanx II-1 absent (0) or present (1).
291. Combined lengths of manual phalanges II-1 and II- 2>length of metacarpal II + carpus (0) or≤length of metacarpal II +carpus (1).
292. Length of manual phalanx II-1<2×length of III-1 (0) or≥2×length of III-1 (1).
293. Length of manual phalanx II-2<2×length of II-1 (0) or≥2×(1).
294. Length of manual phalanx III-1<2×length of phalanx III-2 (0) or>2×(1).
295. Manual phalanx I-1 straight (0) or bowed (palmar surface concave) (1).
296. With proximal articular surface of ungual orientated vertically, dorsal surface of manual ungual I does not (0) or does arch higher than level of dorsal extremity of proximal articular surface (1).
297. With proximal articular surface of ungual orientated vertically, dorsal surface of manual ungual II does not (0) or does arch higher than level of dorsal extremity of proximal articular surface.
298. Manual ungual I strongly curved (0), weakly curved (1), or straight (2).
299. Manual unguals II and III strongly curved (0), weakly curved, (1), or straight (2).
300. Proximodorsal ‘lip’ on manual unguals II and III absent (0) or present (1).
301. Manual digit III with four phalanges (0) or less than four phalanges (1).

302. Manual phalanx III-3 markedly shorter than combined lengths of phalanges III-1 and III-2 (0), subequal in length to their combined lengths (1), or markedly longer (2).
303. Arching of preacetabular iliac blade above height of postacetabular blade absent or small (0) or extreme (1).
304. Shaft of ischium subequal in thickness to the pubis (0), slenderer than the pubic shaft (1), thicker than the pubic shaft (2) (Holtz et al. 2004).
305. Obturator process does not (0) or does form a strongly acute angle in lateral view (1).
306. Obturator process does not (0) or does reach tip of ischium (1).
307. Ventral notch between the distal portion of the obturator process and the shaft of the ischium: present (0), absent (1) (Holtz et al. 2004).
308. Strong kink of pubis at midshaft absent (0) or present, displacing distal half of pubis caudally (1).
309. In adult, femur longer than tibia (0) or shorter (1)
310. Tip of lesser trochanter below level of femoral head (0) or level with femoral head (1) (Holtz et al. 2004).
311. Proximolateral (fibular) condyle of the tibia, development in proximal view: bulge from the main surface of the tibia (0), conspicuous narrowing between the body of the condyle and the main body of the tibia (1) (Holtz et al. 2004).
312. Metatarsus less than half length of femur (0) or more than half femoral length (1).
313. Metatarsal cross-sectional proportions: subequal or wider mediolaterally than craniocaudally at midshaft (0), deeper craniocaudally than mediolaterally at midshaft (1) (Holtz et al. 2004).
314. Shafts of metatarsals not appressed (0) or appressed (1).
315. Length of metatarsal V≥0.5×length of metatarsal IV (0) or<0.5×(1).
316. Marked decrease in transverse width of metatarsus distally, absent (0) or present (1).
317. Plantar surface of hallux faces posteriorly (0) or hallux reorientated so that plantar surface faces medially or anteriorly (1) (Sanz & Buscalioni 1992). This is diagnosable by the degree of torsion in metatarsal I, even in disarticulated specimens (Middleton 2001).
318. Hallucal ungual reduced in size relative to other pedal unguals (0) or not reduced (1).
319. Hallucal ungual weakly curved (0) or strongly curved (1).
320. Length of pedal phalanx II-2 between 0.6×and 1×length of phalanx II-1 (0),≤0.6 ×, or (1)≥1×(2).
321. Total length of pedal phalanx II-2 (not counting posteroventral lip, if any)>2×length of distal condylar eminence (0) or≤2×(1).
322. Pedal phalanx II-2 without posteroventral lip or keel (0) with transversely wide posteroventral lip (1)with transversely narrow posteroventral keel (2) (Makovicky et al. 2005).
323. Pedal phalanx II-1 without dorsal extension of distal condyles (0) or with extension (1).
324. Pedal unguals III and IV straight or weakly curved (0), or strongly curved (1).
325. With fingers extended, tip of ungual III extends no further distally than flexor tubercle of ungual II (0) or extends further (1).
326. Manual ungual III smaller than ungual II (0) or approximately the same size (1).
327. Diameter of non-ungual phalanges of manual digit III>0.5×diameter of non-ungual phalanges of digit II (0) or < 0.5×(1).
328. Manual phalanx II-1 shorter than I-1 (0) or longer (1).
329. Ischial shaft rodlike (0) or flat, platelike (1) (Makovicky et al. 2005).
330. Lateral face of ischial shaft flat (or round in rodlike ischia) (0) or laterally concave (1) or with longitudinal ridge dividing lateral surface into anterior and posterior parts (2) (Makovicky et al. 2005).
331. Contact between pubic apron contributions of both pubes meet extensively (0) or contact interrupted by a slit (1) or no contact (2) (Makovicky et al. 2005).
332. Dorsal margin of postacetabular iliac blade straight or convex (0) or concave (1) (Makovicky et al. 2005).
333. Large, longitudinal flange along caudal or lateral face of metatarsal IV absent (0) or present (1) (Novas & Pol 2005).
334. Distally placed dorsal process along caudal edge of ischial shaft absent (0) or present (1).
335. Length of metatarsus<3.5×transverse midshaft diameter (0) or 3.5–8×midshaft diameter (1) or>8×midshaft diameter (2).

336. Lengths of mid-caudal centra subequal to or less than those of proximal caudal centra (0) or≥twice as long as proximal caudal centra (1).
337. Pubic peduncle of ilium craniocaudally longer (0) or shorter (1) than ischial peduncle of ilium.
338. Phalanges of pedal digit III not blocky (proximal phalanx length≥2×diameter) (0) or blocky (proximal phalanx length<2×diameter) (1).
339. Width of distal humeral expansion<1/3 humeral length (0) or≥1/3 humeral length (1).
340. Lateral epicondyle of humerus not expanded laterally (0) or expanded laterally (1).
341. Distal end of metatarsal I reduced in size relative to distal ends of other metatarsals (0) or comparable in size to distal ends of other metatarsals (1).
342. Pedal phalanx II-1 longer (0) or shorter (1) than pedal phalanx IV-1.
343. Dentary ramus elongate (0) or shortened, not much longer than tall (1).
344. Metacarpal II≥1/3 humeral length (0) or<1/3 humeral length (1).
345. With fingers extended, tip of ungual I does not extend past flexor tubercle of ungual II (0) or extends past flexor tubercle of ungual II but does not extend past tip of ungual II (1) or extends past tip of ungual II (2).
346. Premaxillary teeth serrated (0) or unserrated (1) (Rauhut 2003).
347. Sublacrimal process of jugal dorsoventrally expanded (taller than suborbital bar of jugal) (0) or not dorsoventrally expanded (1) (Rauhut 2003).
348. Flexor tubercles of manual unguals≥1/3×height of articular facet (0) or<1/3 (1).
349. Distal chevrons straight or L-shaped in lateral view (0) or upside-down T-shaped (1).
350. Metacarpal III distally not ginglymoid (0) or ginglymoid (1).
351. Breadth of acromion process perpendicular to long axis of scapular blade: deep (0) or shallow (1).
352. Proximal end of metatarsal IV curls around plantar side of proximal end of metatarsal III (0) or does not (1).
353. Midsagittal ridge formed by dorsal displacement of midline of frontals, nasals and premaxillae, absent (0) or present (1).
354. Ectopterygoid lateral to pterygoid (0) or rostral to pterygoid (1) (Osm´olska et al. 2004).
355. Palatine-pterygoid-ectopterygoid bar does not (0) or does (1) arch below ventral cheek margin (Osm´olska et al. 2004).
356. Co-ossification of angular and surangular absent (0) or present (1) (Osm´olska et al. 2004).
357. Cervical ribs unfused to cervical vertebrae (0) or fused to cervical vertebrae (1) (Osm´olska et al. 2004).
358. Anteroproximal contact between metatarsals II and IV absent (0) or present (1).
359. Anterior caudal vertebrae without pneumatopores (0) or with pneumatopores (1) (Holtz 1998).
360. External mandibular fenestra not rostrally displaced (sits beneath orbit) (0) or rostrally displaced (sits largely anterior to orbit) (1).
361. Ilium, pubic peduncle: substantially larger than (0) or subequal to (1) ischial peduncle
362. Ischium, length relative to pubis: shorter (0) or longer (1)
363. Ischium, shape: distally narrower (0) or distally wider (1) (excluding obturator process)
364. *Proximal elongated anterior process at pubic peduncle, dorsal ¼ formed by ilium pubic peduncle, ventral ¾ formed by pubis iliac peduncle: absent (0) or present (1).*
365. *Posterior sacral articular surface shape: circular or sub circular vertically (0) or horizontally trapezoidal or ovoid (1)*
366. *Anterior face of metatarsal III is flat or convex (0) or concave (1)*

APPENDIX 6. Character matrix from the data set of Gao, et al. (2012), Tsuihji, et al. (2014), and Averianov and Sues (2007), incorporating *Latenivenator mcmasterae*.

Allosaurus_fragilis
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Sinraptor
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Dilong_paradoxus
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Eotyrannus_lengi
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Tyrannosaurus_rex
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Gorgosaurus_libratus
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Tanycolagreus_topwilsoni
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Coelurus_fragilis
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Ornitholestes_hermanni
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Compsognathus_longipes
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Huaxiagnathus_orientalis
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Sinosauropteryx_prima
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Deinocheirus_mirificus
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Harpymimus_okladnikovi
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Pelecanimimus_polyodon
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Shenzhousaurus_orientalis
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Archaeornithomimus_asiaticus
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Garudimimus_brevipes
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Anserimimus_planinychus
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Ornithomimus_edmontonicus
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Struthiomimus_altus
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Gallimimus_bullatus
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Falcarius_utahensis
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Beipiaosaurus_inexpectus
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Alxasaurus_elesitaiensis
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Nothronychus_mckinleyi
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Erliansaurus_bellamanus
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Nanshiungosaurus_brevispinus
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Neimongosaurus_yangi
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Segnosaurus_galbiensis
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Erlikosaurus_andrewsi
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Therizinosaurus_cheloniformis
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Patagonykus_puertai
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Mononykus_olecranus
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Shuvuuia_deserti
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Protarchaeopteryx_robusta
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0???000?000???10??????0????00??1?101??0?0?????1?0?0????????????010?11?0000?001111000??010??10?01000
10000000001011?1?1?000000??00000??0000100?00000011010?1???????0000???

Elmisaurus_rarus
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???0??01?1??100010

??01????0??0??????000010000?0??00??
????????01?0?0000010??11??????1??0??00??0??1???1?????1????????

Caenagnathus_collinsi
???20110?00100?011????3??????????
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???????00??0??????0????0????????????????????????????1?10??
??????????????????????????????????????0?????????????0???0???0??

Rinchenia_mongoliensis
?01?0????0??????????0111?1????1011?10013??00???000?0??????00??1?221120?01100??111?1?3??????
1?????????1???1???1???0??????1?????????111?1??00000???1?0??00?10??1??0??????????????????????????0????0?
???0???????0??10??001????00???0?????????10101???01?01110?010?10?????????????????1????????????????????
????????0??????1??????????????????????????0?????1???1?????11100?11??????

Citipati_osmolskae
?011001001001??2210001111110001011?10013210001100000110011000110221120?0110010111?1?3??
????1011001100101111001??20???002100111?011111?010000100?11000001110021100?110220?0??1010010?11
01000000100?00000100000000100100110?000000000??0???01010110101001110101001??????10????010?001011
0100101000000000000000100??????1??101?00000001011001000001??00000100?10?01?1110?0?1000???

Ingenia_yanshini
?01?0????????????????11111100010?1?1??132??0?1???0?0??0011?????1221120?01100?0111?1?3??????
????0??1??1???1???2???01????2100???0011111111?000000??10000010100211??11?022000011010?11011010000
0?10010000000000000?1100?0?11??000?0?0000?0??101010110?01?01110?010?10?????????0010?0010110100101
000000100000000110000001011?101?00????0010001000000000000000101?10101101100011000???

Khaan_mckennai
?0110??????????????00111?110?01011?1001321000110?000??00110??????21120?01?00?0111?????????
?10110??1??1011110??????1??00210?111001??111110000?00?1100000111002110?1110220001?101??1??110100
?0??100100000000000000100100110?000???000??0??1010101101010011101010?10?????001110010?0010110100
1010000000000000000110000001011?1011000000000100010000000000000000100?10101?0?101011000???

Heyuannia_huangi
??11????????????????????????????????0??????????????0????????????????1120?011?0??1?????3??????1???
????????????0?2???????????0?111?????11??10?00?10??1110?01010021???1??0220??011?1??1??1?010000?0?0??
??0000000?001??01??1????00???0????0??1????????????????????0?1??????00?110010?00?01?0100001000000 1?0
?00?01???00000011?1?1?0?0001000???010?0?00?0000001?1??0?01?0????01?000???

Sinovenator_changii
?0???1002?000011120000101?11100???1??????000011???011?10100?????000?001??????0000021??01?
?????1?111000110100001000110????1?????????010111?0??????????000???21??0111002000111011100?1111000
0???0010001001??000?????0?1??000011?0??0??001100?10?000??010?1?1100??0?00001111??00100????????????
???0?????000000???2011011?101?1???0011??0??1000102?00??000??1?0??110???00??0000??

Mei_long
?0??????????????????11010????00?01?000022100001?10?010??100??????00010010??1?0000?021??01?0
011011110010?1010?01???011012?111011????101?11?[0
1]0?0?1?10000000???2111?1???020??11101110?0111100?0101101?000[0
1]?11011?0?0000?0?00000???00???0001100111???001?0100101?0???????011111?00010011110?0??000??10??000
?00000?01?????1??1?11100?1?1??000011??1?21000000001?010110???0?00000???

Byronosaurus_jaffei
?????101???101?1100110101011?00??????20220?????????????1?100??????0000001??11????00021??01?0
?0???????010110?????????0??02??1????0?0??0??

??????1??????????0????0????100???0?00?100?101100??0100???10?00110???????????????????????????????????
????????????????????????11????????????????????0??11?????0?????????????

Sinornithoides_youngi
?0??0??????????????1?000??1???0????0020?2???????1?0??????????????00??0010???????000110101????
??11?1001??????????0011?12102101??????01?11??0?00??10000000??????????0?200?????1?1???11110?????1?
???0001?11001?0??010????0000???00????30110011011??1?0100??1?000?1?0?011???0?00??01111010010100010
000000000000???0???11?11111000111111000010????21000000001?010110???0?0?000???

MPC-D_100_44_unnamedtroodontid
??????012??1??0????????????????1??11???????1?0??????0??
???10000000???01
?1?001???00??????0?0??1???????3?????????????????????1???0??????????????????????1?0101000?000????00000
?????????????1???0?1111????0?????????0???0?????0?0???????????000???

Troodon_formosus
???1?1112?1101000001???0?010100??????20220000210?00?1?01100????0?10??001?????????01101010
0???1111100101101111?1000?1020??11????????????????010????0??????????1????????????????1??0?011?100????
??0100001210?01????0?0????0??01000???0?30??????0?1???????10?000???1?10??111?????????1?01?0?????????
?????????????????????11?101011110??????0?101??0??000??0?????10???01??0001?0

Saurornithoides_mongoliensis
?01??1?1??1101???0?110001?10000????????2???????????????????1?010?100?0010??1????0001101010?
???????1???0??0?????100??1????0???002000?0101?10??11110????????
??00??211?01??????0??1?0?????00??00?30?0001101100100000??1?0???1?010??1??0??????????????????????????
??????????0011??1???1??01011110????100??0???0????0??01?????000??10????1?0

Saurornithoides_junior
?01101?12?110100?001?000??100?000????2022000?21??0????11100??????100?001???1????0001101010
0???????????????????1?1000?1020???0
1?????????????????00??00???1100???0?30?1001101?0010000001010000?110?0?????0???????????????????????????
????????????????????1???????????????1??????????????0??01?1???0?0??1?????1??

Unenlagia
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?????1111?01????0???????0??????????0?0??1?01????????????01221110?111020101???1112011?01??0?????????
????????0???????11????????????0?0???????????????????????????????????101??0??0?11??????????????????????1?0??
??02???011?????????????1?????1221????0?00???????????1?????????000???

Buitreraptor_gonzalezorum
?0110????????????????00001011??00??????????100?10??0011?0?????????00??001??????????021??100?0
010111100111?010???100011012?021???????01101111010?1?100?0??????11?101??122??1?111?110???11?0??0?
?1?011?011210000????????1??00?0????000????0???????1001001?0?01?0??????0?0?111?00?10011120??????????
??????????????0?101?1????1?0???0?2??????12011021??000?0??1??1?1?0??0?0000?0???

Rahonavis_ostromi
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???011111?0?1?11?011012?02?????????0????11??000?????????01121100111102?001?101??00111?10000??1??10
0011010000????????1?????0??????0?0???????????????????????????????????1111??3?0???130???????????????????
?????0211?011?101?01?10021?????11?11?1100??01??????1?11?????00?000???

Bambiraptor_feinbergi
?0110?????0?0?1??1??00?0?01110000??10?01??10?1????0?01?0?????????00??010??1??0000?01011100?
????0?120011??10??0???0011??110?????0011001011110?001?1010000010?21?001110020001?1021100?1?11000
0??10010001101?0?000?00?0?1??0000????000?0000000?1013001??100101?10?011100011011000?00111201011
010001000001011001010201101101?100001001100?001200101100000100001011110???00000000??

Sinornithosaurus_millenii
?011??????0??????????00???11100????10001?1100?1???0?01???????????00?00100??1????0101011100??
??????1??1???????0???00?1??1???????0111?01031110?00???0?0000010?211?0??10?2?0?111022?0????1???????1
?01000112110?0?000?1001??0000???0??00?0001001101300?0?100101?1?00110?0??????00010011121?00101100
0010001111100001?211111??1?10000120 1?0000012??112?00000100011010 1?0????0??0000??

Microraptor_zhaoianus
1?1????????????????00???0??010?0?1????0?0100000?????
001?1??01?1000?01???0110?11?2111?01?100?1?1?10100?11010000110121 10?011002?0?111022100?11111??00?
1001?10112110??00??010?11?000????0??00?00?100?1????????00??1?1?0???0??0?1111000100111211 0??01100
0010001111001000211111 0?1?10000120111 0000020?11210000010001?0101?0???000?0000??

NGMC91_unnameddromaeosaurid
?011????????????????200????11??00?????001???0??????????????????????0000100??1??0?0?010??10??0?
?????????????????????01???1????1?????10??031?10?00??1?100001?????????????????????????????1???0???????
?????11????0???10????000????10????00010011013?01?1100??1?1?0?1?0?00?????0?0?0011121 10??011000?1000
110100100??????1??1?1??001201110000??????21?0000100011010??0??????0000???

IGM100_1015undescribeddromaeos
?01100100100001201120000101010000 1?100012110110001000??00001?0???00000100?1111000101010
1000????0??2??
?????????????????0??00??00?0?0000???0?0??00010013?0001000001?1???0?0?0???????????????????????????????
???0???1?????0?????????????

Adasaurus_mongoliensis
??1100??????????????????????????0?????001????????????0????0????????????????0?????0?0?0????????01??
?0?2?01?1?????011000????1?????????????0??1?1???????????????00221100 1110???0????021?0??1???00?????????
001100?0010?????0?1??000???????0?000???????????0???????1????0?????01111??00?0???????????????????????
??????02???011?1011000101110????12???01?00??01??????1???0????0?0000???

Velociraptor_mongoliensis
?011001001000012011200001011100001110001211 1?1000100010000111010100000100111100001 0101
110000110001200111110111110001101110211100111001111110100111000000100221100111002000111121100
111100000000100101011010010000000?001100000000000000000000100130000100000101001010000110100001 0
011110100101000100000001100102020010 11?0011000001110000012001011000001000010101 10000?0000000??

Saurornitholestes_langstoni
????????????????????????01110????????????111???????????????11????0???010?????00???010111000?1
1000120011111011011100?1011??11??????????01?1???????10??000100221?0?11?????????????????????????????
????????????0???00?0????00?000?0???0000??????013?????0??00??10?1?1000011????00100?????1?????????????
???11001??0??????????????????1??00?1??010??0?????0??0?0?01?0???0??????01?

Deinonychus_antirrhopus
?0110????1???????11?0000?0111000011100012??????0?1????0?00?11010?000?0100111?1000?0101110
00?1100012001?111011????00110110?21?10???1?01011110100111000000100221100111002000 1110?010011111
000000100100011010000000?00?001100000?0?000?0000??00?0013000?000????000?1?11000100 1??????0111101
0010100010000000110010200001011000110001011100000 12?00001000001000010101100000000000 00??

Achillobator_giganticus
????????????????????????01110??000101??????0
?01200?111100?????????011??1?????????0101?????????????00?010220?0111100100?011010?00?11110?0????00
?000?101????0???????1???0????????0?000??????013?????????????????10??00000??00??0???1???????????0?????
01?0????0000100100?1??????11??????1000000?0??????????0??1?????0???0?????

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Dromaeosaurus_albertensis
        ?0??0010000000000010??0?0?0???0??01110????1111????10001?1001100???00000100111110000?0001010
00?????????????????????????????????????????????????????????????????????????????????????????????????????????
??????1??????00??????00?0?0000???0?00?000?00????0??00?0010010100000???????????????????????????????????
????????????????????????0111????????????????????0??01?????000????0??????

Utahraptor_ostrommaysi
        ?????????????????????0?0???????????00????????????????????????????????????????????01???101??0????
00??1011111?0??????0?1011??????????????01????????????????????2?????11001??0???0??????1???000????00?0?
?????????????????????0????????0???????0?0??????????????????0?????000???????????????????????????????????
????001?00??????????????????10???0???????????0??????????0????????0

Atrociraptor_marshalli
        ??????????????????????????1110???????????????????????????????????????0?1????1????0100011?00????
???????????????????????????????????????????????????????????????????????????????????????????????????????????
????????????????0??????0???0?00??00?00?3??????0?????010?0110????????????????????????????????????????????
????????????????????????????????????????????????????????????????

Epidendrosaurus_ningchengensis
        ?0??????????????????????????????????10000?1?00???????????0????????2??00000?002000??????????????
????????00?010?00???01?01011????1??????1011?10?00??1010000011?1???1??020?0?0?1?02?0??1?0100?0???0
?????000010?000?0110?1??100???00?0?0??0??????????1?????01???10???00?1111???002102010??01000100
0000000000000????011?1?1?0110200001100???0001100000010?11101?0??1?000111???

Epidexipteryx_ningchengensis
        ?0????????????????????????????00???000??00?0011????000????????????110?0?0????0001020??10000?
????????0???0?0?1???102??123??100?1????0101?01000??????00??011?10?????020?0?011?02?0?????????0????0
1111??0?10??00???10??1?1?0?1??000???110??01?????????????01?1???0?1?00?111???0?0021120?????1?0???????
?000000??00???01??10110????????????10?000110?000?0??1?1??11???100?0111???

Archaeopteryx_lithographica
        101?0010??000??112011010??11100?011?00002100010?0000?0??100111?1000000100002?0000020??0
0000?1?1??100?0??010?0???0021012111000????001011110000?11000000101121?0001?002000121011101?111
100000?10010010?0010?0000001001100000?0?0000102001011101000100100101?0??00?0001?11110?3?012113
0110?0100010001000010010202010011?101101112001000001000012100000000110101?000000000000??

Wellnhoferia_grandis
        ?0?????????????????110?0??????????????????????????????????????????00??010???????00020220020???
???????????????0????02?00231??00??????01011110?0????0?0000001??1????1??0??0?1?1?11?01?1?0100?0????0
1001???010?000??010????00?0???1000?0200101?1???????0?00????0???0?0?0??11?1?0310?21130?10?011001000
1000010010202???011?1?110111200?000001??00121000000001?0101???????0?000???

Jeholornis_prima
        10?????????????????1?????0??????????0??????0?????????????????????120?010??00200?1?1?2??0???0??
???????????1???1????02???211?1????1?1?0103?110?00??1100000001221??0???10??0?????21?0?????1?000??1?0
1011??0010?000?0010????1000???00?0102?0?0?1????0?10?1???01?01?0????01?1111?031012113011??011000?1
10011000000002???01??1?1?01112000100101??0?111000000000?10101?0??1??00000???

Sapeornis_chaoyangensis
        ?011???????????????11011????00001?000002??0011???00????????????000?010??00?00000??3??????0
????????0?00?010?2???0??????21?1001????100011110?00??1120000?011?1??01??100?0?1?1021101???010000??
?0??1110000???000?0010?1???000???1010?0??0?0?1101?00100?0??01?0??0?????1?111?0031012113111?101110
0?1110011100?1?02???011?1?110111????1??101?00?01?000000000110?0110??1?00?0000??

Confuciusornis_sanctus
        10110??????????????11000?0???00001???0??2??0?01??0?0???01???????000010000?10?0001?1?3??????
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0???1??1????01110?2???0??????2??111?110100013111400011111000010112101????100?0012103210111??10??1
1?112111101001 0?000000100110?000???001??0??0011?????00100000?01?0?10?????11111?00010121121110101
00000101010110010002???011?1?110111200010 1101??0011?000000000?10?01?0??100?20000??

Protopteryx_fengningensis
10?????????????????110????????????????0?????????????01??????????????000??1???????0?0??2???0??0????
?????0?????1??2???????????2??111?11?11??031?10000??1120000001?????????????0?1?1???????????1???1????????
1110010?0?0??0101???00?????0????2?01?111???00?10?00?01?0???????01?????1?3?012113111??011000?11001
0110001???????11?1?1?0111200?0??10??????1??00000000110?01?0????0??000???

Yanornis_martini
?01?????????????????111?0??????0??????0????????????0?1?0????????????000?011??00????00020??0000??
??11??????????0?2??????????????111?1???0?0031?10?00??1120?00?????????????00???121?32?01???0100?1??11?
?112?00010?000??010????00?????101?1?200001?1???00110?00??1?00?00?0001111??1???012113111??0110?001
1?0?1111101??????01??1?1101??20000???0??????1??00000000110?0??0??10???000???

Hagryphus_giganteus
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??10000001???
????????0???0?0111000000010001?00100?
??????????????????????0?11?????????????????0??0?0????????????????

Alvarezsaurus_calvoi
???1??
?100???????????2?1??2?12?????????????0?0?0?????????????1???00111?0??2?????????????????1?00???0?01??10000
000???0????????1???0??????????0???????????????????????????????????11111 0??0?????????????????????????0?1???
?0???????????1?????000?0???????0??1000???0?????11??1????000???????

Microvenator_celer
???21?10?0?????????????????????011?
0?11000111100???0???1002??????????????1000??01000??????0??1002???0111????0?????10110?0101100?001001
0???????0??0???0???11??0?0????00??0????????????????????????00???????0?111??????011110??0???????????????
0?0???0????011???????????????????????0????00000?1????0????????0??1??????

Avimimus_portentosus
?01?0???10001?00??0??1?1?????????1???1?????00?11??0?00100110??????2?1???00?0??0110???3???????
011011110101?0?00??100???????????????????11?000100???110?????00?211?01??0?2000???010100001100?0???
10011110020???00??0???01?0??00000?00??0?????0???????1?????1011???0?????001?????????111??1??????0????
?????????????00??011?101?0???00000????1000002?0000?0?????????10??011?0000???

Caudipteryx
00110???????????????0?110?010000011?00013210001?00?00??????????????21010?00?????10031?3?????0
0????0?100?????????0???01????210?111000??001010001?00??1000000010020???11?02200?111?10?10?11?01??0
????01000002000000000010?110?000???0?00?0??10001001000110100111?0010?????001110?10?0001110100?01
000000010?0001101?00001011?1011000000000???010000010000000000110101?0??000010000??

Oviraptor_philoceratops
?0110???????????1??00?????111?0?011???0132??0?1?0???0?100?????1????1120?01100?01?1?1?3???????0
??1???1???????1?0???????????????????1?????11?1?0?000001?110?0001???21?00?????????????????????????????????
???????????00100100?????00?0000???????01?1?010??1??1?00?010?10?????0?111?010?00?11?01??10100000000
0000000100?????????????????????????1000??????????00??100?10?01?0?10???1?000??

Conchoraptor_gracilis
?0110???????????1???00111?1100?1011?1001321000110?000?????1?0????221120?010?0?0111?1?3?????
??????????010??1?012?110??1???0?0111???1?11?11000010????????011?00210001?102???0???01001??11010?0?

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???0??000000??0?0???00??0110??0?000000??0???010101l?101001110101??????????????0?????1?1????010?0??
?0?00?0000111000??????1???110???????0?0001000000?????0???0?10?0??0110101?0000??

Chirostenotes_pergracilis
            ????????01?01101??0???1?11??0??????????????????????????01110????0??????????????????1???????????
????1101?11????1?12????????????????????101?????????????00011002l?0001?0220001110?00?0?????0?????10?1
00?00100000????0???1???0?0?00????????????????????????????1?????????1?1????????0??????00??????00001 0?0
?1001000?001?1??101?00000001000 1110000?1?000000??0??0???????001???????

Incisivosaurus_gauthieri
            ?0110???1??01?????100010101000100 1?0?010??00011000?010101101011112001000010 01?1?02022??0
002??????????????????????????????????????????????????????????????????????????????????????????????????????
??????????????00??00??00?0??000???0010?00010?10?0100100101100 10??001????????????????????????????????
?????????????????????????????????????????????????0??11?????0110???0??????

IGM100_42_unnamedoviraptorid
            ?0110??????????????001111110?01011?100132100?11??000???01100?111221120?01100??111?1?3?????
?10??0??1??1?1?1???1???01??00?10?1???01?1111110000?0???10000001100211 0?1110220??1?1010?1??1?01000
???????0000100000001 00?001?0??00?0?0?00?0??101010110101001110101??10?????001010010?001011?100?0
10001?00000000001000000101 1?10110???00000110010?000100010 00100?10101111101011??????

Anchiornis_huxleyi
            001100?????????????11010??111?00?????0?2?000??1????1?1????????????000??01??1?????00020??01??0
?101???00?0??010?01???01101210??011????0111311 10000??1000000010?21?1001102200?1?112112???1?1?000
??1?01?000121100010?1000?1??00?0???0????030110?1101000100100?01?0???0?0?011111101?0001112011 0101
0001010100111001010200101 1?1011000?20?1100001000?121000?00000110101?0??000000000??

Linhevenator_tani
            ?0?????????????????1?????1?????000???02?2??0002101?????0100??1????????????????????0?011010??0??
???????01???1?0?????????????????????????????0??0001??????????????????????????02????11??????????????0?????????
0??211011???????????00???????????0?3?01???????001001?010?1???1???????0???????1?01??????????????????????
???????000????101?0110111?0????10??1?1??00001?????????0????1?????????1

Talos_sampsoni
            ?????????????????????????????????????????????????????????????????????????????????????????????????
?????0011???????????????????????????????????0??????????????????????002??0??00??1?1?????????10??01??001
2110010?????????????????????????????????????????????????????????????001?????????1???????????????????????????
20?1?????11?000001110????11??102??0??00?????????1?????1????01?0

Philovenator
            ?????????????????????????????????????????????????????????????????????????????????????????????????
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11001?????????????????????????????????????????????????????????????????????????????????????????????????
????1101111101011110???????????2??0??01?????????0?????1???????1

Gobivenator_mongoliensis
            ?01101112?110100000??0001011110001100202200002101000101110010100 1??0000101111 0000?02???
010??00?111?0010110111111000110220 02?0???????0001111000?0?10?????????11101111002000101011000?111
1000?00100100001 2?10010?10???0110000011000000?30010?1101100100100101 10001??01??01010?0010011??0
1???????????????????????000110?10111110?011?1?????10?010210?000?0???1?1?110000?100000111

Urbacodon
            ??????????????????????????100?????????????????????????????????????????00?0000??????????021??0101????
?????010111?11?????????22?0??????????????????????1????????????????????????????????????????????????????????0?
12?????0???????????0??????0???0?30?????????????????????00?????10??101?????????????????????????0?????0??????
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Latenivenatrix mcmasterae

?011?1?12?110100000??????????????????2022000021???????11000??????11?0001????????0?001010100
??????????????????11100?????0?????????????????????????????????10?1111011??????????2?11?????????0??1?0
1?00012?1001?????00?1?00???1100??00030?????????????????1011000??0000??????????????1?0???????????????
?????????0????0?????111?101???1???????01???00??000????????1????????0??101