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Description of a partial *Dromiceiomimus* (Dinosauria: Theropoda) skeleton with comments on the validity of the genus

Authors: Ian Macdonald\textsuperscript{a} and Philip J. Currie\textsuperscript{b}

\textsuperscript{a} Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T5N 2E9, Canada; ipmacdon@gmail.com

\textsuperscript{b} Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T5N 2E9, Canada; pjcurrie@ualberta.ca

\textbf{Corresponding author:} Ian Macdonald (e-mail: ipmacdon@gmail.com; phone: 647-221-8626; address: 674-6 Ave E, Drumheller, Alberta T0J 0Y5)

* currently affiliated with the department of Preservation and Research, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, T0J 0Y0
Description of a partial *Dromiceiornimus* (Dinosauria: Theropoda) skeleton with comments on the validity of the genus

Authors: Ian Macdonald and Philip J. Currie

**ABSTRACT**

*Dromiceiornimus brevitertius* is a North American ornithomimid diagnosed primarily by the ratio of tibia length to femur length. It has recently, and perhaps incorrectly, been considered synonymous with *Ornithomimus edmontonicus*, with several authors questioning the utility of limb ratios in diagnosing taxa. While isolated ornithomimosaur material is common, specimens with sufficient diagnostic material to explore the question of synonymy are comparatively rare. The putative *Dromiceiornimus* specimen UALVP 16182 represents one of the few specimens in which diagnostic elements are available. It is therefore an important specimen for assessing the validity of *Dromiceiornimus* and for examining the utility of using limb proportions to diagnose ornithomimid taxa. In this paper, UALVP 16182 is described, the tibia/femur ratio is examined in closely-related ornithomimid taxa, and the ratio is found to distinguish *Dromiceiornimus* from *Gallimimus*, *Ornithomimus*, and *Struthiomimus*. A phylogenetic analysis recovered *Anserimimus* and *Ornithomimus* as sister taxa with *Dromiceiornimus* as an outgroup. Comparison of the manus revealed differences in the morphology of metacarpal I and the flexor tubercle of manual ungual II-3. Differences also appear in the surangular and scapula. An examination of stratigraphic positions of various specimens indicates that *Dromiceiornimus* is generally higher in section than *Ornithomimus*, although there are too few specimens to be statistically significant. This study agrees with other studies in concluding that limb proportions are roughly isometric in small theropods like ornithomimids and that the tibia/femur ratio may therefore be useful for
diagnosing certain small taxa. These findings suggest that *Dromiceiomimus* may indeed be a valid taxon.

Key words: *Dromiceiomimus*, ornithomimid, systematics, allometry
INTRODUCTION

Ornithomimosauria is a group of lightly built, cursorial theropods found mainly in the Cretaceous of Asia and North America (Makovicky et al. 2004). They resemble modern ratites like ostriches in their long necks, their small, edentulous skulls (except in basal forms), and their hind limb proportions. The family Ornithomimidae (Marsh, 1890) contains the five Late Cretaceous North American genera *Dromiceiomimus* (Russell, 1972), *Ornithomimus* (Marsh, 1890), *Rativates evadens* (McFeeters et al. 2016), *Struthiomimus* (Osborn, 1917), and *Tototlmimus packardensis* (Serrano-Brañas et al. 2015). Asian Late Cretaceous ornithomimids include *Anserimimus* (Barsbold, 1988), *Aepyornithomimus* (Tsogtbaatar et al. 2017a), *Archaeornithomimus* (Russell, 1972), *Gallimimus* (Osmólska et al. 1972), *Sinornithomimus* (Kobayashi and Lü, 2003), and *Qiupalong* (Xu et al. 2011). Although *Qiupalong*, *Rativates*, and *Tototlmimus* occur in North America (McFeeters et al. 2017), they are not directly comparable with *Dromiceiomimus* in the context of this study because of limited, non-overlapping fossil material. The type species of *Dromiceiomimus* – *Dromiceiomimus brevijertius* – has recently been considered a synonym of *Ornithomimus edmontonicus* (e.g. Makovicky et al. 2004; Xu et al. 2011; Cullen et al. 2013), while others retain it as a distinct genus (Russell, 1972; Nicholls and Russell, 1981; Watanabe et al. 2015; van der Reest and Currie, 2017). Despite these different conclusions, *Dromiceiomimus brevijertius* will be referred to as such for the sake of clarity. In this study, *Ornithomimus* is defined as *O. edmontonicus* and *O. velox*, plus all descendants of their most recent common ancestor.

Russell (1972) diagnosed *Dromiceiomimus brevijertius* primarily on the basis of it having different limb proportions than those of *Ornithomimus* and *Struthiomimus*. However, there is disagreement regarding the use of limb proportions for distinguishing ornithomimid taxa.
Nicholls and Russell (1981), despite tentatively affirming *Dromiceiomimus* as a valid genus, suggest that limb proportions should be avoided as a diagnostic tool when few specimens are available. They do, however, state cautiously that the ratio between the tibia and femur should be regarded as reasonably diagnostic, as does Osmólska et al. (1972). Both Osmólska et al. (1972) and Russell (1972) found that limb proportions among ornithomimids are roughly isometric during ontogeny, although the latter did not employ any criteria besides absolute size to classify ontogenetic stage. However, isometry does seem reasonable in ornithomimids because there is not so great a disparity between the smallest and largest known specimens for most species; proportions do not have to change as much during growth to accommodate an increase in mass. It is reasonable to propose then that the limb proportions of smaller theropods like ornithomimids can be used to distinguish taxa, particularly if those proportions are linked to other skeletal features. UALVP 16182 is one of a limited number of ornithomimid specimens that has the requisite elements for a proportion-based taxon diagnosis and is therefore a useful specimen for testing both the validity of *Dromiceiomimus* and the utility of limb proportions in diagnosing taxa.

UALVP 16182 is an important ornithomimid specimen in that it has both the femur and tibia preserved, a surprisingly rare condition given the abundance of ornithomimid material in the Upper Cretaceous sediments of southern Alberta. Additionally, it is the only *Dromiceiomimus brevitertius* skeleton for which a manus is preserved. The present study will focus on describing the specimen, which is currently identified on the basis of the tibia/femur ratio as *Dromiceiomimus brevitertius*, discussing the effectiveness of using that ratio for diagnostic purposes, and commenting on the validity of *Dromiceiomimus* as a genus.
MATERIALS AND METHODS

UALVP 16182 is a partial skeleton collected in 1967 by Dr. Richard Fox from what is now known as TMP locality #L2205 (UTM 12U: 366769E; 5757459N (WGS 84)) in the Tolman Member of the Horseshoe Canyon Formation in Dry Island Buffalo Jump Provincial Park east of Huxley, Alberta, Canada (Fig. 1). It was discovered 768 m above sea level, with the tail emerging from the outcrop approximately halfway between prairie level and river level, although laterally removed from either by approximately 500 m (Tanke and Walker, 2011). Besides its palaeontological value, UALVP 16182 is historically noteworthy for being the first dinosaur specimen ever extracted from a field site using a helicopter (Tanke and Walker, 2011). The specimen includes the right nasal, left jugal, right postorbital, posterior halves of the left and right dentaries, left splenial, right surangular, right prearticular, partial hyoid, eight articulated/associated cervical vertebrae, nine articulated dorsal vertebrae, eight articulated proximal caudal vertebrae, ribs, haemal arches, left scapula, ulna, right metacarpal I, left metacarpal II, right metacarpal III, right manual phalanges I-1, II-2 (pathological), II-3, III-3, left manual phalanx II-2, an articulated pelvic girdle, left femur, both tibiae, both fibulae, both astragali, left calcaneum, the left metatarsus, pedal phalanges II-1, II-3, III-2, III-3, III-4, and IV-2.

Measurements of UALVP 16182 were taken twice and averaged (Table 1), whereas those of other specimens were taken from various sources (Table 2). The statistical analyses performed were intended to investigate the null hypothesis that there is no significant difference between limb proportions of specimens that have been referred to either Dromiceiomimus or Ornithomimus. In so doing, this study attempts to replicate previous studies that detected a statistical difference in these proportions. If the null hypothesis can be rejected and the issue of
allometry addressed, then it may be reasonable to interpret the ratios as representative of distinct
taxa, particularly if these proportions co-occur with other anatomical features. The measurements
and proportions were analyzed using a one-tailed t-test with unequal variance to determine
whether the limb proportions of *Dromiceiormimus, Gallimimus, Ornithomimus* and
*Struthiomimus* are significantly different. Although the use of a t-test could be problematic if the
elements being compared exhibit allometric growth through ontogeny, an allometric analysis in
this study indicates that the limb proportions of the ornithomimid taxa examined were roughly
isometric (Table 3). Thus the use of the t-test is justifiable in this case. Allometry of
ornithomimid tibia/femur ratios was assessed using output from RMA 1.21 (Bohonak and van
der Linde, 2004). The allometric exponents (equivalent to the slopes of the regression lines) were
calculated for each of the four ornithomimids in this study and were used in combination with
the 95% confidence intervals (CI) to determine whether the ratios exhibited isometry, positive
allometry, or negative allometry. The ratios were considered positively allometric if the 95% CI
of the slope was greater than 1.0, negatively allometric if the 95% CI of the slope was less than
1.0, and isometric if the 95% CI of the slope included 1.0 (Brown and Vavrek, 2015).

Because the sample size for possible *Dromiceiormimus* specimens is small and displays
relatively little size variation (12%), it was necessary to assess whether such a sample could be
considered representative of a larger, more varied sample. To this end, an ANCOVA test was run
using XLStat to compare the regression lines of a highly variable (approximately 71%) *Gallimimus*
sample and a less varied (11.7%) *Gallimimus* sub-sample comprised of the
specimens MPC-D100/14, MPC-D100/52, and MPC-D Field # 950818. It was assumed that if
the slopes and y-intercepts were not statistically different then the sub-sample could be regarded
as reasonably representative of the full sample. If this was found to be the case, then the limited
Dromiceiomimus sample, and the allometric analysis thereof, could potentially be considered roughly representative of a more variable sample like that of Gallimimus.

Measurements taken from the hind limbs (femur, tibia, and metatarsus) were necessary to explore the validity of Dromiceiomimus and the usefulness of limb proportions in diagnosing a taxon. Measurements were log_{10} transformed before being used in analyses to account for differences in size. The tibia to femur ratios were calculated for four genera (Table 2). One-tailed t-tests with unequal variances were carried out on the tibia/femur ratios of Dromiceiomimus and Gallimimus (D-G), Dromiceiomimus and Ornithomimus (D-O), Dromiceiomimus and Struthiomimus (D-S), Gallimimus and Ornithomimus (G-O) and Ornithomimus and Struthiomimus (O-S).

A phylogenetic test was also conducted with Tree Analysis Using New Technology (TNT; Goloboff et al. 2008) to assess the relationship between Dromiceiomimus and Ornithomimus. The analysis included 285 characters (Appendices 1 and 2). Ten ornithomimosaurian taxa and specimens, one of which was UALVP 16182, were included in the ingroup whereas Allosaurus, Dilophosaurus, Ornitholestes and Tyrannosaurus were used as outgroups for a total of fourteen taxa. The characters used had equal weight and were unordered. A heuristic search with 10,000 replicates was carried out to identify the shortest tree. Bootstrap and Bremer tests were also carried out to assess the degree to which the topology of the resulting tree was supported.

DESCRIPTION
Several of the skull elements are preserved tightly appressed to the vertebral column in such a way as to prevent their removal. Therefore, the descriptions and figures of these elements are necessarily limited to what is visible.

Nasal

The preserved section of the right nasal is narrow, with a transverse width of 9.25 mm and margins that are roughly parallel. The anteroposterior length is unknown due to the incompleteness of the element, only 45 mm of which are preserved. The contact for the other nasal is a straight edge with a shallow groove 21 mm from the posterior border of the narial opening. The contact for the premaxilla is a shallow groove that deepens as it approaches the narial opening and accounts for approximately 1/3 of the transverse width of the nasal in dorsal view.

Jugal

The left jugal (Fig. 2) is roughly sigmoidal in lateral view. Its preserved length measured as a straight line between the contact for the lacrimal and the tip of the dorsal process, is 78.9 mm. The anterior end is compressed dorsoventrally and concave in dorsal view with a deep pit 4.8 mm in diameter at the posterior edge of the concavity. The element bifurcates anteriorly for contacts with the lacrimal and maxilla. The middle suborbital region is shallowly concave on the dorsal margin before becoming laterally compressed and dorsoventrally expanded posteriorly. Posteriorly, the jugal bifurcates into the dorsal and posterior processes for contact with the postorbital and quadratojugal respectively. The contact for the quadratojugal is a groove on the lateral surface of the posterior process.
Postorbital

The height of the right postorbital is 45.6 mm, measured as a straight line from the tip of the ventral process to the midpoint of the dorsal margin of the bone. The dorsal portion expands anteroposteriorly until it is triangular. The anterior process is either absent or not preserved, although the edge seems to be intact. The orbital margin forms a smooth C shape whereas the infratemporal margin is sigmoidal due to the projection of the posterior process and the sharp, anterior deflection of the ventral process. The contact for the jugal on the ventral process begins 34 mm from the dorsal edge of the postorbital.

Mandible

The left dentary (Fig. 2C) was found next to the dorsal vertebrae. It is complete except for the posteroventral tip, and as preserved is 137 mm long. The minimum height, at approximately one third of the length from the front, is 13.7 mm, and the maximum height is 20.5 mm near the posterior end. The distance from the buccal edge ventromedially to the back of the symphysis is 20 mm in height. In lateral view, the upper margin is shallowly convex and the lower edge is shallowly concave behind the symphysis, and like other ornithomimids the front of the lower jaw curves anteroventrally. In dorsal view, the dentary curves slightly anterolaterally in the symphysial region so that it has the ‘shovel-like’ appearance described by Osmólska et al. (1972). The symphysis extends well below the lower margin of the dentary to form a conspicuous chin. On the lateral surface of the dentary, there is a row of a dozen foramina below the buccal margin, each of which penetrates the bone and is exposed on both labial and lingual surfaces. The anterior eight foramina are closely associated, and are separated by as little as 2
mm. However, the more posterior ones spread out, and the last two are separated by almost 9
mm. The line of foramina is close to the buccal edge anteriorly (about 1.5 mm), but shifts
ventrally until the last foramen is 4 mm from the margin. A short (5 mm) canal enters the last
foramen from behind. There is a shallow longitudinal trough on the lateral surface of the
posterodorsal region of the dentary for the anterior process of the surangular. The latter
overlapped the dentary for at least 27 mm, which is much more extensive than the equivalent
contact in *Gallimimus* (Hurum 2001). Another depression along the dorsal margin of the dentary
extends almost as far forward and was presumably for the medial intramandibular process of the
surangular. The posteroventrally sloping symphysis is 32.5 mm long, but the intramandibular
articular surface is only 4.5 mm deep. On the lingual surface, the symphysial articular surface
divides posteriorly to outline the tapering anterior limit of the Meckelian groove. The edge of the
jaw is sharp, and is delineated ventrally on the medial surface by the remnants of the alveolar
shelf. Above the symphysis, the distance between the jaw margin and the shelf is 6.7 mm, but at
the back of the dentary the shelf is only 2 mm below the edge of the jaw. A shallow longitudinal
trough extends along the dorsal surface of the shelf from the symphysis to the back of the
dentary. Ventrally, the shelf overhangs the deep Meckelian canal.

The right surangular (Fig. 3A) was recovered in the chest region of the skeleton close to
the dentary. The preserved portion is 119 mm long and gently curved. As in other
ornithomimids, the dorsal margin is shallowly convex in lateral view. The thin ventral margin
has been somewhat damaged above the lateral mandibular fenestra and is difficult to interpret.
The anterior margin of the articulation for the accessory condyle of the quadrate is mediolaterally
thick (7 mm), sharply defined and vertical. It is about 20 mm anterior to the back of the
retroarticular process. The lateral surface of the surangular has a shallow depression on the
posterior third of the bone that extends to the end of the retroarticular process. This marks the contact for the overlapping suture for the posterior extension of the angular. A lateral ridge extends anteroventrally from the top of the glenoid articulation and forms the lateral margin of a depressed area for the adductor musculature (M. adductor mandibulae externus). The posterior surangular foramen is about 3 mm long and sits beneath this ridge. This foramen is supposedly absent in *Garudimimus* (Kobayashi and Barsbold, 2005a), *Harpymimus* (Kobayashi and Barsbold, 2005b), *Ornithomimus* and *Sinornithomimus* (Kobayashi and Lü, 2003) but is present in *Gallimimus* and *Struthiomimus*. The anterior surangular foramen is separated from the posterior surangular foramen by a distance of 34 mm. It opens anteriorly into an elongate, conspicuous groove that extends to the anterior margin of the surangular. The articular was not fused with the surangular.

The prearticular is gently arcuate, with a length of 82.4 mm measured as a straight line from the anteroventral tip to the dorsal tip of the posterior end. The middle portion is constricted with the anterior and posterior regions expanding dorsoventrally.

A partial hyoid (Fig. 4) was found associated with the left dentary. The posterior end is missing, and the preserved part of the bone is more than 120 mm long. The diameter of the tapering anterior end is 2.6 mm, whereas the diameter is greatest (5 mm) at the posterior end of the preserved section. The anterior end has an oval cross-section, whereas the posterior end of the preserved section is round in section.

**Vertebrae**

The cervical vertebrae (Fig. 5A, Fig. 6) are shorter dorsoventrally relative to their central lengths than either the dorsals or the caudals. This ratio increases in the more posterior cervicals.
until it is similar to the dorsal vertebrae. The centra of the anterior cervicals are long and thin relative to their heights, and the anterior ends flare ventrolaterally to contact the cervical ribs. The transverse processes are short mediolaterally, comparatively wide anteroposteriorly and the distal ends are subrectangular. They have pneumatopores at the bases of the diapophyses, but these are smaller than those of the dorsals and are divided by ridges descending from the distal ends of the transverse processes. In each, one of these ridges extends posteriorly until it forms the ventral margin of the postzygapophysis. The pneumatopore dorsal to the transverse process is simply sunk into the surface rather than being bound by laminae. The transverse processes are confluent with the prezygapophyses. The latter extend more anteriorly from the centrum than in the dorsals, and their articular surfaces are oriented dorsomedially. The postzygapophyses are comparatively short, just barely extending past the centrum, and their articular surfaces face ventrally. In dorsal view, the ridges of the zygapophyses of each cervical form a tall, thin X with the short, subrectangular neural spine in the center. In a representative cervical, the anteroposterior lengths of the neural arch and neural spine are 65.22 mm and 21.98 mm respectively. The more posterior cervicals resemble the dorsals in their proportions and morphology.

The dorsal vertebrae (Fig. 5B, Fig. 7) are taller relative to their central lengths compared to the caudals. The anterior dorsals have on both the left and right sides three deep pneumatopores at the bases of short, distally broad, laterally-directed transverse processes. For two anterior dorsals, the average length of the transverse processes was 49.5% of centrum length and the average width of the transverse process was 47.56% of centrum length. The pneumatopores are divided from one another by distinct laminae that converge into the distal end of the transverse process. The neural spines are short, subrectangular, and point dorsally. The
Prezygapophyses are short, confluent with the anterior margin of the neural spine and enclose a groove between them that is relatively much deeper than the same features on the caudals. The articular surfaces of the prezygapophyses are oriented dorsally. The postzygapophyses are anteroposteriorly longer than those of the cervicals. They are confluent with the posterior margin of the neural spine and neural arch, and are continuous with the triangular blade that extends posterodorsally. Their articular surfaces are oriented ventrally.

The anterior caudal vertebrae (Figs. 5C, D; Fig. 8A, B) lack any visible pneumatization. The nine most anterior caudals have central lengths at least twice as long as their posterior widths, which is consistent with the diagnosis of *Dromiceiomimus* given by Russell (1972). The transverse processes are directed posterolaterally and broaden at their distal ends. The transverse processes become shorter posteriorly along the tail, with those on the first six caudals being the longest. The neural spines are directed dorsally and are subrectangular with posterior extensions of the distal edges at the top. The prezygapophyses are small, extending approximately 10 mm anterior to the centra, and are confluent with the short neural arches in lateral view. Their articular surfaces face mediodorsally. The postzygapophyses are similarly short and their articular surfaces face lateroventrally. The postzygapophyses are confluent with the posterolateral margins of the neural spine, creating a deep groove between them.

Ribs and gastralia (Fig. 9) were recovered with the specimen, but lack any apparent diagnostic characters. About a dozen ribs were found with the specimen.

Scapula
The scapula is mediolaterally thin and strap-like (Fig. 10). It is expanded where the missing coracoid would articulate, and tapers dorsoposteriorly from that point before expanding dorsoposteriorly again, beginning approximately mid-shaft. The lateral surface is convex. The length measured as a straight line is 260 mm, but is 283 mm along the curved lateral surface. The height of the shaft at its narrowest point is 28.3 mm. The scapular portion of the glenoid faces ventrolaterally and the acromion process has a squared-off outline. In contrast with *Ornithomimus* but similar to *Struthiomimus*, the supraglenoid buttress bears an obvious teardrop-shaped depression that is visible in spite of the minor crushing undergone by that portion of the scapula. This feature is poorly developed or absent in *Ornithomimus*.

**Ulna**

The right ulna (Fig. 11) is 280 mm long with a midshaft diameter of 9.7 mm (Table 1). The cross section of the midshaft has the appearance of a rounded equilateral triangle. The proximal half is approximately straight whereas the distal half curves increasingly medially towards where the radius would articulate. Proximally, the dorsal edge curves gently up into the olecranon process, which is triangular in lateral view. The ventral edge is roughly straight but inflects dorsally somewhat into the olecranon process. There is a laterally-projecting ridge that begins at the trochlear notch and blends into the rest of the shaft approximately 10 mm distally. This creates a broad depression between this ridge and the olecranon process. The distal end is somewhat dorsoventrally compressed, becoming an acute triangle in cross section with the base of the triangle formed by the slight dorsoventral expansions on the lateral edge.

**Manus**
The metacarpals (Fig. 12A) are gracile with length/width ratios of 12.6 for metacarpal I and 14.2 for metacarpal III (Table 4). Metacarpal I is roughly triangular in cross section and is dorsoventrally compressed. Its distal portion is inflected medially in dorsal view at an angle of approximately 25° and twists so that the dorsal edge is inclined somewhat medially. Although the right second metacarpal is not present, the straight shaft of the left second metacarpal suggests that metacarpals I and II are closely appressed for most of their lengths, but diverge distally beyond the inflection of the former. This contrasts with *Ornithomimus* in which the two bones seem to be appressed for their entire lengths and is more similar to the condition seen in *Struthiomimus*. Metacarpal I is 101.39 mm long, metacarpal II is 95.85 mm long, and metacarpal III is 92.82 mm long. This condition (Mc I > Mc II > Mc III) is also seen in *Ornithomimus*. All three metacarpals are strongly asymmetrical in distal view, with the lateral condyles being larger than the medial condyles. The shaft of metacarpal III is circular in cross section.

The phalanges are generally similar to those of *Ornithomimus*. However, the ungual of manual digit II is gently curved, noticeably more so than in ROM 851 (*Ornithomimus*), which is nearly straight, although similar to TMP 1995.110.0001, another *Ornithomimus* (Fig. 13). The flexor tubercle is weakly-developed and displaced distally from the articular end. It contrasts with the flexor tubercle of the above-mentioned *Ornithomimus* specimens wherein this structure is noticeably less prominent.

Right phalanx II-2 (Fig. 14) is pathological. The distal end, just proximal to the articular surface, is noticeably inflated and there is a ventrally-projecting spur. There is a fracture extending diagonally through the shaft and the distal portion appears to have been displaced proximally. Despite this, the two portions remained attached although they have since been detached and repositioned somewhat so that the long axes of the segments align, whereas the
proximal segment was originally angled so that the tip was below the ventral surface of the distal
segment. The proximal segment has also been shifted proximally by 4.8 mm in relation to the
distal segment. The broken edges on both sides of the crack seem smooth which may indicate the
presence of a pseudarthrosis. Although it has since been prepared away, there was present what
appeared to be large bony callosity beginning approximately midshaft and ending just proximal
to the distal articular end. Regrettably, the only photographs that survive of this callosity are not
of the highest quality; however, bone texture is still apparent in the swollen area, supporting the
interpretation that it is a pathology rather than a concretion.

Ilium

The length of the ilium (Fig. 15A) is 412.5 mm. The length of the anterior portion of the
ilium, measured from the midpoint of the anterior edge of the iliac blade to a point directly dorsal
to the anterior margin of the acetabulum is 163 mm. The height measured from just anterior to
the acetabular margin to the dorsal edge of the iliac blade is 151.5 mm. The anterior end of the
ilium curves posteroventrally into a distinct hook-like process that ends just ventral to the dorsal
margin of the acetabulum. The supr acetabular crest covers the acetabulum dorsally. The
postacetabular portion of the ilium is subrectangular in lateral aspect. In ventral view, the brevis
fossa is a deep excavation that accommodates the *M. caudofemoralis brevis*, and the brevis shelf
extends ventral to the supraacetabular region resulting in a large overhang, and rendering the
brevis fossa invisible in lateral aspect.

Pubis
The length of the pubis (Fig. 15B) measured from the dorsal corner of the pubic portion of the puboischial contact to the distal end of the shaft is 370 mm. The height of the shaft in lateral aspect is uniform along its entire length, broadening proximally to 52.3 mm distal to the puboischial contact and 52.3 mm distally before it expands into the pubic boot. The shaft is straight until it curves anteriorly close to the pubic boot. Medially, the triangular pubic apron emerges from the shaft 85 mm distal to the bottom of the puboischiadic suture. It expands rapidly to meet its counterpart from the opposite pubis. The conjoined pubic apron extends at least 195 mm distally, and ends just proximal to the pubic boot.

Ischium

The ischium extends posteroventrally and curves anteroventrally at its distal end (Fig. 15B). The length measured from the ischial portion of the puboischial contact is 314 mm. The medial face of the ischial shaft extends into a triangular apron 74 mm distal to the ventral edge of the puboischiadic suture. The apron formed by the two ischia extends to the rounded ischial boot. In lateral aspect the shaft is 9.32 mm thick anteroposteriorly and broadens distally to a maximum of 42.98 mm.

Femur

The total length of the femur is 319 mm. The femoral head is directed medially and has a height of 43.5 mm. It is confluent with the greater trochanter, which is separated from the anterior trochanter by a deep notch. On the medial edge of the anterior trochanter is a small, bulbous accessory trochanter. The fourth trochanter is a distinct ridge on the posterior surface, with a proximodistal length of 83.6 mm and a maximum posterior extension of 13.4 mm (Fig.
16A). The medial side of the fourth trochanter is somewhat inflated. Medial from the distal end of the fourth trochanter is a roughly tear-shaped depression 52.5 mm long proximodistally and 26.6 mm wide that appears to be a point of muscle attachment. At its widest, the femoral shaft has a transverse diameter of 48.9 mm, but is 45.7 mm at its narrowest point. On the posterior surface near the distal end of the femur is a roughened tuberosity on the midline of the bone, just proximal to where the condyles are divided by the posterior intercondylar groove. The lateral condyle is divided posteriorly by a shallow notch, resulting in a thinner fibular flange that is medial to and extends posteriorly past the main portion of the condyle. A similar shallow notch divides the medial condyle anteriorly into the main portion and a thin flange.

Tibia

The following measurements are for the well-preserved left tibia as the right tibia is taphonomically distorted. The maximum length of the tibia (Fig. 16B), measured along the medial side of the shaft, is 468 mm. The cnemial crest extends anteriorly but curves laterally and has an anteroposterior length of 96.4 mm. The fibular crest is approximately a quarter of the way down the shaft and extends laterally from the lateral edge of the anterior surface. The minimum width of the shaft is 32.8 mm, expanding proximally and distally with a maximum proximal width of 41.6 mm and a distal width of 75.2 mm. The lateral malleolus has a D-shaped depression on the lateral side into which the distal end of the fibula fits. Both the astragali are preserved in place and the left calcaneum is also preserved in life position. The left astragalus is 112.4 mm tall, measured as a straight line from the medial side of the base to a point in line with the apex of the ascending process. The ascending process of the left astragalus covers at its base
most of the anterior surface of the tibia, but tapers laterally until it covers only the lateral half of
the tibia shaft.

Fibula

The fibula (Fig. 17) is 441.5 mm long (Table 1). The proximal end is mediolaterally
compressed with a deep medial concavity and measures 67.5 mm anteroposteriorly. The shaft
tapers distally to approximately half that width where it contacts the fibular crest of the tibia and
then tapers further to a midshaft width of 11.8 mm before expanding slightly at the distal end.
The medial aspect of the shaft is concave proximally and distally, but flat through the middle
portion and at the distal end where it contacts the calcaneum.

Metatarsus

The metatarsus (Fig. 16C) is arctometatarsalian as is typical for ornithomimids.

Metatarsal III is pinched proximally in anterior view, although it is visible in anterior view for all
but the proximal 20 mm. The total length as measured along the anterior surface from the centre
of the proximal end to the distal end of metatarsal III is 342 mm. The minimum width across the
metatarsus is 46 mm. Metatarsal II is the shortest and in proximal view makes the biggest
contribution to the ankle articulation, followed by IV then III. The distal portions of metatarsals
II and IV curve medially and laterally, respectively. On the distal end of metatarsal II there is a
posterior, roughly circular depression. A similar but shallower and less defined depression is
found on metatarsal IV.

Pes
All phalangial lengths are measured from the centre of the proximal articular surface to
the larger condyle of the distal end. Phalanx II-1 (Fig. 18A) is 77.1 mm long and tapers from a
proximal height of 38.7 mm to a distal height of 22.8 mm with a slight ventral constriction just
proximal to the distal articular surface. The ventral margin is a smooth arc. In proximal view, the
shallowly concave proximal articular surface is ovoid with the long axis oriented vertically.
There are two ventral processes, the medial being larger, which give the base of the proximal end
a bifurcated appearance. These processes create between them a deep sulcus on the ventral
surface of the phalanx. Phalanx III-2 (Fig. 18B) is 56.6 mm long and tapers from a proximal
height of 23.4 mm to a distal height of 18.3 mm with a strongly convex ventral cross-section of
the shaft. In proximal view, the concave proximal end is roughly hemispherical with a flat base.
Phalanx III-3 (Fig. 18C) is 44.4 mm long with a proximal height of 20.8 mm and a distal height
of 15.5 mm. In proximal view, the proximal articular end is concave and is shaped like an
asymmetrical hemisphere. The ventral surface of the proximal end is slightly concave. The
ventral margin is concave in lateral view from the midpoint of the shaft until it expands ventrally
into the distal articular surface. Phalanx IV-2 (Fig. 18D) is 29.4 mm long with a proximal height
of 26 mm and a distal height of 23.1 mm. In proximal view, the proximal articular surface is
roughly triangular in outline, and the surface is concave with a strong central, vertically-oriented
keel.

The unguals (Fig. 18E and F) are triangular in proximal view and have shallow flexor
depressions on the ventral surfaces. They possess pointed, laterally-oriented protrusions near the
proximal end where the keratin grooves terminate. The ventral margin in lateral view is concave
between these protrusions and the proximal end. The complete ungual is 48.7 mm long.
RESULTS

Due to small sample sizes and the fragmentary nature of many of the specimens, it was not possible to calculate all of the proportions Russell (1972) used to diagnose *Dromiceiomimus*. Therefore the analysis focused primarily on the femur and tibia measurements, which is in any case the ratio that Nicholls and Russell (1981) considered to be most diagnostic for *Dromiceiomimus*. The assignment of UALVP 16182 to *Dromiceiomimus* is based primarily on this ratio; the tibia/femur ratio of UALVP 16182 comports with the same ratio from other specimens assigned to *Dromiceiomimus*, including the holotype ROM 797 (Table 2), more strongly than with other ornithomimid taxa. Comparison of the tibia/femur ratios for the four taxa using a one-tailed t-test with unequal variance (Table 5), revealed a statistically significant difference between *Dromiceiomimus* and *Gallimimus* (*P* = 0.00016), *Dromiceiomimus* and *Ornithomimus* (*P* = 0.00185), *Dromiceiomimus* and *Struthiomimus* (*P* = 0.00124), and *Gallimimus* and *Struthiomimus* (*P* = 0.03083). Comparison of the ratio for *Gallimimus* and *Ornithomimus* (*P* = 0.05191) fell just short of statistically significant difference and the comparison between *Ornithomimus* and *Struthiomimus* revealed no significant difference (*P* = 0.19174). Thus the tibia/femur ratio allows one to delineate between ornithomimid taxa except for *Gallimimus* and *Ornithomimus* (although the results are bordering on significance) and *Ornithomimus* and *Struthiomimus*.

Contrary to Russell (1972), the metatarsal III-femur ratio (Table 6) does not seem to be diagnostic. A one-tailed t-test with unequal variance performed on the ratio (Table 7) yielded results that did not allow rejection of the null hypothesis except between *Dromiceiomimus* and *Gallimimus* (*D-G: P* = 0.03334; *D-O: P* = 0.10605; *D-S: P* = 0.05994; *G-O: P* = 0.31636; *G-S: P* = 0.37808; *O-S: P* = 0.29131). The two data points derived from *Ornithomimus* are similar to...
Struthiomimus. Other ratios were either unhelpful or lacked sufficient samples to obtain statistically significant results.

A comparison (using an ANCOVA test) of regression lines between a Gallimimus sample in which femur length was highly variable (71%) and a sub-sample in which femur length was minimally variable (11.7%) revealed that neither the slopes ($F = 0.62$, $P = 0.45688$) nor the $y$-intercepts ($F = 1.16$, $P = 0.31287$) were significantly different. Output from XLStat indicated that the tibia/femur ratios for the ornithomimid specimens tested were isometric (Table 3), except for Gallimimus which exhibited slight negative allometry. An RMA analysis of the small, minimally variable sub-sample indicated isometry as well.

The phylogenetic analysis recovered a single most parsimonious tree with a length of 274, CI = 0.766, RI = 0.743 and RC = 0.569 (Fig. 19). Dromiceiomimus (represented by UALVP 16182) was recovered as an outgroup to a clade consisting of Anserimimus and Ornithomimus. Bremer support for the ornithomimid clade is strong, but the internal groupings have weak support.

DISCUSSION

Many ornithomimid taxa have been diagnosed using various differences in limb proportions. Russell (1972) diagnosed Ornithomimus by the following length ratios: presacral vertebral column/hindlimb, humerus/scapula, forearm/femur, tibia/femur, antilium/femur, metatarsus/femur, metacarpal I/metacarpals II and III, manual ungual 3/penultimate phalanx of digit 3. Claessens and Loewen (2015) also diagnosed Ornithomimus using the greater length of metacarpal I compared to metacarpal II and the greater length of metacarpal II compared to metacarpal III.
Russell (1972) diagnosed *Dromiceiomimus* by the following length ratios: presacral vertebral column/hindlimb, humerus/scapula, forearm/femur, antilium/femur, tibia/femur, tibia with astragalus/metatarsal III, metatarsus/femur, and pedal digit 3/femur.

Diagnosing taxa on the basis of limb proportions remains problematic because these proportions can vary depending on sex, age, or individual variation (Currie, 2003). This uncertainty can be mitigated when many specimens are available, but, unfortunately, this is not the case with North American ornithomimids. Although many specimens exist, there are comparatively few individuals in which all the elements needed to measure diagnostic proportions have been preserved. In the present study, the only proportion that was measureable in enough specimens to provide statistical significance was the tibia/femur ratio. Before considering the results of comparisons between ornithomimid tibia/femur ratios, however, it was necessary to establish whether or not the ratio was isometric over a range of sizes and whether the *Dromiceiomimus* sample, despite its low size variability, could be considered roughly representative of a more variable sample. Results from RMA 1.21 (Table 3) indicated that the tibia/femur ratio is generally isometric for the ornithomimids examined, meaning that statistical analysis of this ratio could yield useful results. *Gallimimus*, in contrast, exhibited very slight negative allometry. This could perhaps be attributed to its larger body size. However, the isometry indicated by an analysis of the smaller, less variable sub-sample implies that the isometry seen in the other taxa is due to lower sample size, making it ‘soft’ isometry (Brown and Vavrek, 2015). Additionally, Brown and Vavrek (2015) found that allometric analyses indicating isometry were of dubious value when the sample size was small.

The ANCOVA test indicating a lack of significant difference between the slopes and intercepts of the variable *Gallimimus* sample and the winnowed sub-sample indicated that the
Dromiceiomimus sample, although limited in size variability, can nonetheless be regarded as representative of a more variable sample. Thus analysis of the tibia/femur ratio, despite the potentially confounding factors that have been discussed, is not without merit.

The tibia/femur ratio, while not highly diagnostic, does distinguish Dromiceiomimus from Gallimimus, Ornithomimus, and Struthiomimus (Fig. 20). This is in agreement with Nicholls and Russell (1981) who concluded that Dromiceiomimus could be diagnosed on this basis despite also concluding that limb proportions were not generally reliable along with most of the proportions used by Russell (1972). Osmólska et al. (1972) and Russell (1972) found that limb proportions in ornithomimids did not vary significantly with age. These findings suggest that the separate clustering of Dromiceiomimus and Ornithomimus edmontonicus on the basis of the tibia/femur ratio is evidence for the validity of Dromiceiomimus, and the statistical analysis supports this as well.

The differences seen between the tibia/femur ratios of the ornithomimids in this study suggest, as others (Osmólska et al. 1972; Russell, 1972; Nicholls and Russell, 1981) have proposed, that the tibia/femur ratio is diagnostic for ornithomimids. The overlap seen in the error bars (Fig. 20) and the failure of the ratio to distinguish between Ornithomimus and Struthiomimus indicate that caution should still be exercised when diagnosing ornithomimid taxa this way. However, when considered together with other morphological differences, the tibia/femur ratio could still be a useful diagnostic tool. Thus the measurable disparity in tibia/femur ratios between Dromiceiomimus and Ornithomimus edmontonicus, combined with differences in morphology such as those seen in the manus (discussed below), could be sufficient to support Dromiceiomimus as a valid genus.
Even though there were too few sufficiently complete *Ornithomimus* measured to directly compare the femur-MtIII ratio with *Dromiceiomimus*, that ratio does seem to separate *Dromiceiomimus, Gallimimus, and Struthiomimus* to some degree. However the t-test did not reveal a statistically significant difference. Thus, while the femur-MtIII ratio does appear to delineate between these genera to a degree, the ratio cannot be considered sufficiently diagnostic.

The manus of UALVP 16182 is generally more similar to *Ornithomimus* than to *Struthiomimus* in its proportions (Fig. 12), but exhibits some differences. Metacarpals I and III are slightly more gracile in UALVP 16182 than in *Ornithomimus* (Table 4) and much more gracile than in *Struthiomimus*. The manus differs further from that of *Ornithomimus* in the medial inflection of metacarpal I, resulting in the divergence of the distal portion of metacarpal I from metacarpal II. In *Ornithomimus*, these two bones are appressed along their entire length. A slight divergence seems to be present in some *Ornithomimus* specimens, but to a much lesser degree than in UALVP 16182. In fact the divergence of the first metacarpal in UALVP 16182 more closely resembles the condition seen in *Struthiomimus*. However, metacarpal I is longer than metacarpal II (although it should be noted that Mc II is from the left manus) which is in turn longer than metacarpal III, a condition thought to diagnose *Ornithomimus* as a whole (Claessens and Loewen, 2015; Russell, 1972). If this condition is truly diagnostic for *Ornithomimus*, then specimens assigned to *Dromiceiomimus* could instead be referred to as *Ornithomimus brevitertius* (Russell, 1930). The ungual of UALVP 16182 (Fig. 13A) is noticeably curved in contrast with the straight unguals seen in ROM 851, identified as *Ornithomimus edmontonicus* (Fig. 13B). However, it resembles the curvature seen in TMP 1995.110.0001 (Fig. 13C), another specimen identified as *Ornithomimus*. However, in both ROM 851 and TMP 1995.110.0001, the flexor tubercles are low, weakly-developed structures that are barely obvious in lateral aspect. In
contrast, the flexor tubercle of UALVP 16182 is more prominent in lateral view. In this respect it is more similar to the flexor tubercle of *Struthiomimus* (Fig. 13D). These may be significant differences because there is evidence that ornithomimid manual morphology, including that of the unguals, can be diagnostic at a generic level (Russell, 1972; Nicholls and Russell, 1981; Makovicky et al. 2004; Kobayashi and Barsbold, 2006; Longrich, 2008; Tsogtbaatar et al. 2017b; R. Nottrodt, pers. comm., 2017). Manual unguals have not been reported from any *Dromiceiomimus breviterius* specimens other than UALVP 16182, although two unguals, one from digit I and the other from either digit II or III, have been reported for *Dromiceiomimus samueli* (Parks, 1928). The claws differ noticeably from each other, with I-2 being more curved and robust compared to the other ungual. This contrasts with *Ornithomimus* where all three manual unguals are essentially the same shape and more resembles the condition observed in *Struthiomimus*. Unfortunately the ungual from digit II or III is too poorly preserved to properly compare the flexor tubercle to that of UALVP 16182 or *Ornithomimus* specimens.

The topological variability of the trees from study to study (e.g. Kobayashi and Lü, 2003; Cullen et al. 2013; Serrano-Brañas et al. 2015; McFeeters et al. 2016) indicates that the taxonomy of Ornithomimosauria still requires significant attention. The topology of the current tree is roughly similar to other analyses of ornithomimosaurids. However, *Anserimimus* and *Ornithomimus* were recovered as sister taxa with UALVP 16182 as the outgroup. The primary purpose of this analysis was to see whether *Dromiceiomimus* and *Ornithomimus* group as sister taxa, which would support their synonymy, or if they group as more distantly related taxa, which would support the retention of separate genera. The current analysis supports the notion that *Dromiceiomimus breviterius* and *Ornithomimus edmontonicus* could be distinct given that UALVP 16182 was not recovered as the sister taxon to *Ornithomimus*. However, the
discrepancies between different analyses suggest that any phylogenetic hypothesis should be considered tentative. Among the 96 characters (Appendix 1) for which it was possible to compare both taxa, *Dromiceiomimus* and *Ornithomimus* differ in nine instances. These differences appear in features of the skull (108), vertebrae (139, 145), scapula (176), manus (210), and pelvis (219, 220, 231, 242). The morphology of the obturator foramen of the ischium (242) differs between UALVP 16182 and *Ornithomimus*, but the distribution of this character seems to be variable across different specimens referred to *Dromiceiomimus* (B. McFeeters, pers. comm., 2018). The presence of a posterior surangular foramen in UALVP 16182 is shared by *Struthiomimus* but not by *Ornithomimus*, as is the depression found on the supraglenoid buttress of the scapula. The difference in the morphology of the flexor tubercle and curvature of the manual ungual, as well as the distal divergence of the metacarpals, may be significant as other authors have noted the diagnostic potential of the ornithomimid manus. These anatomical differences may serve to bolster distinctions made on the basis of the difference in the tibia/femur ratio.

One possible explanation for two somewhat distinct tibia/femur data clusters that display some overlap in the margins of error is sexual dimorphism. This could also account for the somewhat more gracile metacarpals of UALVP 16182. Although the precise nature of sexual dimorphism is highly variable among the extant phylogenetic bracket for dinosaurs (Barden and Maidment, 2011), sexual dimorphism is far more common than monomorphism (Kaliontzopoulou et al. 2007). It is therefore reasonable to expect it in dinosaurs. Various studies have proposed sexual dimorphism based on femoral morphology. Raath (1990) identified gracile and robust morphs of *Coelophysis rhodesiensis* femora, and Larson (2008) had similar findings in a study of *Tyrannosaurus rex*. Barden and Maidment (2011) found what they consider to be
sexual dimorphism among the femora of *Kentrosaurus aethiopicus*. Although the sample size is limited, the *Ornithomimus* femoral lengths are greater than those of *Dromiceiomimus* in all but two instances (ROM 852 and TMP 1995.110.0001, Table 2), and it is possible that the absolute size differences correlate with sexual differences. However, it should be noted that this apparent difference in size may be misleading. A histological analysis by Cullen et al. (2014) concluded, due to the absence of an outer circumferential layer in any of the elements sectioned, that ROM 852 (the largest specimen assigned to *Dromiceiomimus*) had likely not attained full size when it died. Furthermore, recent studies conclude that detecting sexual dimorphism in dinosaurs may not be feasible given the fossil material available. Hone and Mallon (2017) proposed a number of confounding factors. These included the protracted growth periods of most dinosaurs, which cannot be readily accounted for without sample sizes that are not generally available in the fossil record. They found that, even among the relatively sexually dimorphic *Alligator mississippiensis* and with *a priori* knowledge of sex, detection of sexual dimorphism remained difficult without a minimum of 35 individuals per sex and controls for age. Mallon (2017) notes that (among other methodological shortcomings) no studies of sexual dimorphism in dinosaurs have included skeletochronological determination of age and also emphasizes the importance of large sample sizes. Mallon (2017) concluded that sexual dimorphism was not supported in any of the nine dinosaur taxa he examined, including *Coelophysis, Kentrosaurus*, and *Tyrannosaurus*.

The (possibly) longer femora in *Ornithomimus* could also indicate that the two forms are simply different ontogenetic stages with the younger ontogenetic stage represented by specimens identified as *Dromiceiomimus*. Again, ontogeny could account for the slightly more gracile metacarpals of UALVP 16182 compared to *Ornithomimus*. The lack of fusion between the scapula and coracoid and between pelvic elements, as well as the disarticulated preservation of
the skull elements, suggest an immature animal. Examining bone histology could reveal whether
Ornithomimus bones are consistently at a later ontogenetic stage than Dromiceiomimus bones.
That said, however, the tibia/femur ratio is still able to delineate between the taxa despite the fact
that the femoral sizes of Gallimimus and Struthiomimus overlap substantially with those of
Dromiceiomimus, as do those of Ornithomimus to a lesser extent (Fig. 20). Furthermore, it is not
obvious that morphology of the manus in general should change through ontogeny. Kobayashi
and Barsbold (2006) report that the relative size of the manus compared to the humerus in
Gallimimus bullatus remains consistent between the smallest and largest specimens, although
there is no mention of whether the unguals are notably different.
Examining the stratigraphic position of the two genera informs considerations of sexual
dimorphism and individual variation. If the two genera were generally separated
stratigraphically, this would lend credence to the conclusion that Dromiceiomimus and
Ornithomimus edmontonicus are distinct taxa. Unfortunately, relatively few ornithomimid
specimens are assigned to a particular genus, but it is apparent that Dromiceiomimus breviterti
is generally found higher in section than Ornithomimus edmontonicus (Fig. 21). There is,
however, a slight overlap in the Horsethief Member of the Horseshoe Canyon Formation
(Dromiceiomimus specimen ROM 797 and Ornithomimus specimen CMN 8632). The only
major outlier to this pattern is the presence in the Oldman Formation of ROM 840, which is
assigned by Russell (1972) to Dromiceiomimus samueli. This species was originally identified as
Struthiomimus (Parks, 1928) and was synonymized with Ornithomimus edmontonicus by
Makovicky et al. (2004). It also lacks the elements required for determining the significant limb
ratios that arguably distinguish Dromiceiomimus from Ornithomimus. It is therefore difficult to
be sure of how this specimen impacts the overall pattern, although its stratigraphic position may
suggest that it is more closely linked to *Ornithomimus*. This pattern provides a basis for
tentatively rejecting the explanations of sexual dimorphism and individual variation because it
would not make sense for different sexual or ontogenetic morphs to be stratigraphically
segregated. As noted, however, there are too few specimens assigned to either *Dromiceiomimus*
or *Ornithomimus* to establish a statistically robust pattern in their relative stratigraphic
distributions.

Closely related extant animals with very similar morphology can coexist, and thus the
idea of *Dromiceiomimus* and *Ornithomimus* being distinct but sympatric genera is not
unreasonable. One example of coexistence is between mule deer and white-tailed deer in
southern Alberta, where these two similar species are found in sympatry. However, there is no
competitive interference with one another (Krämer, 1973). Whitney et al. (2011) found that
sympatric white-tailed and black-tailed deer, although they have similar diets and habitat use,
were able to coexist due to spatial segregation whereby competition is mainly avoided because
direct interaction is limited. The difference in manual ungual morphology between the two
groups could indicate distinct ecologies (Tsogtbaatar et al. 2017b), which would agree with the
idea of similar but separate sympatric genera.

Regardless of whether *Dromiceiomimus* is revealed to be a valid taxon or a synonym of
*Ornithomimus edmontonicus*, it should be noted that there are issues with several of the
references cited by various studies in support of the latter case. There appears to be a trend in the
literature to consider the two genera synonymous. However, *Dromiceiomimus* has not been
conclusively invalidated in any publication, and so the current consensus on the matter is
misleading. The majority of papers consider the genera synonymous without any explicit
mention of *Dromiceiomimus* (e.g. Ji et al. 2003; Longrich, 2008; Varricchio et al. 2008;
Bronowicz, 2011). Cullen et al. (2013) mention *Dromiceiomimus* specifically and consider it to be synonymous with *Ornithomimus edmontonicus*, citing Longrich (2008) and Xu et al. (2011) to support this. As noted, Longrich (2008) discusses only *Ornithomimus* and does not make any explicit mention of *Dromiceiomimus*. Although this is an implicit synonymy, no support is offered for the synonymy. Therefore, while this paper conforms to the recent trend, it should not be considered as evidence in favour of synonymy. The focus of Cullen et al. (2013), as with papers that implicitly synonymize the two genera, is not on investigating the distinction between *Dromiceiomimus* and *Ornithomimus* and thus the confusion is understandable.

Xu et al. (2011) also explicitly synonymize the two taxa, citing Makovicky et al. (2004) and Kobayashi et al. (2006). Kobayashi et al. (2006) refer to “some previous studies” which found the ratios used by Russell (1972) to diagnose *Dromiceiomimus* lacked statistical support. Because Kobayashi et al. (2006) is a presentation abstract, it does not explicitly cite these studies. However these “previous studies” seem likely include Makovicky et al. (2004), which is somewhat problematic (discussed in the next paragraph). Kobayashi et al. (2006) also support synonymy by citing *Ornithomimus*-like features of *Dromiceiomimus* specimen CMN 12228, specifically the morphology of the anterior ramus of the postorbital, the dorsal ramus of the quadratojugal and the prequadratic foramen. While synonymy is one explanation for these similarities, they could also be explained by a sister taxon relationship between the two genera or by *Dromiceiomimus brevitertius* being a species of *Ornithomimus*.

Makovicky et al. (2004) seems to be the root of much of the confusion because several papers either cite this source directly (e.g. Xu et al. 2011) or indirectly (e.g. Cullen et al. 2013). When looking at papers that synonymize *Dromiceiomimus brevitertius* and *Ornithomimus edmontonicus*, one finds that they are almost exclusively published after 2004. The issue is that
Makovicky et al. (2004) cite Nicholls and Russell (1981) as an authority for synonymizing the two taxa when in fact Nicholls and Russell (1981) conclude that *Dromiceiomimus* should be considered a valid taxon. More specifically, Nicholls and Russell (1981) report that while limb proportions may not be diagnostic among ornithomimids in general, they seem to be diagnostic for *Dromiceiomimus* in particular. The confusion in Makovicky et al. (2004) is also likely the root of the error in Watanabe et al. (2013), who cite Nicholls and Russell (1981) as synonymizing the two genera. Makovicky et al. (2004) also support the synonymy by making reference to a re-examination of the proportions used by Russell (1972) which revealed no statistically significant differences. Unfortunately, the format of *The Dinosauria* prevented the data from being included in the entry and thus the fact remains that there is still no published data that synonymize *Dromiceiomimus* and *Ornithomimus edmontonicus*. Another note of interest is that *Dromiceiomimus brevitertius* was erected by Parks (1926) and *Ornithomimus edmontonicus* by Sternberg (1933). Thus, if *Dromiceiomimus brevitertius* and *Ornithomimus edmontonicus* are to be considered synonymous, then their designation should properly be *Ornithomimus brevitertius* (Russell, 1930).

**CONCLUSIONS**

Whereas Nicholls and Russell (1981) conclude that limb proportions are not necessarily a reliable diagnostic feature, they qualify that statement by saying that the tibia/femur ratio may be diagnostic for *Dromiceiomimus*. The present study supports these findings and further suggests that limb ratios may be diagnostic for ornithomimids. The t-test provided statistical support for distinguishing *Dromiceiomimus* from *Ornithomimus* (as well as other ornithomimids) on the basis of tibia/femur proportions. This statistical difference is present despite the overlap in
absolute femur sizes across the genera examined. The differences in the skull (the presence of a
posterior surangular foramen), scapula (depression on supraglenoid buttress), and the manus
(strongly divergent metacarpal I, more prominent flexor tubercle in phalanx II-2) could be
significant, although of course the small sample size makes it difficult to assess individual and/or
sexual variation. Additionally, the apparent stratigraphic separation of *Dromiceiomiinus
brevitertius* and *Ornithomimus edmontonicus* supports a taxonomic distinction. At minimum, this
study has replicated the finding that there are two morphs (in terms of tibia/femur ratio) present
in specimens generally assigned to *Ornithomimus*, regardless of whether or not these morphs
represent inter- or intraspecific variation. Based on the points discussed, it is not unreasonable to
conclude that these two morphs do indeed represent distinct taxa. Although there are doubts
regarding the utility of limb ratios in diagnosing taxa, it appears that the tibia/femur ratio,
especially when considered in conjunction with other anatomical differences, is useful in
distinguishing between ornithomimid taxa. Despite the recent consensus in the literature,
*Dromiceiomiinus* has not been invalidated as a genus by any published data and, in light of the
present study, it seems advisable, as proposed by Nicholls and Russell (1981), to retain the genus
*Dromiceiomiinus* until data are published that do so. Conversely, if the relative lengths of the
metacarpals is diagnostic for *Ornithomimus* as a genus, then it would also be reasonable (based
on the findings of this study) to refer to *Dromiceiomiinus* specimens as *Ornithomimus
brevitertius*.

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INSTITUTIONAL ABBREVIATIONS

AMNH, American Museum of Natural History, New York; BHI, Black Hills Institute of Geological Research, Hill City, South Dakota; CMN, Canadian Museum of Nature, Ottawa; GI, Geological Institute, Academy of Sciences, Ulan Bator, Mongolia; ROM, Royal Ontario Museum, Toronto; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta; UCMZ (VP), University of Calgary Museum of Zoology, Calgary, Alberta.
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variation in growth marks and osteocyte lacunar density in a theropod dinosaur


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Alberta, Canada: implications for the study of dissociated dinosaur remains.


TABLE 1. Measurements taken from UALVP 16182, all of which were taken twice and averaged.

<table>
<thead>
<tr>
<th>Source</th>
<th>Preserved length (mm)</th>
<th>Min height (mm)</th>
<th>Max height (mm)</th>
<th>Distance from buccal edge to symphysis (mm)</th>
<th>Distance of foramina from buccal edge (mm)</th>
<th>Length of symphysis (mm)</th>
<th>Depth of intramandibular articular surface (mm)</th>
<th>Distance between jaw margin and alveolar shelf (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dentary</strong></td>
<td>137</td>
<td>13.7</td>
<td>20.5</td>
<td>20</td>
<td>1.5 – 4</td>
<td>32.5</td>
<td>4.5</td>
<td>6.7 (anteriorly) – 2 (posteriorly)</td>
</tr>
<tr>
<td><strong>Surangular</strong></td>
<td>119</td>
<td>27</td>
<td>7</td>
<td>20</td>
<td>3</td>
<td>34</td>
<td></td>
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<tr>
<td><strong>Hyoid</strong></td>
<td>120</td>
<td>2.6</td>
<td>5</td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td><strong>Scapula</strong></td>
<td>283</td>
<td>28.3</td>
<td>9.7</td>
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<td><strong>Ulna</strong></td>
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<td>280</td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Metacarpals</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td><strong>Manual phalanges</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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<tr>
<td><strong>Ilium</strong></td>
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<td></td>
<td></td>
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</tr>
<tr>
<td><strong>Pubis</strong></td>
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<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><strong>Femur</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Tibia</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td><strong>Fibula</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Metatarsus</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
TABLE 2. Femur and tibia lengths of *Dromiceiomimus*, *Gallimimus*, *Ornithomimus* and *Struthiomimus*, as well as the ratios of the log_{10} transformed measurements and the sources of the measurements used in this study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Specimen #</th>
<th>Source</th>
<th>Tibia length (mm)</th>
<th>Femur length (mm)</th>
<th>Tibia/femur</th>
<th>Log_{10} tibia/Log_{10} femur</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. brevitertius</em></td>
<td>AMNH 5201</td>
<td>Currie pers. obs.</td>
<td>438</td>
<td>387</td>
<td>1.13</td>
<td>1.02</td>
</tr>
<tr>
<td><em>D. brevitertius</em></td>
<td>ROM 797</td>
<td>Parks 1926, Clive Coy</td>
<td>470</td>
<td>390</td>
<td>1.21</td>
<td>1.03</td>
</tr>
<tr>
<td><em>D. brevitertius</em></td>
<td>UALVP 16182</td>
<td>Macdonald pers. obs.</td>
<td>469</td>
<td>410</td>
<td>1.14</td>
<td>1.02</td>
</tr>
<tr>
<td><em>D. brevitertius</em></td>
<td>CMN 12068</td>
<td>Currie pers. obs. (PJC 2004)</td>
<td>493</td>
<td>416</td>
<td>1.19</td>
<td>1.03</td>
</tr>
<tr>
<td><em>D. brevitertius</em></td>
<td>ROM 852</td>
<td>Parks 1933</td>
<td>520</td>
<td>440</td>
<td>1.18</td>
<td>1.03</td>
</tr>
<tr>
<td><em>G. bullatus</em></td>
<td>MPC-D100/10</td>
<td>Currie pers. obs.</td>
<td>218</td>
<td>192</td>
<td>1.14</td>
<td>1.02</td>
</tr>
<tr>
<td><em>G. bullatus</em></td>
<td>D-I/94</td>
<td>Currie pers. obs.</td>
<td>292</td>
<td>270</td>
<td>1.08</td>
<td>1.01</td>
</tr>
<tr>
<td><em>G. bullatus</em></td>
<td>MPC-D KID 499</td>
<td>Currie pers. obs.</td>
<td>350</td>
<td>332</td>
<td>1.05</td>
<td>1.01</td>
</tr>
<tr>
<td><em>G. bullatus</em></td>
<td>Zpal MgD-I/1</td>
<td>Currie pers. obs.</td>
<td>384</td>
<td>360</td>
<td>1.07</td>
<td>1.01</td>
</tr>
<tr>
<td><em>G. bullatus</em></td>
<td>MPC-D100/14</td>
<td>Currie pers. obs.</td>
<td>403</td>
<td>391</td>
<td>1.03</td>
<td>1.00</td>
</tr>
<tr>
<td><em>G. bullatus</em></td>
<td>MPC-D100/52</td>
<td>Currie pers. obs.</td>
<td>400</td>
<td>400</td>
<td>1.00</td>
<td>1.00</td>
</tr>
<tr>
<td><em>G. bullatus</em></td>
<td>Field # 950818</td>
<td>Currie pers. obs.</td>
<td>450</td>
<td>443</td>
<td>1.02</td>
<td>1.00</td>
</tr>
<tr>
<td><em>G. bullatus</em></td>
<td>MPC-D100/12</td>
<td>Currie pers. obs.</td>
<td>508</td>
<td>500</td>
<td>1.01</td>
<td>1.00</td>
</tr>
<tr>
<td><em>O. edmontonicus</em></td>
<td>TMP 1995.110.0001</td>
<td>Currie pers. obs.</td>
<td>465</td>
<td>425</td>
<td>1.09</td>
<td>1.02</td>
</tr>
<tr>
<td><em>O. edmontonicus</em></td>
<td>ROM 851</td>
<td>Parks 1933, Clive Coy, Russell 72, PJC 2005</td>
<td>475</td>
<td>435</td>
<td>1.09</td>
<td>1.01</td>
</tr>
<tr>
<td><em>O. edmontonicus</em></td>
<td>UALVP 52531</td>
<td>Currie pers. obs.</td>
<td>520</td>
<td>480</td>
<td>1.08</td>
<td>1.01</td>
</tr>
<tr>
<td><em>O. edmontonicus</em></td>
<td>CMN 12441</td>
<td>Currie pers. obs. (PJC 2004)</td>
<td>550</td>
<td>507</td>
<td>1.08</td>
<td>1.01</td>
</tr>
<tr>
<td><em>S. altus</em></td>
<td>AMNH 5385</td>
<td>Currie pers. obs.</td>
<td>408</td>
<td>370</td>
<td>1.10</td>
<td>1.02</td>
</tr>
<tr>
<td><em>S. altus</em></td>
<td>TMP 1990.026.0001</td>
<td>Currie pers. obs.</td>
<td>506</td>
<td>467</td>
<td>1.08</td>
<td>1.01</td>
</tr>
<tr>
<td><em>S. altus</em></td>
<td>AMNH 5339</td>
<td>Osborn 1917</td>
<td>540</td>
<td>480</td>
<td>1.13</td>
<td>1.02</td>
</tr>
<tr>
<td><em>S. altus</em></td>
<td>UCMZ (VP) 1980.1</td>
<td>Currie pers. obs.</td>
<td>556</td>
<td>502</td>
<td>1.11</td>
<td>1.02</td>
</tr>
<tr>
<td><em>S. altus</em></td>
<td>AMNH 5257</td>
<td>Currie pers. obs.</td>
<td>555</td>
<td>512</td>
<td>1.08</td>
<td>1.01</td>
</tr>
<tr>
<td><em>S. sedens</em></td>
<td>BHI 1266</td>
<td>van der Reest et al. 2016</td>
<td>700</td>
<td>632</td>
<td>1.12</td>
<td>1.02</td>
</tr>
</tbody>
</table>
TABLE 3. Allometric analysis of tibia-femur ratio for *Dromiceiomimus*, *Gallimimus*, *Ornithomimus* and *Struthiomimus* using RMA 1.17.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>R²</th>
<th>Slope</th>
<th>Intercept</th>
<th>Lower CI</th>
<th>Upper CI</th>
<th>Growth Pattern</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dromiceiomimus</em></td>
<td>0.841</td>
<td>1.22</td>
<td>-0.51</td>
<td>0.33</td>
<td>2.12</td>
<td>isometry</td>
</tr>
<tr>
<td><em>Gallimimus</em></td>
<td>0.996</td>
<td>0.87</td>
<td>0.34</td>
<td>0.82</td>
<td>0.92</td>
<td>-ve allometry</td>
</tr>
<tr>
<td><em>Ornithomimus</em></td>
<td>0.999</td>
<td>0.95</td>
<td>0.18</td>
<td>0.88</td>
<td>1.01</td>
<td>isometry</td>
</tr>
<tr>
<td><em>Struthiomimus</em></td>
<td>0.991</td>
<td>1.04</td>
<td>-0.07</td>
<td>0.93</td>
<td>1.15</td>
<td>isometry</td>
</tr>
</tbody>
</table>
TABLE 4. Ratios of the manus for *Dromiceiomimus*, *Ornithomimus* and *Struthiomimus* derived from measurements which were taken twice and averaged.

<table>
<thead>
<tr>
<th>Ratio</th>
<th><em>Dromiceiomimus</em> (UALVP 16182)</th>
<th><em>Ornithomimus</em> (ROM 851)</th>
<th><em>Struthiomimus</em> (BHI 1266)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mc I length/Mc I width</td>
<td>12.64</td>
<td>11.40</td>
<td>–</td>
</tr>
<tr>
<td>Mc III length/Mc III width</td>
<td>14.17</td>
<td>11.76</td>
<td>–</td>
</tr>
<tr>
<td>Mc I length/Mc III length</td>
<td>1.09</td>
<td>1.06</td>
<td>0.98</td>
</tr>
<tr>
<td>Mc I length/Femur length</td>
<td>0.25</td>
<td>0.24</td>
<td>0.18</td>
</tr>
<tr>
<td>Mc III length/Femur length</td>
<td>0.23</td>
<td>0.22</td>
<td>0.19</td>
</tr>
<tr>
<td>Ph I-1 length/Mc I length</td>
<td>1.04</td>
<td>1.08</td>
<td>1.09</td>
</tr>
<tr>
<td>Ph I-1 length/Mc III length</td>
<td>1.13</td>
<td>1.14</td>
<td>1.07</td>
</tr>
<tr>
<td>Ph I-1 length/Ph II-2 length</td>
<td>1.41</td>
<td>1.30</td>
<td>1.24</td>
</tr>
<tr>
<td>Ph I-1 length/Ph III-3 length</td>
<td>1.67</td>
<td>1.53</td>
<td>1.56</td>
</tr>
<tr>
<td>Ph I-1 length/Femur length</td>
<td>0.26</td>
<td>0.26</td>
<td>0.20</td>
</tr>
<tr>
<td>Ph II-3 outer length/straight length</td>
<td>1.10</td>
<td>1.00</td>
<td>1.07</td>
</tr>
</tbody>
</table>
TABLE 5. Results from a one-tailed t-test with unequal variance comparing the tibia/femur ratios of different pairs of genera.

<table>
<thead>
<tr>
<th>Genera</th>
<th>t</th>
<th>P</th>
<th>t critical</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dromiceiomimus</em> (n=5) – <em>Gallimimus</em> (n=8)</td>
<td>5.13</td>
<td>0.00016</td>
<td>1.79</td>
</tr>
<tr>
<td><em>Dromiceiomimus</em> (n=5) – <em>Ornithomimus</em> (n=4)</td>
<td>6.08</td>
<td>0.00185</td>
<td>2.13</td>
</tr>
<tr>
<td><em>Dromiceiomimus</em> (n=5) – <em>Struthiomimus</em> (n=7)</td>
<td>4.99</td>
<td>0.00124</td>
<td>1.94</td>
</tr>
<tr>
<td><em>Gallimimus</em> (n=8) – <em>Ornithomimus</em> (n=4)</td>
<td>1.87</td>
<td>0.05191</td>
<td>1.89</td>
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<tr>
<td><em>Gallimimus</em> (n=8) – <em>Struthiomimus</em> (n=7)</td>
<td>2.13</td>
<td>0.03083</td>
<td>1.83</td>
</tr>
<tr>
<td><em>Ornithomimus</em> (n=4) – <em>Struthiomimus</em> (n=7)</td>
<td>0.92</td>
<td>0.19174</td>
<td>1.86</td>
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</tbody>
</table>
TABLE 6. Metatarsal III and femur lengths (measured twice and averaged) of *Dromiceiomimus*, *Gallimimus*, *Ornithomimus* and *Struthiomimus*, as well as the ratios of those two elements.

<table>
<thead>
<tr>
<th>Species</th>
<th>Specimen #</th>
<th>Mt III length (mm)</th>
<th>Femur length (mm)</th>
<th>Femur/MtIII</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dromiceiomimus brevitertius</em></td>
<td>CMN 12068</td>
<td>356</td>
<td>416</td>
<td>1.168539</td>
</tr>
<tr>
<td><em>Dromiceiomimus brevitertius</em></td>
<td>ROM 797</td>
<td>298</td>
<td>390</td>
<td>1.308725</td>
</tr>
<tr>
<td><em>Dromiceiomimus brevitertius</em></td>
<td>ROM 852</td>
<td>370</td>
<td>440</td>
<td>1.189189</td>
</tr>
<tr>
<td><em>Dromiceiomimus brevitertius</em></td>
<td>UALVP 16182</td>
<td>341</td>
<td>410</td>
<td>1.202346</td>
</tr>
<tr>
<td><em>Gallimimus bullatus</em></td>
<td>Zpal MgD-I/1</td>
<td>280</td>
<td>360</td>
<td>1.285714</td>
</tr>
<tr>
<td><em>Gallimimus bullatus</em></td>
<td>D-I/8</td>
<td>510</td>
<td>635</td>
<td>1.245098</td>
</tr>
<tr>
<td><em>Gallimimus bullatus</em></td>
<td>D-I/94</td>
<td>220</td>
<td>270</td>
<td>1.227273</td>
</tr>
<tr>
<td><em>Gallimimus bullatus</em></td>
<td>MPC-D100/10</td>
<td>157</td>
<td>192</td>
<td>1.22293</td>
</tr>
<tr>
<td><em>Gallimimus bullatus</em></td>
<td>MPC-D100/11</td>
<td>530</td>
<td>665</td>
<td>1.254717</td>
</tr>
<tr>
<td><em>Gallimimus bullatus</em></td>
<td>MPC-D100/12</td>
<td>360</td>
<td>500</td>
<td>1.388889</td>
</tr>
<tr>
<td><em>Gallimimus bullatus</em></td>
<td>MPC-D100/52</td>
<td>283</td>
<td>400</td>
<td>1.413428</td>
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<tr>
<td><em>Gallimimus bullatus</em></td>
<td>Field # 950818</td>
<td>305</td>
<td>443</td>
<td>1.452459</td>
</tr>
<tr>
<td><em>Ornithomimus edmontonicus</em></td>
<td>ROM 851</td>
<td>310</td>
<td>435</td>
<td>1.403226</td>
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<tr>
<td><em>Ornithomimus edmontonicus</em></td>
<td>RTMP 95.110.1</td>
<td>332</td>
<td>425</td>
<td>1.28012</td>
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<tr>
<td><em>Struthiomimus altus</em></td>
<td>UCMZ (VP) 1980.1</td>
<td>398</td>
<td>502</td>
<td>1.261307</td>
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<tr>
<td><em>Struthiomimus altus</em></td>
<td>ROM 1790</td>
<td>300</td>
<td>395</td>
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<tr>
<td><em>Struthiomimus altus</em></td>
<td>AMNH 5257</td>
<td>370</td>
<td>512</td>
<td>1.383784</td>
</tr>
<tr>
<td><em>Struthiomimus altus</em></td>
<td>AMNH 5339</td>
<td>370</td>
<td>480</td>
<td>1.297297</td>
</tr>
<tr>
<td><em>Struthiomimus altus</em></td>
<td>RTMP 90.26.1</td>
<td>375</td>
<td>467</td>
<td>1.245333</td>
</tr>
</tbody>
</table>
TABLE 7. Results from a one-tailed t-test with unequal variance comparing the metatarsal III/femur ratios of different pairs of genera.

<table>
<thead>
<tr>
<th>Genera</th>
<th>t</th>
<th>P</th>
<th>t critical</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dromiceiornimus (n=4) – Gallimimus (n=8)</td>
<td>2.12</td>
<td>0.03334</td>
<td>1.86</td>
</tr>
<tr>
<td>Dromiceiornimus (n=4) – Ornithomimus (n=2)</td>
<td>1.81</td>
<td>0.10605</td>
<td>2.92</td>
</tr>
<tr>
<td>Dromiceiornimus (n=4) – Struthiornimus (n=4)</td>
<td>1.81</td>
<td>0.05994</td>
<td>1.94</td>
</tr>
<tr>
<td>Gallimimus (n=8) – Ornithomimus (n=2)</td>
<td>0.41</td>
<td>0.36136</td>
<td>2.92</td>
</tr>
<tr>
<td>Gallimimus (n=8) – Struthiornimus (n=4)</td>
<td>0.32</td>
<td>0.32014</td>
<td>1.83</td>
</tr>
<tr>
<td>Ornithomimus (n=2) – Struthiornimus (n=4)</td>
<td>0.65</td>
<td>0.29131</td>
<td>2.92</td>
</tr>
</tbody>
</table>
FIGURE 1. Map of the area from which UALVP 16182 was collected. A, an overview of Alberta with an inset of the immediate area surrounding the collection site, including an outline of Dry Island Buffalo Jump Provincial Park. Modified from Google Maps. Scale bar equals 10km; B, a satellite image from Google Maps with the collection site marked by an X. Scale bar equals 1km.

FIGURE 2. Skull elements from UALVP 16182. A, right jugal in dorsolateral view; B, right jugal in lateral view; C, left dentary and splenial in medial view. d, dentary; pn, pneumatopore; qj, quadratojugal; sp, splenial. Shaded grey area represents contact with another bone. Scale bars equal 5cm.

FIGURE 3. Skull elements from UALVP 16182. A, right surangular in lateral view; B, right dentary in medial view; C, right prearticular in medial view; D, right nasal in dorsal view and right postorbital in lateral view. mf, mandibular fenestra. Shaded grey area represents contact with another bone. Scale bars equal 5cm.

FIGURE 4. Hyoid in lateral view. Scale bar equals 5 cm.

FIGURE 5. Vertebrae from UALVP 16182. Light grey indicates matrix A, right lateral view of cervical vertebra; B, left lateral view of seventh dorsal vertebra; C, anterior view of caudal vertebra; D, right lateral view of caudal vertebra. C and D are based primarily on the sixth caudal but are composite images of three proximal caudals. cpf, central pneumatic foramen; id, infradiapophysial fossa; ipo, infrapostzygapophyssial fossa; ipr, infraprezygapophyssial fossa; ns, neural spine; po, postzygapophyses; pr, prezygapophyses; tr, transverse process. Scale bars equal 5 cm.

FIGURE 6. Cervical vertebrae, arranged from caudalmost to cranialmost. A, dorsal view; B, right lateral view. Scale bar equals 10 cm.

FIGURE 7. Dorsal vertebrae. A, dorsal view; B, right lateral view. Scale bar equals 10 cm.

FIGURE 8. Caudal vertebrae and haemal arches. A, caudal vertebrae in dorsal view; B, caudal vertebrae in right lateral view; C, haemal arches in left lateral view; D, haemal arches in posterior view. Scale bar equals 10 cm.

FIGURE 9. Ribs and gastralia. A, ribs; B, gastralia. Scale bar equals 10 cm.
FIGURE 10. Left scapula in lateral view. Hashing indicates areas that have been reconstructed. ac, acromion; gl, scapular portion of glenoid; scb, scapular blade. Scale bar equals 10 cm.

FIGURE 11. Right ulna. A, dorsal view; B, lateral view. cp, coronoid process; op, olecranon process; tr, trochlear notch. Scale bar equals 10 cm.

FIGURE 12. Comparison of ornithomimid manus. All appear in lateral view. A is a right manus while B, C, and D are left manus reversed along a vertical axis for more direct comparison with A. A, Dromiceiomimus, UALVP 16182, right manus; B, Ornithomimus, ROM 851; C, Struthiomimus, UCMZ (VP) 1980.1; D, Gallimimus, G.I. No. DPS 100/11. Modified from Nicholls and Russell (1981). Scale bar equals 10 cm.

FIGURE 13. Comparison of ornithomimid manual ungual II-3 in lateral view. A, Dromiceiomimus brevitertius, UALVP 16182; B, Ornithomimus edmontonicus, ROM 851; C, Ornithomimus edmontonicus, TMP 1995.110.0001; D Struthiomimus altus, TMP 1990.026.0001. ft, flexor tubercle; kg, keratin groove. Scale bar equals 5cm.

FIGURE 14. Right manual phalanx II-2. A, right lateral view; B, left lateral view; C, dorsal view; D, ventral view, after the bony callous was prepared away.

FIGURE 15. Pelvic girdle of UALVP 16182. Light grey areas indicate matrix, hashed areas indicate reconstruction. A, left ilium in lateral view; B, pelvic girdle in right lateral view. ac, acetabulum; bf, brevis fossa; bs, brevis shelf; cf, cuppidicus fossa; il, ilum; ip, ischial peduncle; isc, ischium; isa, ischial apron p, pubis; pp, pubic peduncle; pua, pubic apron; ss, supraacetabular shelf. Scale bars equal 10 cm.

FIGURE 16. Hind limb elements of UALVP 16182. Light grey areas indicate matrix, hashed areas indicate reconstruction. A, left femur in posteromedial view; B, left tibia-fibula in medial view; C, left metatarsus in anterior view. Note that Mt II is shifted proximally in the illustration compared to the photograph. This is the result of preparation subsequent to the illustration being done and repositioning of the element into its proper position. a, astragalus; cn, cnemial crest; f, fibula; fh, femoral head; ft, fourth trochanter; ig, intercondylar groove; II, metacarpal II; III, metacarpal III; IV, metacarpal IV; lc, lateral condyle; mc, medial condyle; t, tibia. Scale bars equal 10 cm.
FIGURE 17. Left tibia-fibula in lateral view. a, astragalus; cal, calcaneum; cn, cnemial crest; f, fibula; fc, fibular crest; t, tibia. Scale bar equals 10 cm.

FIGURE 18. Pedal phalanges. All phalanges appear first in lateral, then dorsal, ventral, proximal and finally distal view. A, Ph II-1; B, Ph III-2; C, Ph III-3; D, Ph IV-2; E, Ph II-3; F, Ph III-4. Scale bar equals 5 cm.

FIGURE 19. Most parsimonious tree recovered from a heuristic analysis of ten ornithomimosaur and four other theropods outgroups with bootstrap and Bremer values added (Bootstrap/Bremer).

FIGURE 20. Comparison of tibia-femur ratios between Dromiceiomimus, Ornithomimus and Struthiomimus. Ratios were calculated from log_{10}-transformed measurements to account for differences in size. Reduced major axis (RMA) regression lines were calculated to assess how well correlated data clusters were. The different taxa cluster separately despite overlapping in absolute femur size, although the error bars overlap. A and B represent the same data, but the scales of the axes have been altered in B for visual clarity.

FIGURE 21. Stratigraphic position of ornithomimid specimens. Dromiceiomimus specimens seem to appear generally higher in section than Ornithomimus specimens, however the sample of ornithomimids identified to genus is too small to reveal a statistically significant pattern. Specimen locations are based on Table A1 from Eberth et al., 2013. The figure is made in the same style as Figure 6 from Cullen et al., 2013.
APPENDIX 1 – Characters used in phylogenetic analysis

1. Skull compared with length of neck: 0, neck less than double length of skull; 1, neck at least twice length of skull (Perez-Moreno et al., 1994).
2. Skull vs Femur lengths: 0, falls on or near tyrannosaurid bivariate line $y=0.9638x + 0.09$; 1, falls well below this line (new, this paper).
3. Hand (mc II plus digit II) to humerus plus radius length: 0, less than 59%; 1, more than 60% (Perez-Moreno et al., 1994).
4. Tibia plus Metatarsal III to Femur lengths in comparison with tyrannosaurids: 0, less than in tyrannosaurids; 1, the same as tyrannosaurids or greater.
5. Narial opening, posterior margin: 0, more anterior than, or nearly reaching anterior border of the antorbital fossa; 1, overlapping.
6. Antorbital fossa, lateral view: 0, dorsal border formed by the lacrimal and maxilla; 1, by the lacrimal and nasal; 2, by maxilla, premaxilla, and lacrimal.
7. Antorbital fenestra size compared with orbit: 0, falls close to tyrannosaurids on line $y=1.14x-.05$; 1, falls significantly below line; 2, smaller yet (oviraptorids).
8. Lateral temporal fenestra: 0, postorbital bar parallels quadrate, lower temporal fenestra rectangular; 1, jugal and postorbital approach or contact quadratojugal-squamosal flange to constrict fenestra.
9. Upper temporal fossa: 0, limited extension onto dorsal surfaces of frontal and postorbital; 1, covers most of frontal process of the postorbital and extends anteriorly onto dorsal surface of frontal
10. Upper temporal fenestra: 0, bounded laterally and posteriorly by the squamosal; 1, supratemporal fenestra extended as a fossa on to the dorsal surface of the squamosal.
11. External mandibular fenestra: 0, present; 1, reduced; 2, absent.
12. Premaxillary symphysis: 0, acute, V-shaped; 1, rounded, U-shaped.
13. Premaxilla, crenulate margin on buccal edge of premaxilla: 0, absent; 1, present. Only applies in taxa with edentulous premaxilla.
14. Premaxilla, main body: 0, anteroposteriorly longer than high or approximately as long as high; 1, significantly higher than long. (Turner, et al., 2012, character 260).
15. Premaxilla, maxillary process: 0, contacts nasal to form posterior border of nares; 1, reduced so that maxilla participates in external naris; 2, extends posteriorly to separate maxilla from nasal behind naris.
16. Premaxilla, maxillary process: 0, posterior end terminates anterior to anterior border of antorbital fossa; 1, extends more posteriorly (Kobayashi and Lü, 2003).
17. Premaxilla: 0, internarial bar rounded; 1, flat.
18. Maxilla: 0, participates in external narial opening; 1, separated from opening by maxilla-nasal contact (Xu et al., 2002).
19. Maxilla, series of foramina along ventral edge of lateral surface: 0, present; 1, absent (Kobayashi and Lü, 2003).
20. Maxilla, promaxillary fenestra: 0, absent; 1, present.
21. Maxilla, promaxillary fenestra: 0, visible in lateral view; 1, obscured by ascending ramus of maxilla (Witmer, 1997).
22. Maxilla, maxillary fenestra: 0, situated at anterior border of antorbital fossa; 1, situated posterior to anterior border of fossa.
23. Maxilla, maxillary fenestra displaced dorsally: 0, absent; 1, present.
24. Maxilla, jugal process ventral to antorbital fossa: 0, dorsoventrally shallow; 1, dorsoventrally deep.
25. Maxilla, secondary palate: 0, short; 1, long, with extensive palatal shelves on maxilla.
26. Nasals: 0, unfused; 1, at least partially fused.
27. Nasals, dorsal surface of nasals: 0, smooth; 1, ornamented with irregular sculpting [taxa with a mid-line crest are considered inapplicable].
28. Nasals in dorsal view: 0, with parallel outer edges posterior to narial region; 1, hourglass shaped with constriction at midlevel and expanded ends.
29. Nasals, series of pneumatic foramina along lateral edge of nasal: 0, absent; 1, present.
30. Nasals: 0, narial region apneumatic or poorly pneumatized; 1, with extensive pneumatic fossae, especially along posterodorsal rim of naris.
31. Jugal: 0, does not participate in margin of antorbital fenestra; 1, participates in antorbital fenestra.
32. Jugal, sublacrimal part: 0, tapering; 1, expanded (Turner, 2012, character 262 simplified).
33. Jugal pneumatic recess in posteroventral corner of antorbital fossa: 0, present; 1, absent.
34. Jugal: 0, medial jugal foramen present on medial surface ventral to postorbital bar; 1, absent.
35. Jugal beneath lower temporal fenestra, 0, at least twice as tall dorsoventrally as it is wide transversely; 1, rod-like.
36. Jugal and postorbital: 0, contribute equally to postorbital bar; 1, ascending process of jugal reduced and descending process of postorbital ventrally elongate.
37. Lacrimal: 0, supraorbital crests in adult individuals absent; 1, dorsal crest above orbit; 2, dorsal crest present and surmounted by cornual process.
38. Lacrimal, enlarged foramen or foramina opening laterally at the angle of the lacrimal above antorbital fenestra: 0, absent; 1, present.
39. Lacrimal posterodorsal process: 0, absent (inverted 'L' shaped); 1, lacrimal 'T' shaped in lateral view; 2, anterodorsal process much longer than posterior process.
40. Lacrimal, prominence on lateral surface: 0, present; 1, absent (Xu et al., 2002).
41. Jugal and quadratojugal: 0, separate; 1, jugal fused and not distinguishable from one another.
42. Prefrontal: 0, large, dorsal exposure similar to that of lacrimal; 1, greatly reduced in size; 2, absent.
43. Frontals: 0, narrow posteriorly as a wedge between nasals; 1, end abruptly posteriorly, suture with nasal transversely oriented.
44. Frontal, anterior emargination of supratemporal fossa onto frontal: 0, straight or slightly curved; 1, strongly sinusoidal and reaching onto postorbital process.
45. Frontal, position of frontoparietal suture relative to postorbital processes of frontal: 0, well posterior; 1, level with; 2, anterior to (Turner, 2012, Character 464).
46. Frontal: 0, broadly exposed along orbital margin; 1, excluded from orbital margin as prefrontal and postorbital almost meet or contact each other.
47. Postorbital, anterior process: 0, projects into orbit; 1, does not project into orbit.
48. Postorbital, lateral view of anterior frontal process: 0, straight; 1, curves anterodorsally and dorsal border of temporal bar is dorsally concave.
49. Postorbital bar: 0, relatively narrow and similar to preorbital bar (lacrimal) in anteroposterior length; 1, anteroposteriorly long and plate-like, about twice as long as preorbital bar.

50. Parietals: 0, separate; 1, fused.

51. Parietals: 0, dorsal surface flat, lateral ridge borders supratemporal fenestra; 1, dorsally convex with low sagittal crest along midline; 2, dorsally convex with well-developed sagittal crest.

52. Squamosal, descending process: 0, parallels quadrate shaft; 1, nearly perpendicular to quadrate shaft.


54. Quadratojugal: 0, without horizontal process posteroventral to ascending process (reversed 'L' shape); 1, with process (inverted 'T' or 'Y' shape).

55. Quadratojugal: 0, mediolaterally compressed and flat; 1, with distinct flexure near posterior border, so that posterior edge faces posteriorly rather than laterally.

56. Quadrate: 0, vertical; 1, strongly inclined anteroventrally so that distal end lies far forward of proximal end.

57. Quadrate head: 0, covered by squamosal in lateral view; 1, quadrate cotyle of squamosal open laterally exposing quadrate head.

58. Quadrate: 0, solid; 1, hollow (pneumatic), with foramen on posterior surface.

59. Quadrate pneumatization: 0, none; 1, single large pneumatopore on posteromedial surface of body (Turner, 2012, character 301).

60. Quadrate, lateral border of shaft: 0, straight; 1, with broad, triangular process along lateral edge of shaft contacting squamosal and quadratojugal above enlarged quadrate foramen.

61. Quadrate fenestra: 0, small, slit-like, fully or almost fully enclosed by quadrate; 1, very large, circular with broad participation of quadratojugal in lateral margin; 2, large but contained within quadrate.

62. Quadrate and quadratojugal ascending rami: 0, meet squamosal to form straight border to the lateral temporal fenestra; 1, kinked into fenestra at midheight.

63. Basisphenoid-parasphenoid, base of cultriform process: 0, not highly pneumatized; 1, base of cultriform process (parasphenoid rostrum) expanded and pneumatic (parasphenoid bulla present).

64. Basioccipital, subcondylar recesses: 0, absent; 1, present.

65. Prootic, opisthotic crista interfenestrals: 0, confluent with lateral surface of prootic and opisthotic; 1, distinctly depressed within middle ear opening.

66. Basisphenoid in ventral view: 0, basisphenoid longer than wide, or with subequal proportions; 1, basisphenoid clearly wider than long.

67. Basisphenoid recess: 0, present between basisphenoid and basioccipital; 1, entirely within basisphenoid; 2, absent.

68. Basisphenoid with pronounced muscle scars flanking basisphenoid recess: 0, no; 1, yes.

69. Basisphenoid, posterior opening of basisphenoid recess: 0, single; 1, divided into two small, circular foramina by a thin bar of bone.

70. Basipterygoid processes: 0, ventral or anteroventrally projecting; 1, lateroventrally projecting.
71. Basipterygoid processes: 0, well developed, extending as a distinct process from the base of the basisphenoid; 1, processes abbreviated or absent.
72. Basipterygoid processes: 0, solid; 1, hollow.
73. Basipterygoid recesses on dorsolateral surfaces of basipterygoid processes: 0, absent; 1, present.
74. Braincase, accessory tympanic recess dorsal to crista interfenestralis: 0, absent; 1, small pocket present; 2, extensive with indirect pneumatization.
75. Braincase, prootic depression for pneumatic recess: 0, absent; 1, present as dorsally open fossa on prootic/opisthotic; 2, present as deep, posterolaterally directed concavity.
76. Braincase, subotic recess (pneumatic fossa ventral to fenestra ovalis): 0, absent; 1, present.
77. Braincase, preotic pendent: 0, absent; 1, present but small; 2 robust ORDERED (Turner, 2012, character 448).
78. Braincase, posterior tympanic recess: 0, absent; 1, present as opening on anterior surface of paroccipital process; 2, extends into opisthotic posterodorsal to fenestra ovalis, confluent with this fenestra.
79. Braincase, exits of C. N. X-XII: 0, flush with surface of exoccipital; 1, cranial nerve exits located together in a bowl-like depression.
80. Braincase, foramen magnum: 0, subcircular, slightly wider than tall; 1, oval, taller than wide.
81. Braincase, occipital condyle: 0, without constricted neck; 1, subspherical with constricted neck.
82. Supraoccipital, median ridge: 0, absent or low; 1, pronounced, strongly demarcated (Holtz 1998).
83. Basiooccipital, basal tubera: 0, far apart, level with or beyond lateral edge of occipital condyle (connected by web of bone or separated by large notch); 1, small, directly below condyle, and separated by narrow notch.
84. Paroccipital process: 0, elongate and slender, with dorsal and ventral edges nearly parallel; 1, process short, deep with convex distal end.
85. Paroccipital process: 0, straight, projects laterally or posterolaterally; 1, distal end curves ventrally, pendant.
86. Paroccipital process: 0, with straight dorsal edge; 1, with dorsal edge twisted anterolaterally at distal end.
87. Vomer: 0, contacts premaxilla; 1, does not contact premaxilla (Turner, 2012, character 279).
88. Ectopterygoid: 0, with constricted opening into fossa; 1, with open ventral fossa in the main body of the element.
89. Ectopterygoid: 0, dorsal recess absent; 1, present.
90. Pterygoid flange: 0, well developed; 1, reduced in size or absent.
91. Palatine and ectopterygoid: 0, separated by pterygoid; 1, contact.
92. Mandibles: 0, occlude for their full length; 1, diverge anteriorly due to kink and downward deflection in dentary buccal margin.
93. Mandible: 0, without coronoid prominence; 1, with coronoid prominence.
94. Mandible, accessory mandibular condyle, lateral to lateral condyle of quadrate: 0, absent; 1, present (Kobayashi and Lü, 2003).
95. Mandibular fenestra: 0, heart-shaped with a short and wide process of the dentary at the anterior part of the external mandibular fenestra; 1, oval shaped.
96. Dentary: 0, subtriangular in lateral view; 1, with subparallel dorsal and ventral edges.
97. Dentary, dorsal border in transverse cross-section: 0, rounded and lacks "cutting edge"; 1, sharp with "cutting edge".
98. Dentary symphyseal region: 0, in line with main part of buccal edge; 1, symphyseal end downturned leaving gap between upper and lower jaws.
99. Dentary: 0, symphyseal region of dentary broad and straight, paralleling lateral margin; 1, medially recurved slightly; 2, strongly recurved medially.
100. Dentary: 0, separate interdental plates; 1, interdental plates fused; 1, lost.
101. Dentary, posterior end: 0, no posterodorsal process dorsal to external mandibular fenestra; 1, dorsal process above anterior end of mandibular fenestra; 2, elongate dorsal process extending over most of fenestra.
102. Splenial forms notched anterior margin of internal mandibular fenestra: 0, absent; 1, present.
103. Splenial, posterior extent: 0, ends anterior to external mandibular fenestra; 1, extends posterior to middle of external mandibular fenestra (new character).
104. Coronoid ossification: 0, large; 1, only a thin splint; 2, absent.
105. Surangular, laterally inclined flange along dorsal edge for articulation with lateral process of lateral quadrate condyle: 0, absent; 1, present.
106. Surangular, foramen in lateral surface of surangular anterior to mandibular articulation: 0, absent; 1, present; 2, enlarged into a fenestra.
107. Surangular, foramen on dorsal edge dorsal to mandibular fenestra: 0, absent; 1, present.
108. Surangular, posterior surangular foramen: 0, absent; 1, present.
109. Angular: 0, exposed almost to end of mandible in lateral view, reaches or almost reaches articular; 1, excluded from posterior end, angular suture turns ventrally and meets ventral border of mandible anterior to glenoid.
110. Angular, exposure on medial surface of mandible: 0, virtually none; 1, considerable along the ventral edge of mandible.
111. Articular, tall slender medial, posteromedial or mediodorsal process on retroarticular process: 0, absent; 1, present.
112. Articular, retroarticular process: 0, points posteriorly; 1, curves gently posterodorsally.
113. Articular, retroarticular process: 0, short, stout; 1, rod-like, elongate and slender.
114. Articular, mandibular articulation surface: 0, as long as distal end of quadrate; 1, two or more times longer than quadrates surface, allowing anteroposterior movement of mandible.
115. Teeth: 0, constricted between root and crown; 1, edges of root and crown confluent.
116. Teeth, premaxilla: 0, present; 1, absent.
117. Teeth, premaxilla: 0, subequal to anterior maxillary teeth in size; 1, significantly smaller.
118. Teeth, premaxilla: 0, serrated; 1, unserrated.
119. Teeth, premaxilla: 0, basal cross section sub-oval to sub-circular; 1, asymmetrical (J-shaped in cross section) with flat lingual surface; 2, D-shaped. Ordered.
120. Teeth, premaxilla, first tooth size compared with crowns of premaxillary teeth 2 and 3: 0, slightly smaller or same size; 1, much smaller; 2, much larger.
121. Teeth, premaxilla: 0, second tooth approximately equivalent in size to other premaxillary teeth; 1, second tooth markedly larger than third and fourth premaxillary teeth.
122. Teeth, maxilla: 0, present; 1, edentulous.
123. Teeth, maxillary tooth height: 0, highly variable with gaps evident for replacement; 1, almost isodont with no replacement gaps.
124. Teeth, maxilla and dentary: 0, serrated; 1, some without serrations anteriorly (except at base in Saurornithoides mongoliensis); 2, all without serrations.
125. Teeth, maxilla and dentary, tooth size: 0, large; 1, small (25-30 in dentary).
126. Teeth, dentary teeth: 0, in separate alveoli; 1, set in open groove; 2, no sockets (modified).
127. Teeth, dentary: 0, present and ziphodont; 1, restricted to front, peglike and thin enamel; 2, absent.
128. Vertebrae, anterior postaxial prezygapophyses: 0, straight; 1, anteroposteriorly convex, flexed ventrally anteriorly (Turner, 2012, character 264).
129. Vertebrae pneumatism: 0, cervicals only; 1, cervical centra and anterior dorsals but not posterior dorsal vertebrae; 2, all presacral centra pneumatic.
130. Vertebrae, cervical, axial neural spine: 0, flared transversely; 1, compressed mediolaterally.
131. Vertebrae, cervical, axis, epineurapophyseal processes (on either side of distal end of neural spine): 0, absent; 1, present.
132. Vertebrae, cervical, axial epipophyses: 0, absent or poorly developed, not extending past posterior rim of postzygapophyses; 1, large and posteriorly directed, extend beyond postzygapophyses.
133. Vertebrae, cervicals, axial neural spine: 0, sheet-like; 1, anteroposteriorly reduced and rod-like (Turner, 2012, character 263).
134. Vertebrae, cervical, epipophyses: 0, distal on postzygapophyses above postzygapophyseal facets; 1, positioned proximal to postzygapophyseal facets.
135. Vertebrae, cervical centra, anterior: 0, posterior intercentral articulation level with or shorter than posterior extent of neural arch; 1, centra extending beyond posterior limit of neural arch.
136. Vertebrae, cervical, hypapophysis (carotid process) on posterior cervicals: 0, absent; 1, present.
137. Vertebrae, cervical, anterior centra: 0, subcircular or square in anterior view; 1, distinctly wider than high, kidney shaped.
138. Vertebrae, cervical neural spines: 0, anteroposteriorly long; 1, short and centered on neural arch, giving arch an 'X' shape in dorsal view.
139. Vertebrae, anteroposterior length of cervical neural spines: 0, more than 1/3 of neural arch length; 1, less than 1/3 of neural arch length (Pérez-Moreno et al., 1994).
140. Vertebrae, cervical centra: 0, one pair of pneumatic openings; 1, two pairs of pneumatic openings.
141. Vertebrae, cervical and anterior trunk vertebrae: 0, amphiplatyan; 1, opisthocoelous; 2, heterocoelous.
142. Vertebrae, dorsal, neural spines: 0, not expanded distally; 1, expanded to form 'spine table'.
143. Vertebrae, dorsal, anterior trunk vertebrae: 0, with low hypapophyses (carotid processes); 1, with large, prominent hypapophyses.
144. Vertebrae, dorsal, parapophyses of posterior dorsals: 0, flush with neural arch; 1, distinctly projected on pedicels.
145. Vertebrae, dorsal, transverse processes of anterior dorsals: 0, long and thin; 1, short, wide, and only slightly inclined.
146. Vertebrae, dorsal, zygapophyses: 0, abutting above neural canal, opposite hyposphenes meet via lamina; 1, lateral to neural canal, separated by groove for interspinous ligaments, hyposphenes separate.
147. Vertebrae, sacral, number of sacrals: 0, 5 or less; 1, 6; 2, 7; 3, 8; 4, 9.
148. Vertebrae, sacral, pleurocoels: 0, absent on sacral vertebrae; 1, present on some sacrals; 2, present on all sacrals.
149. Vertebrae, sacral: 0, with unfused zygapophyses; 1, with fused zygapophyses forming a sinuous ridge in dorsal view.
150. Vertebrae, sacral; 0, ventral surface of posterior centra gently rounded, convex; 1, ventrally flattened, sometimes with shallow sulcus; 2, centrum strongly constricted transversely, ventral surface keeled.
151. Vertebrae, caudal: 0, more than 40; 1, 25-40; 2, no more than 25; 3, very short tail.
152. Vertebrae, caudal pygostyle: 0, not present; 1, two or more terminal caudals coossified.
153. Vertebrae, caudal neural spines: 0, simple, undivided; 1, separated into anterior and posterior alae throughout much of caudal sequence.
154. Vertebrae, caudal: 0, caudal transition point distal to 10th caudal; 1, between the 7th and 10th vertebrae; 2, proximal to the 7th.
155. Vertebrae, caudal, anterior centra: 0, tall, oval in cross section; 1, box-like in caudals I-V; 2, centra laterally compressed with ventral keel.
156. Vertebrae, caudal, neural spines on distal caudals: 0, form a low ridge; 1, spine absent; 2, midline sulcus in center of neural arch.
157. Vertebrae, caudal, prezygapophyses of distal caudals: 0, 30-100% centrum length; 1, long extensions of prezygapophyses (up to 10 vertebral segments long); 2, strongly reduced as in Archaeopteryx.
158. Vertebrae, caudal, midcaudal prezygapophyses: 0, extend less than one half centrum length; 1, extend more than one half but less than one centrum length (Kobayashi and Barsbold, 2005).
159. Haemal arches, anterior chevrons: 0, proximal ends short anteroposteriorly, shaft cylindrical or narrow blade; 1, proximal end elongate anteroposteriorly, flattened and plate-like.
160. Haemal arches, distal caudal chevrons: 0, anteriorly bifurcate; 1, bifurcate at both ends.
161. Ribs, shafts of mid-cervical ribs: 0, slender and longer than vertebrae to which they articulate; 1, broad and shorter than vertebrae.
162. Ribs, ossified ventral (sternal) rib segments: 0, absent; 1, present.
163. Ribs, ossified uncinate processes: 0, absent; 1, present
164. Gastralia: 0, lateral gastral segment shorter than medial one in each arch; 1, distal segment longer than proximal segment.
166. Sternum: 0, without distinct lateral xiphioid process posterior to costal margin; 1, with lateral xiphioid process.
167. Sternum: 0, anterior edge grooved for reception of coracoids; 1, sternum without grooves.

168. Sternum, articular facet for coracoid (conditions may be determined by the articular facet on coracoid in taxa without ossified sternum): 0, anterolateral or more lateral than anterior; 1, almost anterior

169. Scapula and coracoid, glenoid fossa: 0, faces posteriorly or posterolaterally; 1, laterally.

170. Scapula and coracoid: 0, form a continuous arc in anterior and posterior views; 1, coracoid inflected medially, scapulocoracoid 'L' shaped in lateral view.

171. Scapula, acromion process of scapula: 0, large and projects perpendicular to scapular shaft; 1, deep and broadly rounded; 2, pointed and extends in continuation of anterior edge of scapular blade.

172. Scapula, acromion process: 0, long, either tapering or horizontal triangle; 1, truncated, with deep base but short reach beyond scapular blade and squared-off profile. State 1 occurs in ornithomimids.

173. Scapula, acromion margin: 0, continuous with blade in anterior aspect; 1, anterior edge laterally everted relative to plane of scapular blade.


175. Scapula, flange on supraglenoid buttress: 0, absent; 1, present.

176. Scapula, depression on dorsal surface of supraglenoid buttress of scapula: 0, weak/absent; 1, present.

177. Coracoid, infraglenoid buttress: 0, alligned with posterior process; 1, offset laterally from line of posterior process (Kubayashi and Lü, 2003).

178. Coracoid in lateral view: 0, subcircular, with shallow ventral blade; 1, subquadrangular with extensive ventral blade; 2, shallow ventral blade with elongate posteroventral process; 3, 'strut'-like.

179. Coracoid, posterior edge: 0, not or only shallowly indented below glenoid; 1, posterior edge of coracoid deeply notched just ventral to glenoid, glenoid lip everted.

180. Coracoid, posterior process: 0, short; 1, long (Pérez-Moreno et al., 1994).

181. Coracoid, biceps tubercle: 0, positioned close to base of posterior process; 1, positioned more anteriorly (Kobayashi and Lü, 2003).

182. Coracoid, posterolateral surface ventral to glenoid fossa: 0, unexpanded; 1, edge expanded above triangular subglenoid fossa bounded laterally by enlarged coracoid tuber.

183. Coracoid, dorsal surface (= posterior surface of basal maniraptoran theropods): 0, strongly concave; 1, flat to convex (Turner, 2012, character 342).

184. Coracoid, medial surface, area of the foramen n. supracoracoideus (when developed): 0, strongly depressed; 1, flat to convex. (Turner, 2012, character 350).

185. Humerus, proximal end, head in anterior or posterior view: 0, strap-like, articular surface flat, no proximal midline convexity; 1, head domed proximally (Turner, 2012, Character 357)).

186. Humerus, ratio of width of proximal end to total length: 0, greater than 0.2; 1, less than 0.2 (Kobayashi and Lü, 2003).

187. Humerus, internal tuberosity: 0, pointed; 1, expanded along humeral shaft with straight medial edge
188. Humerus, deltopectoral crest, anterior view: 0, large with quadrangular proximal end; 1, less pronounced, forming an arc; 2, weakly developed with rounded edges; 3, long, rectangular 4, proximal end of humerus broad, triangular.
189. Humerus, deltopectoral crest, anterior surface: 0, smooth; 1, with distinct muscle scar near lateral edge along distal end of crest for insertion of biceps muscle.
190. Humerus, radial condyle: 0, larger than ulnar condyle; 1, approximately equal; 2, smaller.
191. Humerus, entepicondyle: 0, weak; 1, strong.
192. Radius and ulna: 0, well separated; 1, with distinct adherence or syndesmosis distally.
193. Radius/Humerus ratio: 0, more than 0.5; 1, less than 0.5 (Turner, 2012, Character 268).
194. Ulna, distal articular surface: 0, flat; 1, convex, spherical surface.
195. Carpus, lateral proximal carpal (ulnare?): 0, quadrangular; 1, triangular in proximal view.
196. Carpus: 0, two recognizable distal carpals in contact with metacarpals I, II; 1, single principal distal carpal capping mc I and II or mc II and III.
197. Carpus: 0, principal distal carpal semilunate in lateral view with trochlear proximal surface; 1, discoid, with flat proximal surface.
198. Carpus, distal carpal: 0, large, covering proximal ends of metacarpals I and II; 1, small, covers base of metacarpal I and about half of II; 3, shifted to cover metacarpals II and III.
199. Metacarpal I: 0, less than 55% the length of metacarpal II; 1, 60-94%; 2, 95% or more (modified for ornithomimids).
201. Metacarpal I, distal end: 0, ginglymoid articulation with distinct condyles; 1, relatively large convex phalangeal articulation with reduced condyles (Pérez-Moreno and Sanz, 1995, pp. 115-117).
202. Metacarpal I and phalanx I-1 joint: 0, ginglymoid; 1, ginglymous articulation reduced on phalanx I-1; 2, proximal articulation of I-1 is spherical, smooth.
203. Metacarpal I and II: 0, ginglymoid; 1, rounded; II ginglymoid and mc I shelf (Turner, 2012, character 213).
204. Metacarpal II: 0, shorter than metacarpal III; 1, longer than metacarpal III.
205. Manus, phalanx I-1: 0, shorter than metacarpal II; 1, longer than metacarpal II.
206. Manus: 0, tetradactyl; 1, tridactyl, or with less digits.
207. Manus, phalanx I-1 shaft diameter compared with shaft diameter of radius: 0, less; 1, greater.
208. Manus, third digit: 0, phalanges present; 1, reduced to no more than metacarpal splint.
209. Manus, third digit, (III3/III1+III2): 0, less than 1.0; 1, more than 1.0; 2, third finger lost (Perez-Moreno et al., 1994).
210. Manus, unguals: 0, strongly curved, with large flexor tubercles; 1, weakly curved with weak flexor tubercles displaced distally from articular end; 2, straight with weak flexor tubercles displaced distally from articular end.
211. Manus, unguals with proximodorsal 'lip' (some, not all) - a transverse ridge immediately dorsal to the articulating surface: 0, absent; 1, present.
212. Iliac blades: 0, roughly vertical; 1, inclined dorsomedially, dorsal edges approach or meet each other above sacrum.
213. Ilium, tuberosity along dorsal edge, dorsal or slightly posterior to acetabulum; 0, absent; 1, present.
214. Ilium, vertical midline ridge on lateral face above acetabulum: 0, absent; 1, present.
215. Ilium, pubic and ischiadic peduncles: 0, of comparable anteroposterior lengths at ventral ends; 1, pubic peduncle expanded, at least twice as wide as ischiadic peduncle.
216. Ilium, supraacetabular crest: 0, as a separate process from antitrochanter, forms hood over femoral head; 1, reduced, not forming hood; 2, absent.
217. Ilium, supraacetabular shelf: 0, extends along most or all of the edge of the pubic peduncle; 1, distinctly offset from acetabular edge of pubic peduncle.
218. Ilium, antitrochanter posterior to acetabulum: 0, absent or poorly developed; 1, prominent.
219. Ilium, pubic peduncle articular facet: 0, flexed with two facets set at obtuse angle to each other; 1, convex; 2, flat or concave.
220. Ilium, pubic peduncle of ilium: 0, uniform in anteroposterior length (i.e. unexpanded) in lateral view; 1, broadly flared toward pubic articular surface.
221. Ilium, preacetabular ala, anterior end: 0, gently rounded or straight: 1, strongly convex, lobate; 2, pointed at anterodorsal corner with concave anteroventral edge; 3, distinctly concave dorsally.
222. Ilium, preacetabular ala, anterior end: 0, straight or concave; 1, with notch at anterodorsal corner.
223. Ilium, preacetabular ala, ventral edge: 0, straight or gently curved; 1, with shallow, obtuse process; 2, process strongly hooked. Ordered.
224. Ilium, preacetabular ala, brevis fossa: 0, shelf-like; 1, deeply concave with lateral overhang.
225. Ilium, preacetabular ala, brevis fossa: 0, shallow with no lateral overhang, medial edge visible in lateral view; 1, well developed full length of postacetabular blade, lateral overhang along full length covers medial edge in lateral view.
226. Ilium, postacetabular ala, lateral view: 0, 'square'; 1, acuminate.
227. Ilium, postacetabular ala, cuppedicus fossa: 0, deep, ventrally concave; 1, fossa shallow or flat, with little or no lateral overhang; 2, absent. See (Hutchinson, 2001) for explanation of related changes in pelvic musculature.
228. Pubis, obturator foramen: 0, present; 1, open to become a notch between pubic shaft and ischiadic peduncle; 2, neither notch nor foramen present.
229. Pubis orientation: 0, propubic; 1, vertical; 2, opisthopubic (posteroventral).
230. Pubis, shaft: 0, straight; 1, distal end curves anteriorly, anterior surface of shaft concave; 2, shaft curves posteriorly, anteriorly convex curvature.
231. Pubis, apron (shelf on pubic shaft proximal to symphysis): 0, extends medially from middle of cylindrical shaft; 1, shelf extends medially from anterior edge of anteroposteriorly flattened shaft.
232. Pubis, apron: 0, about half of pubic shaft length; 1, less than 1/3 of shaft length.
233. Pubic boot: 0, projects anteriorly and posteriorly; 1, has little or no anterior process; 2, no anteroposterior projections.
234. Pubis, tip of anterior extension of pubic boot: 0, at the level of anterior border of pubic shaft; 1, more extended anteriorly.
235. Pubis, acute angle between pubic shaft and boot: 0, small; 1, large.
236. Pubis, ventral border of pubic boot: 0, nearly straight or slightly convex; 1, strongly convex with ventral expansion.

237. Ischium to pubis length ratio: 0, more than two-thirds; 1, two-thirds or less of pubis length.

238. Ischium, acetabular rim: 0, convex or beveled; 1, with longitudinal sulcus or depression.

239. Ischium: 0, slightly concave or flat proximal articular surface that contacts ilium; 1, deep socket for reception of peg-like ischial peduncle of ilium.

240. Ischium, scar on posterior edge of the proximal end of the ischium 0, absent; 1, present.

241. Ischium, obturator process: 0, does not contact pubis; 1, contacts pubis.

242. Ischium, obturator foramen: 0, present; 1, reduced to notch; 2, notch or foramen absent, U shaped gap between pubic peduncle and obturator process.

243. Ischium, obturator process: 0, absent; 1, proximal in position; 2, near middle of ischiadic shaft; 3, at distal end of ischium.

244. Ischium, obturator process: 0, square (with distinct posterior edge or notch); 1, triangular with posterior end confluent with shaft.

245. Ischium: 0, rod-like shaft distal to acetabulum; 1, wide, flat, and plate-like shaft.

246. Ischium shaft: 0, roughly straight or only gently arced; 1, curves ventrodistally anteriorly; 2, hooked posteriorly with deeply concave caudal margin.

247. Ischium, lateral face of blade: 0, flat, round in rod-like ischia; 1, laterally concave; 2, with longitudinal ridge subdividing lateral surface into anterior (including obturator process) and posterior parts.

248. Ischium, posterior edge: 0, straight; 1, with proximal median posterior process.

249. Ischium, distal ends 0, form symphysis; 1, approach one another but do not form symphysis; 2, widely separated.

250. Femur/Humerus ratio: 0, more than 2.5; 1, between 1.2 and 2.2; 2, less than 1 (Turner, 2012, character 266).

251. Femur, patellar groove: 0, absent; 1, present (Turner, 2012, character 415).

252. Femur head: 0, fovea capitalis for attachment of capital ligament; 1, circular fovea present in center of medial surface; 2, vertical ridges on anterior and posterior edges of medial surface of head.

253. Femur, lesser trochanter: 0, separated from greater trochanter by deep cleft; 1, trochanters separated by small groove; 2, completely fused (or absent) to form a trochanteric crest.

254. Femur, lesser trochanter height: 0, below height of greater trochanter; 1, level with or dorsal to top of greater trochanter.

255. Femur, lesser trochanter, vertical ridge on lateral face: 0, present; 1, absent.

256. Femur, fourth trochanter: 0, present; 1, absent.

257. Femur, anterior surface of distal end of shaft proximal to medial distal condyle: 0, without longitudinal crest; 1, crest extending from medial condyle.
262. Tibia, lateral fossa of proximal end (incisura tibialis): 0, deeply notched; 1, wide and shallow, nearly absent.
263. Tibia, medial cnemial crest: 0, absent; 1, present.
264. Fibula, medial surface of proximal end: 0, concave along long axis; 1, flat.
265. Fibula, deep oval fossa on medial surface of fibula near proximal end: 0, absent; 1, present.
266. Astragalus and calcaneum: 0, separate from tibia; 1, fused to each other and to the tibia in late ontogeny.
267. Astragalus and calcaneum, condyles on distal ends: 0, separated by shallow, indefinite sulcus; 1, distinct condyles separated by prominent tendinal groove on anterior surface.
268. Astragalus, ascending process: 0, tall, extending proximally for at least a quarter of tibia’s total length; 1, short, extending proximally for less than a quarter of tibia’s total length.
269. Astragalus, ascending process: 0, broad, covering anterior surface of distal tibia; 1, covering only lateral portion of anterior surface of distal tibia.
270. Astragalus, ascending process: 0, confluent with condylar portion; 1, separated by transverse groove or fossa across base.
271. Distal tarsals: 0, separate, not fused to metatarsals; 1, form metatarsal cap with intercondylar prominence that fuses to metatarsus early in postnatal ontogeny.
272. Metatarsus, shafts of major metatarsals: 0, not appressed against each other beyond proximal half; 1, appressed throughout most or all of metatarsus, adjacent surfaces of shafts flattened for contacts.
273. Metatarsus: 0, shaft of mt III with straight medial border in extensor view; 1, with medial expansion forming convexity or bulge along distal part of shaft.
274. Metatarsus, distal end of metatarsal III: 0, smooth, not ginglymoid; 1, with developed ginglymus.
275. Metatarsus, metatarsal I: 0, present; 1, absent (Turner, 2012, character 447).
276. Metatarsus, mt I attachment on mt II: 0, middle of medial surface; 1, posterior surface of distal quarter; 2, medial surface near proximal end; 3, mt I absent.
277. Mt II, distal extent relative to MT IV: 0, approximately equal; 1, shorter than mt IV, but reaching distally further than base of metatarsal IV trochlea; 2, shorter than mt IV, extending to base of mt IV trochlea. (Turner, 2012, #438).
278. Metatarsus, mt III: 0, exposed between mt II and mt IV along entire height; 1, proximal shaft constricted and narrower than mt II or mt IV, exposed along entire height, subarctometatarsal; 2, pinched, arctometatarsal; 3, prox part of mt III lost.
279. Metatarsus, mt III: 0, straight medial border in dorsal view; 1, with a medial expansion forming a convexity or bulge along distal part of the shaft.
280. Metatarsus, mt IV, large, longitudinal flange along posterior or lateral face: 0, absent; 1, present.
281. Metatarsus, mt IV shaft: 0, round or thicker dorsoventrally than wide in cross section; 1, mediolaterally wide and flat in cross section.
282. First pedal digit: 0, present; 1, absent.
283. Length of pedal phalanx II-2: 0, more than 60% of pedal phalanx II-1; 1, less.
284. Pedal ungual and penultimate phalanx of pedal digit II: 0, similar to those of III; 1, penultimate phalanx highly modified for hyper-extension, ungual more strongly curved and significantly larger than that of digit III.
285. Pedal unguals: 0, curved in lateral view, pointed; 1, straight with flat or concave bottoms but pointed tips; 2, flat or concave ventrally, broad and blunt tips.
APPENDIX 2 – Character matrix used in the analysis and the coded character states. Dashes represent missing data, polymorphisms are indicated by A, (0,1) and B, (1,2)

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