A Problematic Tyrannosaurid (Dinosauria: Theropoda) Skeleton and its Implications for Tyrannosaurid Diversity in the Horseshoe Canyon Formation (Upper Cretaceous) of Alberta

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ABSTRACT

Several published censuses have noted the presence of two tyrannosaurids, Daspletosaurus sp. and Albertosaurus sarcophagus, within the Upper Cretaceous Horseshoe Canyon Formation of Alberta. Although A. sarcophagus is known from more than a dozen major discoveries in these strata, Daspletosaurus sp. is known from just a single problematic skeleton (lacking most of the skull) of a young individual. Here we describe and figure this skeleton, and marshal a variety of osteohistologic, morphometric, and phylogenetic methods to accurately determine its taxonomic status. Although none of these methods individually provides convincing evidence regarding the affinities of the specimen, together (and including other historical and biostratigraphic considerations) they strongly imply that the skeleton instead pertains to a young A. sarcophagus. In this way, we show that only a single species of tyrannosaurid is definitively present in the Horseshoe Canyon Formation, greatly simplifying interpretations of tyrannosaurid evolution and ecology in this setting. Anat Rec, 303:673–690, 2020. © 2019 The Authors. The Anatomical Record published by Wiley Periodicals, Inc. on behalf of American Association of Anatomists.

Key words: Tyrannosauridae; osteohistology; taxonomy; Horseshoe Canyon Formation; morphometrics

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Abbreviations: CMN = Canadian Museum of Nature, Ottawa, Ontario; ROM = Royal Ontario Museum, Toronto, Ontario; TMP = Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta

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In 1926, Charles M. Sternberg discovered the partial skeleton of an immature tyrannosaurid (CMN 11315; Fig. 1) within a sandstone on the south bank of the Red Deer River, Alberta, upstream of the Tolman Bridge (SW 1/8, Section 20, Township 34, Range 21, west of the 4th meridian). These coordinates place the specimen within the lower Maastrichtian Tolman Member of the Horseshoe Canyon Formation (Eberth et al., 2013). Sternberg initially attributed the specimen to *Albertosaurus sarcophagus* (1926 field notes, CMN archives), likely based on the fact that no other tyrannosaurids had yet been described from those strata. However, Russell (1970) later reassigned CMN 11315 to *Daspletosaurus cf. D. torosus*, based on the proportions of the forelimb, ilium, femur, and on the curvature of the claw of the first manual digit. The holotype of *D. torosus* otherwise comes from the middle Campanian Oldman Formation of Alberta.

The classification of CMN 11315 as *D. torosus* has become widely cited in the literature (Makovicky and Currie, 1998; Currie, 2003a; Claessens, 2004; Nesbitt et al., 2009), although others (Madsen Jr, 1974; Holtz Jr, 2000; Currie, 2003b; Eberth et al., 2013; Persons IV and Currie, 2016) have accepted Sternberg’s original assessment of the specimen as *A. sarcophagus*. The reasons for this disagreement are unclear, but in all likelihood reflect the fact that diagnostic skeletal characters are often not expressed in immature individuals (Hone et al., 2016). Importantly, several censuses (Russell, 1984; Carpenter, 1992; Ryan and Russell, 2001; Weishampel et al., 2004a; Weishampel et al., 2004b; Brown et al., 2015) have listed both *A. sarcophagus* and *Daspletosaurus sp.* as present in the Horseshoe Canyon Formation, presumably on the basis of Russell’s (1970) initial assessment, which is the only published instance citing evidence for *Daspletosaurus* in the formation.

The ramifications concerning the identity of CMN 11315 are not insignificant. First, if the specimen truly is *Daspletosaurus sp.*, it would provide evidence for the presence of two co-occurring large apex-predators within the Horseshoe Canyon Formation, which introduces a presence of two co-occurring large apex-predators within the Horseshoe Canyon Formation (Eberth et al., 2013). Importantly, several treatments of postcrania can be found in Lambe (1917), Parks (1928), Brochu (2003), and Brusatte et al. (2012). The forelimb is described here in greater detail, given that it is often missing in tyrannosaurid specimens, and in light of the interest it has garnered concerning its potential uses (or lack thereof) (Vance, 1989; Carpenter and Smith, 2001; Carpenter, 2002; Lipkin and Carpenter, 2008). Anatomical reference planes for individual elements follow Brochu (2003). General measurements of the various skeletal elements are given in Table 1.

**Skull**

The skull is incomplete, being represented by just the few bones described below. Evidently, it had mostly eroded away before it could be collected.

The triradiate quadratejugal (Fig. 2A–C) is like that of Albertosaurus and other tyrannosaurines, in several ways (Currie, 2003b; Carr et al., 2017). First, the wing-like dorsal process is greatly expanded, creating an elongate dorsal contact for the squamosal. Second, the thickened ridge that runs along the rostral surface of the dorsal process attenuates dorsally, and does not meet the squamosal contact. Third, the dorsal contact surface for the jugal along the rostral process of the quadratejugal does not approach the posteroventral corner of the infratemporal fenestra. This process appears to taper rostrally, again as in albertosaurines, but the bone is obviously damaged in this region. There is a small (~4 mm) foramen that perforates the center of the fossa on the dorsal process. This foramen has not been described elsewhere in a tyrannosaurid, but it is variably present in *Albertosaurus sarcophagus* (present: TMP 1981.010.0001, TMP 1985.085.0001; absent: TMP 1988.063.0084). The foramen is distinct from the quadratejugal pneumatopore seen in *Daspletosaurus horneri* and *Nanotyrannus lancensis*, which occurs lower on the lateral surface of the dorsal process, beyond the bounds of the fossa (Larson, 2013; Carr et al., 2017).

The quadrate (Fig. 2C–F) is of typical tyrannosaurid construction, being vaguely P-shaped in outline, and sporting a large fenestra laterally. The fenestra is displaced from the jaw joint by more than two times the height of the quadrate condyles, a condition common in...
TABLE 1. Measurements for CMN 11315

| Measure                      | Value (mm) |
|------------------------------|------------|
| Left quadrat height          | 164        |
| Left quadrat jugal foramen height | 37.2  |
| Left dentary maximum height  | 65         |
| Left scapula-coracoid length | 580        |
| Left scapular blade length   | 470        |
| Left scapula shaft width     | 32.7       |
| Left scapula distal width    | 85         |
| Left coracoid height         | 116.5      |
| Furcula width                | 180        |
| Left humerus length          | 222        |
| Left humerus proximal width  | 47.4       |
| Left humerus transverse shaft width | 25.3  |
| Left humerus distal width    | 38.3       |
| Left radius length           | 96.2       |
| Left radius proximal width   | 18.6       |
| Left radius transverse shaft width | 13.1  |
| Left radius distal width     | 19.3       |
| Left ulna length (including olecranon) | 119.5 |
| Left ulna proximal width     | 30.4       |
| Left ulna anteroposterior shaft width | 13.6   |
| Left ulna distal width       | 21         |
| Left metacarpal I length     | 35.7       |
| Left metacarpal II length    | 61.5       |
| Left metacarpal III length   | 40         |
| Left manual phalanx I-1 length | 58     |
| Left manual phalanx I-2 length (straight) | 54.5  |
| Left manual phalanx I-2 length (outside curve) | 57   |
| Left manual phalanx II-1 length | 29     |
| Left manual phalanx II-2 length | 40     |
| Left manual phalanx II-3 length (straight) | 54     |
| Left manual phalanx II-3 length (outside curve) | 58  |
| Left ilium length            | 675        |
| Left ilium height over pubic peduncle | 325  |
| Pubis length                 | 560*       |
| Pubis boot length            | 360        |
| Left ischium length          | 495        |
| Femur length                 | 680a       |
| Femur proximal width         | 120a       |
| Femur shaft width (anteroposterior) | 66a   |
| Femur shaft width (transverse) | 112a  |
| Femur minimum shaft circumference | 314a |
| Femur distal width           | 124a       |
| Tibia length                 | 690a       |
| Right tibia-astragalus length | 720      |
| Tibia proximal width         | 150a       |
| Tibia transverse shaft width | 62a        |
| Tibia distal width           | 155a       |
| Fibula length                | 630a       |
| Fibula proximal width        | 130a       |
| Fibula shaft width           | 27a        |
| Fibula distal width          | 39a        |
| Astragalus width             | 190a       |
| Calcaneum width              | 137a       |
| Calcaneum maximum height     | 61a        |
| Metatarsal I length          | 14a        |
| Metatarsal II length         | 73.5a      |
| Metatarsal III length        | 410a       |
| Metatarsal III length        | 445a       |
| Metatarsal IV length         | 422a       |
| Metatarsal V length          | 165.3      |
| Phalanx I-1 length           | 71         |
| Phalanx II-1 length          | 118        |
| Phalanx II-2 length          | 80.6       |
| Phalanx II-3 length (straight) | 96     |

TABLE 1. Continued

| Measure                      | Value (mm) |
|------------------------------|------------|
| Phalanx II-3 length (outside curve) | 110  |
| Phalanx III-1 length         | 128        |
| Phalanx III-2 length         | 81.5       |
| Phalanx III-3 length         | 63         |
| Phalanx III-4 length (straight) | 79    |
| Phalanx III-4 length (outside curve) | 89    |
| Phalanx IV-1 length          | 78         |
| Phalanx IV-2 length          | 61         |
| Phalanx IV-3 length          | 41         |
| Phalanx IV-4 length          | 28         |
| Phalanx IV-5 length (straight) | 66     |
| Phalanx IV-5 length (outside curve) | 73    |

Asterisk (*) indicates estimated value. Letter ‘a’ indicates averaged length (between right and left sides).

...early tyrannosauroids and some tyrannosaurids (e.g., D. horneri and Teratophoneus curriei) (Loewen et al., 2013). The pterygoid ala is posteromedially excavated by a deep fossa, a condition common with A. sarcophagus and Bistahieversor sealeyi (Loewen et al., 2013).

The rostral portion of the dentary is preserved (Fig. 3), as well as pieces of the more caudal region; however, the latter are too fragmentary to be of diagnostic value. The rostral margin of the dentary is straight and faces anteroventrally at an angle of approximately 45 degrees relative to the horizontal dorsal margin, and in this way is reminiscent of A. sarcophagus and Tyrannosaurus rex; the rostral margin is rounded in D. torosus. However, CMN 11315 is unlike A. sarcophagus and T. rex in that the transition between the rostral and ventral margins of the dentary occurs below the first and second alveolus, as it does in D. torosus (Carr and Williamson, 2010). The confluence of the rostral and ventral margins of the dentary is marked by a weakly developed “chin” that is seen in most other tyrannosaurids (Brusatte et al., 2010). The chin is absent in the juvenile “Raptorex kriegsteini” (=Tarbosaurus bataar). Medially, the surface of the dentary symphysis is smooth as in albertosauroids and some more primitive tyrannosaurids; it is not as rugose as in tyrannosaurines (Brusatte et al., 2010).

**Gastralia**

A portion of the gastral cuirass is preserved, consisting of 12 free ribs from the left side and nine from the right (Fig. 4). In life, the count would likely have been closer to 19 per side, as reported in Gorgosaurus libratus (Lambe, 1917). Each rib consists of a medial and lateral portion. The medial portions are elongate with spatulate heads that overlap or rest at the midline. The ventral surface of each head bears a large, rugose attachment site for the adjoining rib head, which itself bears a smaller corresponding attachment site on the ventral surface. Each medial element quickly narrows laterally to form the rib shaft, which curves caudolaterally and slightly dorsally along its length. Approximately mid-way along the length of the rib shaft, an elongate facet occurs laterally for the attachment of the lateral gastralia. These elements are largely missing, although a few preserved examples show them to be little more than slender bony rods. Moving caudally along the series, the gastralia
decrease in size, with narrower heads and a more pronounced caudal curvature. The caudalmost gastralia are indistinguishably fused about the midline, forming an inverse U-shape. The individual gastralia are considerably less robust than reported in *Ty. rex* (Brochu, 2003) or *Ta. bataar* (Maleev, 1974).

**Pectoral Girdle**

The scapula (Fig. 5) is tightly appressed to the coracoid; the contact is open ventrally, but closed (with a visible suture) dorsally. The area of the acromion process of the scapula is badly damaged due to crushing, but field photos showing the outline of the comparatively intact element prior to removal (Fig. 5(E)) indicate that the process was not particularly well developed, being less than three times the minimum dorsoventral depth of the blade. The scapula is broken in two at midlength, but can be rejoined along a thin splint of bone ventrally; a large portion of the dorsal surface of the scapular blade is missing. The slender scapular blade is concave ventrally as in albertosaurines; the blade is approximately straight in *D. torosus* and *Ty. rex* (Russell, 1970; Brochu, 2003). The caudal end of the scapula is modestly expanded and broadly rounded, but it is doubtful whether this character is of taxonomic significance; in *G. libratus*, the caudal end of the scapula may be either slightly expanded and rounded (as in CMN 11315), or more widely expanded and squared off (Lambe, 1917; Matthew and Brown, 1923). In *D. torosus*, the caudal end of the scapula is slightly expanded and squared off (Russell, 1970), and in the only described postcranium of *A. sarcophagus*, it is broadly expanded and rounded (Parks, 1928). Variation in the caudal shape the scapula probably reflects variation in ossification of the scapular cartilage (Romer, 1956).

The quadrangular coracoid (Fig. 4) is weakly hooked at its anteroventral corner and broadly rounded, but, again, this character appears to be intraspecifically variable in *G. libratus* (Parks, 1928). The oval coracoid foramen, visible adjacent to the scapular contact medially, is obscured by local crushing of the lateral surface. The coracoid only contributes to approximately a quarter of the surface area of the humeral glenoid, which is reniform and faces ventrolaterally.
The furcula (Fig. 5D,E) was described in some detail by Makovicky and Currie (1998). It measures 163 mm transversely, with an interclavicular angle of 115 degrees. Compared with that of adult tyrannosaurids (e.g., *G. libratus*, TMP 1994.012.0602; *D. torosus*, CMN 8506), the furcula is slenderer with more poorly developed epicleideal facets.

**Forelimb**

The left humerus (Fig. 6) has suffered some crushing in the craniocaudal plane. It is 33% the length of the femur, which is comparable to relative lengths reported in *A. sarcophagus* and *D. torosus*, but shorter than those reported in *T. bataar* or *Ty. rex* (Sereno et al., 2009). The humeral head is low and poorly differentiated from the remainder of the humerus, which is typical of early tyrannosaurids; however, the head overhangs (albeit weakly) both the cranial and caudal surfaces, as in tyrannosaurids (Sereno et al., 2009). The deltopectoral crest, partially reconstructed with plaster, is not as pronounced as in mature *A. sarcophagus* (e.g., ROM 807). The apex of the crest is located approximately 39% along the length of the humerus from the proximal end. In most tyrannosaurids, this value is typically on the order of less than 25% (Sereno et al., 2009). There are no additional muscle tubera distal to the deltopectoral crest, which are clearly visible in *Ty. rex* (Brochu, 2003). In *A. sarcophagus* and “*R. kriegsteini,*” the medial condyle of the distal end of the humerus reportedly expands farther than the lateral one (Brusatte et al., 2010), which does not appear to be the case in CMN 11315, in which the condyles are equidimensional. There are two small (~9 mm) bones at the distal end of the humerus, apressed to each condyle. That adjacent to the lateral condyle is roughly spherical, and the other, adjacent to the medial condyle, is rather amorphous, partially obscured by plaster. The latter may simply be a loose fragment of the damaged medial condyle. The spherical bone near the lateral condyle is not obviously from another part of the skeleton, and is plausibly interpreted as a sesamoid bone (Gudmundsen and Østensen, 1987).

The relatively straight ulna (Fig. 7A,B) is 52% the length of the humerus. Even taking into account crushing of the medial surface of the element, the ulna is quite slender compared to that of mature *A. sarcophagus* (Parks, 1928) and particularly *Ty. rex* (Brochu, 2003). The olecranon process is modest in size. There are no obvious tuberousities on the shaft of the element, as reported in *Ty. rex* (Brochu, 2003).

The rod-like radius (Fig. 7C,D) is rather featureless, owing in part to mediolateral crushing of the main shaft. The proximal articulation for the humerus is D-shaped, with a flattened lateral contact for the ulna. The radius narrows slightly at midlength before expanding again distally. In *Ty. rex*, the shaft is typically twisted about its long axis so that the distal end is oriented transversely (Carpenter and Smith, 2001); however, this does not appear to be the
case in CMN 11315 or larger A. sarcophagus (ROM 807), in which the shaft is relatively straight along its length.

Three, possibly four, carpals are preserved. Their precise homologies are difficult to establish, given the varied interpretations that have been given from both neontological and palaeontological perspectives (Botelho et al., 2014; Xu et al., 2014). One carpal (Fig. 7C,D), shaped like a right triangle in distal outline, is associated with the distal end of the radius. It measures 11 mm wide \( \times \) 9 mm long \( \times \) 4 mm thick. It is interpreted as a scapholunare, a product of the fusion of the radiale and intermedium (Botelho et al., 2014). The largest carpal (Fig. 8A–C) straddles the proximal ends of metacarpals I and II, but does not completely overlap either. It is 14 mm wide \( \times \) 12 mm long \( \times \) 7 mm thick. The proximal surface, which has suffered some crushing, appears to bear a shallow, transversely oriented trochlea. This element has been interpreted as a “semilunate” carpal (Holtz Jr, 2000; Holtz Jr, 2004), and has also been reported in the basal tyrannosauroid Guanlong wucaii (Xu et al., 2006)—an identification with which we concur.

However, in this case, the “semilunate” carpal appears to consist only of distal carpal 1, and is not a fusion of distal carpals 1 and 2 as reported elsewhere (Botelho et al., 2014). Rather, the smaller (9 mm wide \( \times \) 5 mm long \( \times \) 4 mm thick) distal carpal 2 (Fig. 8A,B) clearly lies immediately lateral to the “semilunate” carpal, centered proximal to metacarpal II. This arrangement goes to support the contention of Xu et al. (2014) that the “semilunate” carpal is not strictly homologous across all maniraptoriformes. The scapholunare and distal carpal 2 are markedly smaller than the semilunate carpal, whereas these elements are subequal in size in mature A. sarcophagus (ROM 807). There is possibly a fourth carpal (3–4 mm in all dimensions) apressed to the proximal end of metacarpal III, but this region is not particularly well preserved, so the perceived bone may be an artifact of crushing. If genuine, this element would likely represent distal carpal 3.

The metacarpals (Fig. 8B,C) are tightly apressed and preserved as a single block. The shaft of metacarpal I is wider than tall. The proximal articular surface is lunate, with a concave palmar surface. The distal condyles are greatly expanded dorsoventrally so that they are twice as
deep here as elsewhere along the shaft. The lateral condyle extends farther distally than the medial one, forming an asymmetrical trochlea. This configuration would have restricted the first digit to operating at an angle of 15 degrees from the second one. The medial surface of the medial condyle is incised by a shallow ligament pit that is dorsally offset. Metacarpal II is 1.7 times longer than the first, and is slightly wider in the proximal half. The proximal articular surface is also lunate. The distal articular surface is more symmetrical than in the first metacarpal, although the lateral condyle is nevertheless slightly larger than the medial one. The shallow ligament pits on either side of the distal trochlea are centrally located compared to those of metacarpal I. Metacarpal III is a thin splint of bone that is intermediate in length between metacarpals I and II. The proximal articulating surface is deeper dorsoventrally, rather than mediolaterally as in the other two metacarpals. Metacarpal III does not reach as far proximally as metacarpals I and II, which has been a matter of small contention in the tyrannosaurid literature (Brochu, 2003). The proximal end of metacarpal III expands ventrally into a pointed tubercle, and the element gradually tapers distally before terminating in advance of the distal trochlea of metacarpal II. There is no distal trochlea on metacarpal III.

The manus is functionally didactyl, as only the first two digits are preserved (phalangeal formula = 2-3-0-X-X) (Fig. 8B,C). Phalanx I-1 is the longest element in the manus, being very slightly longer than metacarpal II. The proximal articular surface is deeply concave, with a subtle, medially offset ridge extending dorsoventrally; this shape corresponds well to that of the articulating trochlea of the adjoining metacarpal. The prominent dorsal and ventral rims of the proximal articulating surface ensure a firm articulation with metacarpal I. The shaft of phalanx I-1 is slightly concave ventrally. The distal trochlea is rotated clockwise about the long axis of the element, offset from the proximal articulating surface by approximately 25 degrees. The lateral condyle is slightly larger than the medial one, and the articular surface of the trochlea extends well onto the ventral surface of the phalanx, evidently more so than in Ty. rex (Brochu, 2003). The deep ligament pits are positioned centrally on either side of the trochlea. Phalanx I-2 is developed into a mediolaterally narrow, decurved ungual (Fig. 8B–D). The proximal articulating surface is teardrop-shaped, and is overhung dorsally by a subtle bony lip. The flexor tubercle, located proximoventrally, is modestly developed, less exaggerated than in early tyrannosauroids. The flexor margin of the claw is weakly concave; the ratio of the maximum height of the flexor margin to claw length (measured from flexor tubercle to claw tip) is 0.12. Deep grooves incise each side of the ungual, the medial groove being slightly more ventrally positioned than the lateral groove.
The non-ungual phalanges of digit II resemble phalanx I-1 in gross morphology, although they are considerably smaller and more robust. The distal trochlea of phalanx II-1 does not extend far onto the ventral surface of the element, and ligament pits are missing entirely. Phalanx II-2 is slightly longer than its proximal homologue, and the distal end is missing. Phalanx II-3 is again developed into a claw (Fig. 8B,C,E), albeit more gracile and more pointed than that of digit I. The exor tubercle is slightly better defined than that of the ungual of digit I. The aforementioned measure of convexity is 0.21. The medial and lateral grooves are symmetrically positioned on the surface of the claw. Overall, the manual unguals are sub-equal in size, whereas in mature A. sarcophagus (e.g., ROM 807), the ungual of digit I is markedly larger than that of digit II.

Pelvic Girdle

The maximum length of the ilium (Fig. 9) is 98% the length of the femur. In most adult tyrannosaurs, this value is on the order of 105%–115% (Holtz Jr, 2001). There is a strong, anterodorsally extending ridge on the lateral surface of the iliac blade, dorsal to the acetabulum. This ridge is present in most tyrannosaurs except “R. kriegsteini” and Qianzhousaurus sinensis (Carr et al., 2017). The antitrochanter of the acetabular crest is very weakly developed, in contrast with those of early tyrannosaurs (Holtz Jr, 2001; Carr et al., 2017). The base of the pubic peduncle is much longer craniocaudally than the ischial peduncle, similar to the condition seen in the juvenile “R. kriegsteini” and early tyrannosaurs (Brusatte et al., 2010; Li et al., 2010). The ventral margin of the postacetabular process forms a subtle lobe, as in most tyrannosaurs except Alioramus remotus, G. libratus, Q. sinensis, and “R. kriegsteini” (Brusatte et al., 2010). The dorsal margin of the ilium is likewise convex cranially, and not flat along its entire margin as it is in “R. kriegsteini” and early tyrannosaurs (Brusatte et al., 2010).

The conjoined pubes (Fig. 10) are both broken at a third of their lengths and cannot be reassembled due to missing bone. There is evidently more bone missing from the left side. The pubic shaft is bowed caudally, unlike “R. kriegsteini” and early tyrannosaurs in which it bows cranially (Carr and Williamson, 2010; Carr et al., 2017). The pubic tubercle, present on the anterolateral face of the element, is low (15 mm) and projects laterally. It is not caudally bordered by heavy rugosities as it is in adult tyrannosaurs (Carr and Williamson, 2010).

The midshaft diameter of the ischium (Fig. 11) is less than half that of the pubis, as in adult tyrannosaurs, and in contrast with the condition of the juvenile “R. kriegsteini,” in which the midshaft diameter of both bones is more nearly equal (Sereno et al., 2009). The ischial shaft is straight, as in Alb. sarcophagus and Te. curriei (Loewen et al., 2013).

Hindlimb

The femora (Fig. 12) are mostly complete, although some parts are missing, particularly about the midshaft. Regardless, they appear to be accurately restored, and much of the missing or distorted morphology on one element is intact on its counterpart. The proximal face of the femur is straight and oriented at an obtuse angle to the long axis of the shaft (i.e., dorsally or proximally inclined head), which contrasts with the condition in D. torosus and Ty. rex, in which this surface is concave (Brusatte and Carr, 2016). The trochanteric fossa, located caudally between the femoral head and greater trochanter,
The pes (Figs. 15 and 16) differs from those of B. sealeyi and D. horneri in that the distal surface of metatarsal IV is approximately square in outline (it is craniocaudally elongate in the other two taxa) (Brusatte et al., 2010; Carr et al., 2017). Metatarsal IV also bears a proximodistally elongate, narrow muscle scar, located centrally along the shaft, and covering only a third of it (the scar is much wider and longer in D. torosus and Ty. rex) (Loewen et al., 2013). Also unlike these taxa, the proximal pedal phalanges are slender, having a length: width ratio greater than 3.0 (Brusatte et al., 2010).

OSTEOHISTOLOGICAL ANALYSIS

Methods

We attempted an osteohistological age assessment of CMN 11315 using a thin section from the distal third of the left fibula. This element was chosen because it was already broken and, because it is a non-weight-bearing bone, is arguably less likely to have remodeled the cortex with growth (Erickson et al., 2004; but see Chinsamy-Turan, 2005). Prior to cutting, we scanned the element in three-dimensions using a Go!Scan 20 handheld scanner and VXelements v. 6.1 software (Creaform, Lévis, Quebec). The 3D file and color 3D print are available at the CMN.

To produce the thin section, an ~5 mm-thick sample was cut using a Buehler Isomet 1000 Precision Saw. To remove saw marks and prepare it for mounting, the sample was lapped with a Hillquist 8 in lapidary using MetTech Silicon Carbide Grit in the sequence of 320 to 1,000. Once close to desired thickness, polishing continued with 320 grit. Once close to desired thickness, 400 grit silicon carbide was used. Constant checking of the thin section with the microscope allowed determination of the desired thickness of approximately 30–35 μm. After this thickness was reached, polishing continued with 1,000 grit silicon carbide on a glass plate. The final polishing was done with 0.05 μm colloidal silica to obtain a sample surface suitable for SEM work. As a final step, the thin section was placed in the ultrasonic bath for 10–15 sec to remove any grit, colloidal silica, and dust from the sample.
Large-area transmitted light microscopy image mosaics of the fibular section were acquired using a Zeiss AXIO Zoom.V16 light microscope. The mosaics were acquired with ZEN Pro software using the Plan Apo Z 1.0/0.25 objective (FWD 60 mm) at a resolution of 410 nm/pixel with plane-polarized and cross-polarized transmitted light. Each of the light microscopy image mosaic of the fibula thin section consists of 522 individual tiles.

A large-area SEM image mosaic of the fibular section was acquired with ZEISS Atlas 5 software using a ZEISS Gemini 450 FE-SEM at Fibics Incorporated (Ottawa, Canada). The large area light microscopy mosaics were imported into the respective Atlas 5 correlative workspace project, aligned with the sample in the SEM, and the large-area SEM image mosaic of the whole sample was imaged with an accelerating voltage of 20 kV simultaneously using the backscattered electron (BSE) detector, at a working distance of 9.917 mm, a 3.2 nA beam current, a 3 μsec dwell time, and a resolution of 65 nm/pixel. The resulting mosaics comprise 834 image tiles each, with each tile consisting of 10,240 × 10,240 pixels (666.7 × 666.7 μm), and a total pixel count of 87.5 gigapixels. Once the image mosaics were acquired, stitched, and corrected, the entire Atlas 5 data set was exported to an autonomous series of files called the

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Fig. 11. Left ischium of CMN 11315 in lateral (A), caudal (B), and medial (C) views. (D) Close-up of peduncles in dorsal view. Abbreviations: ilal, ilac ala; it, ischial tuberosity; obfl, obturator flange; obtp, obturator process; pp, pubic process.
Browser-Based Viewer (BBV), which allows anyone on a PC and a web browser to view the complete data set at full resolution in a similar manner to that of the Google Earth application. The computer mouse is used for zooming in and out as well as for navigating through the large area image mosaic.

The BBV data sets of the fibula thin section can be viewed at the following link: http://www.petapixelproject.com/mosaics/museumofnature/TSB/TyrannosaurShinBone/index.html.

**Results**

The transverse thin section of the fibula (Fig. 17) is approximately D-shaped, with the flat surface facing medially, toward the tibia. The bone is dense, composed entirely of cortical tissue (i.e., lacking both a medullary cavity and spongiosa). Vascularization is longitudinal and occurs throughout the bone, most clearly demonstrated in the BSE SEM imagery. The cortex is zonal, the deepest zone making up ~70% of the section and being tan colored under plain

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**Fig. 12.** Femora of CMN 11315. Right femur in caudal (A), lateral (B), cranial (C), medial (D), proximal (J), and distal (K) views. Left femur in caudal (E), lateral (F), cranial (G), and medial (H) views. (I) Close-up of shaft of left femur. Abbreviations: ctf, crista tibiofibularis; ct1, circular tuberosity on femur 1; icf, intercondylar fossa; tf, fibular trochlea; tc2, greater trochanter; tc1, lesser trochanter; t4, fourth trochanter.

**Fig. 13.** Shin and tarsal elements of CMN 11315. Right shin elements in medial (A), caudal (B), lateral (C), cranial (D), and proximal (J) views. Left tibia in medial (E), caudal (F), lateral (G), and cranial (H) views. (I) Tarsal elements in ventral view. Left fibula not shown because it was sectioned for osteohistological analysis. Abbreviations: ast, astragalus; calc, calcaneum; cnc, cnemial crest; f, fibula; fbc, fibular crest; t, tibia.

**Fig. 14.** Astragali of CMN 11315. Left astragalus in cranial (A) and caudal (B) views. (C) Right astragalus in cranial view. Abbreviations: ast, astragalus; calc, calcaneum; f, fibula.
polarized light. Here, the primary bone is fibrolamellar with abundant primary osteons; however, remodeling is pervasive with overlapping secondary osteons scattered throughout, particularly toward the medial side. External to this, the cortical tissue is stained brown, and the zonation is somewhat finer, with three distinguishable zones of varying thickness. All three are composed of fibrolamellar primary tissue. The layers are separated by one or possibly two annuli, but it is difficult to trace them circumferentially because remodeling has obliterated the primary tissue medially. There is no sign of an external fundamental system near the periosteal surface.

MORPHOMETRIC ANALYSIS

Methods

Russell (1970) attributed CMN 11315 to *Daspletosaurus* cf. *D. torosus* based on the long humerus, radius-ulna, ilium, and circumference of the femur relative to femur length, all of which he argued are shorter in *Albertosaurus sarcophagus*. He also argued that ungual I-1 of CMN 11315 is less recurved than in *A. sarcophagus*, and that the metatarsus is slightly shorter than expected for the genus. However, although Russell did provide raw measurements for some tyrannosaurids, he did not otherwise show his work. Using the more extensive data set of Currie (2003a), we investigated the scaling relationships between log-transformed femur length and minimum shaft circumference, humeral length, radio-ulnar length, ilium length, and metatarsal III length for both albertosaurines (including *A. sarcophagus*) and tyrannosaurines (including *D. torosus*). The allometric series were subjected to analysis of covariance to assess the significance of differences between groups. Where significance was achieved ($\alpha = 0.05$), we calculated the distance ($e_c$) of CMN 11315 to both the albertosaurine and tyrannosaurine regression lines to determine with which clade it is most closely associated. All regressions and statistical analyses were conducted in PAST 3.15 (Hammer et al., 2001).

Results

Albertosaurines and tyrannosaurines are statistically indistinguishable with respect to both humerus and radius length; however, the two clades differ in the lengths of the ulna, ilium, metatarsal III, and in the circumference of the femur (Table 2). Proportionally, the ulna and ilium of CMN 11315 are more similar to those of albertosaurines, yet the specimen more closely resembles tyrannosaurines with respect to the proportions of metatarsal III and femur circumference (Fig. 18; Table 3).

PHYLOGENETIC ANALYSIS

Methods

We further assessed the phylogenetic affinities of CMN 11315 by scoring the specimen for 105 of 386 (27.2%) characters in the tyrannosaurid character matrix of Carr et al. (2017) (Supplementary Data 1). We conducted a parsimony-based cladistic analysis using the "traditional search" function in TnT v. 1.1 (Goloboff et al., 2008). The number of trees held in memory was set to the maximum (99,999). We used Wagner trees as starting trees with a random seed of 0, and specified 10,000 replicates with 1,000 trees saved per replicate. Tree bisection reconnection was retained as the swapping algorithm. Character ordering and taxon exclusion followed the specifications given in Carr et al. (2017), with the exception of including "*Raptorex kriegsteini*" to assess its placement and inferred maturity relative to CMN 11315. We also performed a second phylogenetic analysis, discounting ontogenetically variable characters by excluding all 49 ordered characters (*sensu* Currie et al., 2016); other variables were maintained as before. Standard bootstrap values were calculated using 1,000 replicates, and reported as absolute frequencies. Bremer support was calculated using the Bremer.run script in TnT.

Results

The initial search returned 480 most parsimonious trees (MPTs) of 837 steps each (consistency index = 0.535, retention index = 0.804). The strict consensus tree was not particularly well resolved, so the 50% majority rule consensus
tree is shown in Figure 19 (left). CMN 11315 falls outside of Tyrannosauridae (sensu Brusatte and Carr, 2016), in a polytomy with Appalachianaurus montgomeriensis, Bistahieversor sealeyi, Dryptosaurus aquilunguis, and an unnamed taxon from Iren Dabasu. It is slightly more derived than the recognized immature tyrannosaurid “Raptorex kriegsteini.” Support for the least inclusive clade containing CMN 11315 and T. rex is low, with <50% bootstrap support and a Bremer support value of 0. Forcing CMN 11315 to be the sister taxon to Albertosaurinae (Albertosaurus sarcophagus + Gorgosaurus libratus) in Mesquite v. 3.04 (Maddison and Maddison, 2015) requires an additional step, and forcing it to be the sister taxon to Al. sarcophagus requires an additional two-steps. By contrast, forcing the same specimen to be the sister taxon to both Daspletosaurus spp. and Da. torosus requires 12 additional steps, and to Da. horneri requires 10 steps. CMN 11315 uniquely shares with Albertosaurinae a caudally concave ischium, and with Al. sarcophagus a lobe-like flange of the postacetabular process of the ilium.

The second phylogenetic analysis, excluding all ordered characters, produced 16 MPTs of 646 steps each. The strict consensus tree (CI = 0.470, RI = 0.805) (Fig. 19 right) recovered CMN 11315 as the sister taxon to Tyrannosauridae + (B. sealeyi + Lythronax argestes). Support for this grouping is again low (bootstrap <50%,
Fig. 17. Osteohistology of the left fibula of CMN 11315. (A) Thin section under plane-polarized light (inset shows possible growth lines, indicated by arrows); (B) large-area backscattered electron SEM image mosaic of the thin section showing bone porosity (see link to Atlas 5 BBV data set for high-resolution images).

Fig. 18. Results of morphometric analyses. Regressions depict log-transformed humerus length (A), radius length (B), ulna length (C), ilium length (D), femur circumference (E), and metatarsal III length (F) plotted against log-transformed femur length for albertosauromorphs and tyrannosaurids. CMN 11315 indicated by the red X. $e_\text{X}$ of CMN 11315 is given for those analyses of covariance (ANCOVA) in which significant differences were detected between albertosauromorphs and tyrannosaurids (see Table 2).
Bremer support = 0). “Raptorex kriegsteini” was once again recovered as somewhat more basal. CMN 11315 shares the following synapomorphies with the clade Tyrannosauridae + (B. sealeyi + L. argestes): rotation of humeral shaft absent; concave notch between external tuberosity and deltopectoral crest absent; vertical linear ridge on lateral surface of ilium dorsal to acetabulum present; anterodorsal notch on ilium present; ventral margin of pubic boot straight; caudal surface of ischium concave; lateral distal condyle of femur with an cranial bulge that is slightly separated from the remainder of the condyle; and lateral malleolus of tibia extends significantly further distally than medial malleolus.

**DISCUSSION**

**Age of CMN 11315**

CMN 11315 is evidently a subadult tyrannosaurid, based on its relatively small size (femur and ilium <750 mm long) and reduced muscle scarring; the latter generally becomes more pronounced with age. Fusion of the skull and vertebral bones is often used as an indicator of skeletal maturity (Hone et al., 2016), but unfortunately these are missing. Importantly, none of the aforementioned indicators of skeletal maturity are infallible, and supplementary osteohistological age assessment is typically advised when possible (Hone et al., 2016).

**TABLE 2. ANCOVA results**

| Element            | Slopes Means |            |            |
|--------------------|--------------|------------|------------|
|                    | F-stat       | P (same)   | F-stat     | P (same)   |
| Femur circumference| 2.73         | 0.104      | 9.664      | **0.00291**|
| Metatarsal III     | 0.842        | 0.366      | 8.423      | **0.00646**|
| Humerus            | 0.520        | 0.478      | 1.01316    | 0.720      |
| Radius             | 0.437        | 0.527      | 1.744      | 0.219      |
| Ulna               | 0.0486       | 0.829      | 6.864      | **0.0202** |
| Ilium              | 0.0233       | 0.880      | 25.05      | **1.82x10^-5** |

Comparisons between Albertosaurinae and Tyrannosaurinae, using femur length as the independent variable. Significant *P*-values are given in bold.
TABLE 3. Residual calculations for CMN 11315 from the albertosaurine and tyrannosaurine regression lines, using femur length as the independent variable

| Element       | Albertosauroids | Tyrannosauroids |
|---------------|-----------------|-----------------|
| Ulna length   |                  |                 |
| Observed      | 2.08             | 2.08            |
| Predicted     | 2.09             | 2.01            |
| Residual (ex) | −0.0164          | Residual (ex)   |
|               |                  | 0.0629          |
| Ilium length  |                  |                 |
| Observed      | 2.83             | 2.85            |
| Predicted     | 2.82             | 2.87            |
| Residual (ex) | 0.0139           | Residual (ex)   |
|               |                  | −0.0368         |
| Femur circumference |      |                 |
| Observed      | 2.50             | 2.50            |
| Predicted     | 2.36             | 2.38            |
| Residual (ex) | 0.139            | Residual (ex)   |
|               |                  | 0.114           |
| Metatarsal III|                  |                 |
| Observed      | 2.65             | 2.65            |
| Predicted     | 2.67             | 2.65            |
| Residual (ex) | −0.0210          | Residual (ex)   |
|               |                  | −0.00265        |

Bolded values indicate the smaller residual and the likely affinity of CMN 11315.

Histology of the fibula of CMN 11315 shows that the animal was young and still growing when it died, indicated by the lack of prolific Haversian bone or of an external fundamental system. Thus, CMN 11315 is definitely not a "pygmy," as has been suggested for some small tyrannosaurid species (e.g., Bakker et al., 1988; Fiorillo and Tykoski, 2014). Notably, the age inferred from osteochronology (at least 2 years from counted annuli) is appreciably younger than that obtained from the tyrannosaurid growth curves of Erickson et al. (2004). Using development mass estimation (Erickson and Tumanova, 2000), and calibration data from Erickson et al. (2004), the inferred mass of CMN 11315, assuming it is Albertosaurus sarcophagus, is 501 kg. This corresponds to an age of ~13 years (Erickson et al., 2004). Similarly, if CMN 11315 is Daspletosaurus sp., the same method provides a mass estimate of 636 kg and an age of ~10 years. In either case, the animal plots within the exponential portion of its growth curve.

The age disparity between the osteochronological and growth curve estimates might be explained in one of two ways. First, it is possible that the complete growth record of CMN 11315 is not entirely reflected by the annuli, and that some growth marks (annuli or lines of arrested growth) are missing. This would not be terribly surprising, given that growth marks often vary in number between skeletal elements in any individual (Horner et al., 2000). Alternatively, it may be that the osteochronological age estimate is accurate, and that the logistic growth model of Erickson et al. (2004) is erroneous (Myhrvold, 2013). There may be some reason to suspect this, given that the model predicts almost no growth in the first five years of the animal's life. Regardless of the source of error, the point remains that CMN 11315 does not represent a skeletally mature individual.

Identity of CMN 11315

Although CMN 11315 is recovered as a non-tyrannosaurid tyrannosaurid in the cladogram, this unqualified identification is quite unlikely considering no such animal has ever been found in Upper Cretaceous strata of Laramidia (Brusatte and Carr, 2016). Most certainly, this basal positioning is an upshot of the young ontogenetic age of CMN 11315, as it is lacking many of the relevant apomorphies that develop in adults (Gould, 1977). Such a phenomenon has been reported in tyrannosaurs elsewhere (e.g., Sereno et al., 2009; Tsuihiji et al., 2011), and is common in animals more widely (Hennig, 1999).

Accepting that CMN 11315 is a tyrannosaurid, the question remains as to which species it pertains. The historically varied classification of CMN 11315 as either A. sarcophagus (Madsen Jr., 1974; Holtz Jr., 2000; Currie, 2003b; Persons IV and Currie, 2016) or Daspletosaurus sp. (Russell, 1970; Makovicky and Currie, 1998; Currie, 2003a; Claessens, 2004; Nesbitt et al., 2009) makes sense in light of the equivocal morphometric results presented here. The specimen evidently shares a mix of features with both albertosaurines and tyrannosaurines. Importantly, although several of the albertosaurine and tyrannosaurine regression lines are significantly different, they are nonetheless often quite close, and the points overlap such that some plot closer to the opposite regression line. Thus, it is unsurprising that CMN 11315 should be variably allied with different taxa, particularly given the few variables considered here.

The greater number of variables included in the cladistic analysis might lead one to expect that it should provide a more exact identification, but this is not obviously the case. The number of plesiomorphic (and missing) character states is such that CMN 11315 falls outside of Tyrannosauridae, rather than with any particular taxon within it. Even so, the fewer steps necessary to unite CMN 11315 with A. sarcophagus than with Daspletosaurus spp. suggests that the former is a more parsimonious interpretation, all else being equal. Notably, CMN 11315 shares several skull characters (which are often considered the most useful for taxonomic identification; Currie et al., 2003) with A. sarcophagus, to the exclusion of tyrannosaurines. It shares only one (transition between the rostral and ventral margins of the dentary occurs below the first and second alveolus) with Daspletosaurus spp., to the exclusion of albertosaurines.

One must not be too careless with this phylogenetic line of reasoning. "Raptorex kriegsteini," a recognized juvenile Tarbosaurus bataar (Fowler et al., 2011; Tsuihiji et al., 2011), is also recovered outside of Tyrannosauridae, and (using the methods above) it takes ~50 fewer steps to unite it with any albertosaurine than with T. bataar. However, this does not mean that "R. kriegsteini" is instead an albertosaurine; biostratigraphic and biogeographic evidence strongly indicates that albertosaurines were not otherwise contemporaneous with "R. kriegsteini" (Brusatte and Carr, 2016). It is therefore imperative that...
CONCLUSIONS

Tyrannosauridae is rife with examples of species that have been coined on the basis of undiagnostic immature material, which has often led to overestimates of diversity (Currie and Dong, 2001; Currie, 2003b; Fowler et al., 2011). Although Russell (1970) did not name a new species specifically to receive CMN 11315, the effect of assigning it to Daspletosaurus cf. D. torosus was largely the same, in addition to artificially inflating the longevity of the genus. To be sure, accurate classification of immature skeletal material is often made quite difficult by the fact that diagnostic character states are typically not expressed until adulthood (Carr, 1999; Hone et al., 2016). Although none of the methods applied here was individually able to provide a satisfactory answer concerning the taxonomic status of CMN 11315, their combined application (in addition to historic and biostratigraphic considerations) yields a more definitive answer. We therefore stress the use of such “total evidence” approaches when taxonomic information is not forthcoming.

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