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**A juvenile cf. *Edmontosaurus annectens* (Ornithischia,
Hadrosauridae) femur documents a poorly represented growth stage
for this taxon**

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ABSTRACT

A nearly complete, but isolated, femur of a small hadrosaurid from the Hell Creek Formation of Montana is tentatively referred to *Edmontosaurus annectens*. At 28 cm long, the element can be classified as that from an “early juvenile” individual, approximately 24 percent of the maximum known femur length for this species. Specimens from this size range and age class have not been described previously for *E. annectens*. Notable trends with increasing body size include increasingly distinct separation of the femoral head and greater trochanter, relative increase in the size of the cranial trochanter, a slight reduction in the relative breadth of the fourth trochanter, and a relative increase in the prominence of the cranial intercondylar groove. The gross profile of the femoral shaft is fairly consistent between the smallest and largest individuals. Although an ontogenetic change from relatively symmetrical to an asymmetrical shape in the fourth trochanter has been suggested previously, the new juvenile specimen shows an asymmetric fourth trochanter. Thus, there may not be a consistent ontogenetic pattern in

trochanteric morphology. An isometric relationship between femoral circumference and femoral length is confirmed for *Edmontosaurus*. Overall ontogenetic trends in the femur of *Edmontosaurus* are concordant with patterns seen in other Hadrosauridae, supporting a fairly conserved pattern of development for this element within the clade.

Key words: *Edmontosaurus*, ontogeny, femur, Hadrosauridae, Dinosauria, Hell Creek Formation, Ornithischia

INTRODUCTION

Ontogenetic changes in hadrosaurid dinosaurs are known in substantial detail for several species, supported by the study of isolated elements, articulated skeletons, and multi-individual bonebed assemblages. Documentation of gross morphology, osteohistology, and allometric trends permit inference of heterochrony, life history traits, functional changes, and other attributes both within species and across species. Among hadrosaurine hadrosaurids, growth series are particularly broad (i.e., preserving individuals spanning a spectrum from very small and early in life to very large and presumably adult) for *Maiasaura peeblesorum*, *Saurolophus angustirostris*, and *Edmontosaurus annectens* (Bell, 2011; Guenther, 2014; Prieto-Márquez, 2014; Dewaele et al., 2015; Woodward et al., 2015; Prieto-Marquez and Guenther, 2018; Wosik et al., 2018). Here, we describe a femur identified as an early juvenile *Edmontosaurus annectens* from the Hell Creek Formation of Montana, which fills a size gap in the described specimens for this taxon.

Edmontosaurus annectens is a common component of the faunal assemblage for the Hell Creek, Lance, Frenchman, and Scollard formations (late Maastrichtian) of western North

America (Campione and Evans, 2011). Cranial changes during ontogeny have received particular attention, due to their relevance in taxonomic problems. Postcranial changes are more sparsely documented. Although bonebed assemblages have the potential to document a range of body sizes for *E. annectens*, none of these have been formally described with respect to gross skeletal morphology (Colson et al., 2004; Stanton Thomas and Carlson, 2004; Wosik, 2018). Instead, most information on postcranial ontogenetic changes in *E. annectens* is based upon exceptionally preserved articulated individuals, particularly for the first half of ontogeny. Most notably, Prieto-Marquez (2014) described a nearly complete skeleton from a late juvenile-sized individual (~47% of maximum known femur length for the taxon). This was followed by Wosik et al. (2018)'s description of the partial articulated postcranium from a nestling-sized individual (~12% of maximum known femur length for *E. annectens*). Thus, despite the reputation of *E. annectens* as a common fossil, the postcrania are still rather sparsely described for most size classes. Similarly, described postcranial elements from the closely related *Edmontosaurus regalis*, *Shantungosaurus giganteus*, and *Ugrunaaluk kuukpikensis* generally are for individuals at 50 percent or more of maximum known element length (Baert et al., 2014; Hone et al., 2014; Vandervén et al., 2014; Mori et al., 2015).

The femur has figured prominently in studies of dinosaurian ontogeny (and hadrosaurid ontogeny) for multiple reasons. First, it is a robust and frequently well preserved element with morphology that permits confident assignment to the family (and often subfamily) level when found in isolation. Additionally, the femur is an attachment site for major muscles that function in locomotion, so it is useful for understanding functional changes during ontogeny. Finally, as a major load bearing bone, it can be used to estimate the biologically informative parameter of body mass. Thus, detailed study of this element is particularly worthwhile.

This paper focuses on RAM 9396, an isolated femur tentatively assigned to *Edmontosaurus annectens*. At approximately 28 cm long, it falls precisely in the middle of a size gap between the previously described smallest (UCMP 128181, 15 cm long, at the “late nestling” ontogenetic stage, *sensu* Wosik et al. 2018) and next smallest (LACM 23504, 56 cm long, at the “late juvenile” ontogenetic stage, *sensu* Wosik et al. 2018) femora. Thus, the fossil provides new information on ontogenetic changes in *E. annectens*, as well as data relevant to ontogenetic comparisons across hadrosaurids.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, New York, USA; CCM, Carter County Museum, Ekalaka, Montana, USA; CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; CMNH, Cleveland Museum of Natural History, Cleveland, Ohio, USA; DMNH, Denver Museum of Nature and Science, Denver, Colorado, USA; FPDm, Fukui Prefectural Dinosaur Museum, Katsuyama, Japan; LACM, Natural History Museum of Los Angeles County, Los Angeles, California, USA; MOR, Museum of the Rockies, Bozeman, Montana, USA; RAM, Raymond M. Alf Museum of Paleontology, Claremont, California, USA; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; SDSM, Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota, USA; UALVP, University of Alberta Laboratory of Vertebrate Paleontology, Calgary, Alberta, Canada; UCMP, University of California Museum of Paleontology, Berkeley, California, USA; USNM, National Museum of Natural History, Washington, D.C., USA.

Ontogenetic terminology

Here, we use terminology for ontogenetic stages as defined by Wosik et al. (2018), which was modified in turn from that of Horner et al. (2000). Because the specimen was not sectioned for histological study, stage referrals are based upon element length.

Geological background

RAM 9396 was collected in 2000 by a team from the Raymond M. Alf Museum of Paleontology and The Webb Schools, at RAM locality V200029. This site is within the basal lag of a channel sandstone situated within the upper part of the Hell Creek Formation of McCone County, Montana, USA. Although RAM 9396 was collected *in situ*, no other bones referable to this individual were recovered at the site. Detailed locality data are on file at RAM, available upon request.

Taxonomic referral

Because the Hell Creek Formation yields numerous tetrapod taxa that have femora within the size range of RAM 9396, we briefly justify our assignment of this specimen to *Edmontosaurus annectens*. Overall shape of the fossil (e.g., comparatively straight diaphysis, prominent fourth trochanter, etc.) excludes identification as a turtle, choristodere, or crocodyliiform, and the solid cross-section further excludes assignment to a pterosaur or theropod. The non-pendant fourth trochanter differs from that seen in “basal” ornithopods such as *Thescelosaurus*, pachycephalosaurids, and neoceratopsians such as *Leptoceratops*. Furthermore, the fourth trochanter is more pronounced than seen in ceratopsids (e.g., *Triceratops*) or ankylosaurians. Thus, in overall form, major aspects of the femoral anatomy match those seen in much larger *Edmontosaurus annectens* (as outlined below). Although the

femur itself does not hold autapomorphies that permit assignment to the species or even genus level, *E. annectens* is currently the only valid hadrosaurid known from the Hell Creek Formation (Campione and Evans, 2011). Thus, we tentatively refer RAM 9396 to this taxon.

DESCRIPTION

RAM 9396 is a nearly complete left femur, missing only the posterior parts of the distal condyles (Figures 1, 2). It has a maximum length of 277 mm, as measured along the lateral surface; comprehensive measurements are illustrated in Figure 3 and provided in Table 1. Here, we describe the element beginning with the proximal end and compare RAM 9396 with other specimens of *Edmontosaurus* spp.

In dorsal view the femoral head of RAM 9396 is roughly rectangular and set at a 90 degree angle relative to the greater trochanter, which is roughly triangular (Figures 1E, 2E). In larger individuals of *Edmontosaurus* spp., the two structures are separated in dorsal view by a distinct constriction of the bone on both its cranial and caudal surfaces (e.g., LACM 23504; also see Fig. 13.20F,L in Campione, 2014). In RAM 9396, the constriction is much less pronounced, and the head and greater trochanter are less distinctly separated (Figures 1E, 2E). The bone surface in this region is gently abraded, so it is not possible to gauge the extent of cartilaginous surfaces. When the main body of the femoral shaft is oriented vertically and viewed cranially (Figures 1A, 2A), the femoral head is set slightly ventrally (distally) relative to the greater trochanter, and the two are separated by a slight depression. The condition in larger individuals is hard to assess due to crushing in many specimens. For instance, the head is ventral relative to the greater trochanter in the subadult *E. annectens* LACM 23504 and in the left femur of the large *E. regalis* individual CMN 2289, but at nearly the same level in the right femur of CMN 2289. In

lateral view (Figures 1D, 2D), the dorsal (proximal) end of the greater trochanter on RAM 9396 has a semicircular profile, comparable in shape and proportions to the greater trochanter in larger juvenile (LACM 23504) and adult-sized (AMNH 5886, USNM 2414) individuals of *E. annectens*. The tab-like cranial trochanter is well defined and placed ventral to the greater trochanter, at approximately the same level as the femoral head (Figures 1A, 2A). This cranial trochanter of RAM 9396 is proportionately smaller than the condition in larger individuals; in large *Edmontosaurus*, the cranial trochanter sometimes approaches the same width as the greater trochanter (e.g., CMN 2289; AMNH 5886), although it may also be smaller (USNM 2414). A distinctly rimmed fossa immediately medial to the cranial trochanter occurs on the cranial surface of the femur (Figure 1A), which may represent the insertion for *m. iliofemoralis* (following muscle maps from Maidment et al., 2014).

The femoral shaft of RAM 9396 is fairly straight in lateral view (Figures 1D, 2D). In cranial view (Figures 1A, 2A), the lateral surface is also fairly straight, whereas the medial surface has a concave profile. Thus, the overall conformation of the shaft matches that seen in smaller and larger *Edmontosaurus* (e.g., UCMP 128181; LACM 23504). The fourth trochanter is centered at approximately midshaft (comparable with individuals across all sizes in *Edmontosaurus annectens*) and occupies just over a quarter of the length of the femur along its caudomedial surface (Figures 1B, 2B). The trochanter occupies a proportionately smaller percentage of the femoral shaft length in larger individuals, around 20% of the shaft length in the juvenile LACM 23504 and adult AMNH 5886. The trochanter has a broad-based, asymmetrically triangular profile, with the tip of the triangle placed distally relative to the center of the triangle (Figure 4A). The base of the trochanter is relatively narrower in some larger individuals (Figure 4B, 4C), which creates a more prominent appearance for the structure. The

outline is also asymmetrical in some large individuals (Prieto-Márquez, 2014; Wosik et al., 2018), but this varies with specimen, possibly due to taphonomic effects. For instance, the greater trochanters of large *E. annectens* (AMNH 5886, RAM 318, RAM 7150, and USNM 2414; Figure 4C,D,E) are asymmetric with the apex positioned distally, whereas the same structure is fairly symmetrical in the large *E. regalis* CMN 2289 and the subadult *E. annectens* LACM 23504 (Figure 4B). A slight concavity occupies most of the medial surface of the fourth trochanter in RAM 9396, which presumably represents the insertion for *m. caudofemoralis longus* (Maidment et al., 2014). The femoral shaft of RAM 9396 is uncrushed and has a teardrop-shaped cross-section at mid-shaft (when the trochanter is ignored), with the lateral surface broadest and slightly flattened. Shape could not be compared reliably with that in larger specimens, because no uncrushed examples were accessible.

In distal view, the medial condyle in RAM 9396 is slightly more prominent than the lateral condyle, and they are separated by a prominent cranial intercondylar groove (Figures 1F, 2F); both conditions match that seen in larger *Edmontosaurus annectens* (e.g., RAM 318, 7150). One distinct difference between RAM 9396 and larger *Edmontosaurus* (LACM 23504, AMNH 5886, USNM 2414) is that larger individuals sometimes have a slight cranial protrusion of the condyles. With the lateral surface of the shaft oriented vertically, the lateral condyle is in approximately the same vertical plane as the greater trochanter, and the medial condyle is very slightly lateral to the vertical plane that contains the femoral head (Figures 1A, 2A), matching the condition in larger individuals. The caudal surfaces of the distal condyles and the associated caudal intercondylar groove are not preserved.

STATISTICAL ANALYSIS

A previous analysis of femoral allometry in *Edmontosaurus* was heavily skewed towards large individuals (Wosik et al., 2018), which can hamper interpretations of allometry. Thus, RAM 9396 was incorporated into the dataset of Wosik et al. (2018), regressing femoral circumference onto femoral length. Two additional femora (UALVP 50988 and 52758) from *E. regalis* were added to the sample, using published measurements (Baert et al., 2014; Vandervén et al., 2014). Measurements were log-transformed with a natural log function, and then analyzed with RMA (reduced major axis) regression. Regressions were calculated within PAST 3.22 (Hammer et al., 2001), using samples with all *Edmontosaurus* spp. (*E. annectens* and *E. regalis*) as well as a sample with just *E. annectens*.

The new regression (Figure 5) had a slope indistinguishable from isometry when considering all *Edmontosaurus* (1.041; 95% confidence interval of 0.7802–1.079; $r^2=0.96$; $n=21$) and when including just *E. annectens* (1.0183; 95% confidence interval of 0.407–1.087; $r^2=0.98$; $n=15$). These results do not differ significantly from the finding of isometry by Wosik et al. (2018).

BODY MASS ESTIMATE

We used Developmental Mass Extrapolation (Erickson and Tumanova, 2000) to estimate the body mass of RAM 9396. Following the assumptions of Wosik et al. (2018), we used the large CCM specimen for comparison. Depending on the metric used for scaling, body mass for RAM 9396 is estimated as 68 kg (when scaled by femoral circumference) or 96 kg (when scaled by femoral length).

DISCUSSION

The description and comparisons of a femur referred to a small juvenile *Edmontosaurus annectens* help to clarify both previously documented and previously unrecognized patterns in the ontogeny of the femur in this taxon. Major changes with increasing body size include a more distinct separation of the femoral head and greater trochanter with increasing body size, relative increase in the size of the cranial trochanter, a slight reduction in the relative size of the fourth trochanter, and a relative increase in the prominence of the cranial intercondylar groove. The gross profile of the femoral shaft is fairly consistent between the smallest and largest individuals. Although a major shift from relatively symmetrical to asymmetrical shape in the fourth trochanter has been described in the literature (noted by Prieto-Márquez, 2014; Wosik et al., 2018), the asymmetric shape in the relatively small RAM 9396 indicates that this is probably not a clear trend, but instead may just reflect individual variation in the shape of the trochanter independent of ontogeny (Figure 4).

Inclusion of RAM 9396 in an allometric analyses of femoral proportions in *Edmontosaurus* does not change previous interpretations of isometry in femoral circumference versus length in this animal (Wosik et al., 2018). Nonetheless, the fossil is important for filling a size gap in the dataset (Table 2 and Figure 5); the collection and measurement of other specimens will undoubtedly help to firm up interpretations of femoral allometry for *Edmontosaurus*.

Based on the overall sample in the literature, the general ontogenetic trajectory for femora in *Edmontosaurus* is consistent with that observed other hadrosaurines. Femoral ontogeny was quite similar in *Maiasaura* and *Edmontosaurus* (Dilkes, 2001; Guenther, 2014; Prieto-Marquez and Guenther, 2018), and indeed even similar to that in the lambeosaurine *Hypacrosaurus* (Guenther, 2014). Thus, overall ontogenetic trends for the femur were probably

conserved across Hadrosauridae, as noted previously (Brett-Surman and Wagner, 2006; Guenther, 2009, 2014).

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248 **Figure 1.** RAM 9396, left femur of cf. *Edmontosaurus annectens*, photographed in A) anterior;
 249 B) medial; C) posterior; D) lateral; E) proximal; and F) distal views. Scale bar equals 10 cm.
 250 Abbreviations: cig, cranial intertrochanteric groove; ct, cranial trochanter; fh, femoral head; ft,
 251 fourth trochanter; gt, greater trochanter; lc, lateral condyle; mc, medial condyle; mf, muscular
 252 fossa.

254 **Figure 2.** RAM 9396, left femur of cf. *Edmontosaurus annectens*, drawn in A) anterior; B)
255 medial; C) posterior; D) lateral; E) proximal; and F) distal views. Missing portions of the
256 condyles are indicated with gray shading. Scale bar equals 10 cm. Illustrated by Phillip
257 Krzeminski, used with permission.

258

260 **Figure 3.** Measurement parameters for RAM 9396, left femur of cf. *Edmontosaurus annectens*,
 261 drawn in A) anterior; B) medial; C) lateral; and D) proximal views. Numbers correspond with
 262 measurements in Table 1.

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264

265 **Figure 4.** Comparative line drawings of the fourth trochanter from *Edmontosaurus annectens*,
266 showing variation in the proximo-distal position of the trochanter's apex. Proximal is towards the
267 top of the drawing, and caudal is to the left. Specimens are arranged from smallest (left) to
268 largest trochanter (right), for A) RAM 7967; B) LACM 23504; C) USNM 2414; D) RAM 318;
269 E) RAM 7150. Scale bar equals 5 cm.

270 **Figure 5.** Linear regression (RMA) showing femur length versus femur circumference for
 271 *Edmontosaurus* spp. Data presented in Table 2.

273 **Table 1.** Measurements of RAM 9396, left femur of cf. *Edmontosaurus annectens*, in
 274 millimeters. Measurement standards illustrated in Figure 3.

275

	Description	Measurement (mm)
1	Maximum length, medial surface	252.0
2	Maximum length, lateral surface	277.1
3	Medio-lateral width at midshaft	35.9
4	Circumference of shaft, just below fourth trochanter	105.0
5	Distance between cranial edges of medial and lateral distal condyles	11.7
6	Maximum width of distal end	55.5
7	Maximum length of fourth trochanter	76.2
8	Maximum height of fourth trochanter	11.4
9	Maximum width of iliofemoralis insertion fossa	20.5
10	Maximum proximo-distal length of cranial trochanter	24.4
11	Maximum cranio-caudal length of cranial trochanter	16.8
12	Maximum cranio-caudal length of proximal end	48.1
13	Maximum medio-lateral width of proximal end	64.1
14	Maximum cranio-caudal width of femoral head	24.8

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278 **Table 2.** Measurements of femora from *Edmontosaurus*, in millimeters, used for regression anal-
 279 ysis. All measurements from Wosik et al. (2018), except for UALVP specimens (Baert et al.,
 280 2014; Vandervén et al., 2014) and RAM 9396 (this study).

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Specimen	Species	Length (mm)	Circumference (mm)
AMNH 5730	<i>E. annectens</i>	1148	512.3
CCM disarticulated	<i>E. annectens</i>	875	337.5
CCM mount	<i>E. annectens</i>	1152	490
CMN 8509	<i>E. annectens</i>	995	417.5
CMNH 10178	<i>E. annectens</i>	910	330
DMNH 1493	<i>E. annectens</i>	1035	459.5
FPDM	<i>E. annectens</i>	990	344
LACM 23504	<i>E. annectens</i>	559	220
MOR 2939	<i>E. annectens</i>	1175	509
RAM 9396	<i>E. annectens</i>	277	105
SDSM 4917	<i>E. annectens</i>	1032	381
UCMP 128181	<i>E. annectens</i>	148	60
UCMP 137278	<i>E. annectens</i>	995	425
USNM 2414	<i>E. annectens</i>	1025	388.5
YPM 2182	<i>E. annectens</i>	1025	490
CMN 2289	<i>E. regalis</i>	1243	532
CMN 8399	<i>E. regalis</i>	1140	374
ROM 801	<i>E. regalis</i>	1280	480
ROM 867	<i>E. regalis</i>	990	422.5
UALVP 52758	<i>E. regalis</i>	860	266
UALVP 50988	<i>E. regalis</i>	515	208

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