MORPHOLOGY AND OSTEOHISTOLOGY OF A LARGE-BODIED CAENAGNATHID (THEROPODA, Oviraptorosauria) FROM THE HELL CREEK FORMATION (MONTANA): IMPLICATIONS FOR SIZE-BASED CLASSIFICATIONS AND GROWTH RECONSTRUCTION IN THEROPODS

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Typescript received 14 July 2019; accepted in revised form 1 December 2019

Abstract: Oviraptorosaurs, like many coelurosaurians, are frequently diagnosed using incomplete or fragmentary skeletal remains, with factors such as body size often used to assign material to a particular taxon or as a basis for describing new species. Here we describe a partial skeleton, ROM VP 65884, from the Hell Creek Formation (Montana, USA), and through morphological and phylogenetic comparisons identify it as belonging to Caenagnathidae, and probably referable to Anzu wyliei. We perform multi-element osteohistological sampling of the tibia, fibula, manual phalanx, rib and gastralium of ROM VP 65884 to determine the ontogenetic status of the individual, and to perform a detailed assessment of the intra-skeletal variation present in a series of histological proxies for growth and development. Skeletochronological analysis suggests ROM VP 65884 was still actively growing at time of death. Lacunar area was variable, but consistent with values reported for other dinosaurs and vertebrates. Osteocyte lacunar density was found to be relatively similar to the few previous measurements known from coelurosaurian dinosaurs, and preserved no ontogenetic pattern. Osteocyte lacunar density (OLD) was much higher in sampled rib and gastralium elements when compared to limbs, and the high variability in OLD overall lends further support against the hypothesis of this feature acting as a proxy for mass-specific growth rate. Our results stress the importance of using osteohistological analyses to constrain variation and permit ontogenetic assessment, and suggest caution be taken when using size as a determinant for referral of disassociated elements to specific or new coelurosaur taxa.

Key words: Caenagnathidae, osteohistology, theropod, taxonomy, Cretaceous, osteocyte lacunar density.

Caenagnathidae is a clade of oviraptosaurian theropods known primarily from the Upper Cretaceous of Asia and North America (Currie & Russell 1988; Currie 1989; Currie et al. 1993; Sullivan et al. 2011; Longrich et al. 2013; Funston et al. 2015a). The clade is characterized by slender hands, long hind limbs and feet, and distinctive lower jaws with toothless beaks (Currie & Russell 1988; Funston & Currie 2014). Historically, isolated caenagnathid elements from the Campanian–Maastrichtian of North America have been misidentified as belonging to a variety other theropod taxa, such as ornithomimids, small tyrannosaurs, or even birds (Gilmore 1924; Sternberg 1932, 1940; Cracraft 1971). The discovery and description of more complete specimens in the last four decades years has led to a better understanding of caenagnathids and their position within the clade Oviraptorosauria (Currie & Russell 1988; Sues 1997; Zanno & Sampson 2005; Lamanna et al. 2014; Funston & Currie 2016).

Despite these several notable associated skeletons, the osteology and variability of caenagnathids remains poorly known due to a dearth of material. Most of the available skeletons are far from complete, with many named taxa represented by extremely fragmentary material. Studies of ontogeny and other aspects of growth-related variation are
therefore limited, although exquisitely preserved embryos have recently been described (e.g. Zelenitsky et al. 2017). Osteohistological descriptions of caenagnathids have been constrained to single limb bones in two taxa of caenagnathid, Gigantoraptor from the Early Cretaceous of China (Xu et al. 2007) and an indeterminate tibia from the Horseshoe Canyon Formation (Funston & Currie 2018), as well as isolated dentaries from the Dinosaur Park Formation (Funston et al. 2019). As such, intra-element variation of osteohistological traits is unknown in Caenagnathidae, but is of interest due to the presence of both putatively extremely small-bodied taxa (e.g. Longrich et al. 2013) and gigantism in the clade (Xu et al. 2007). This issue, combined with the description of, or referral of specimens to, taxa from fragmentary material where size is a major differentiating component, may lead to significant misestimations of caenagnathid diversity, and consequently may have broader implications for our understanding of North American terrestrial diversity at the end of the Mesozoic. Thus, it is imperative that thorough analyses of ontogenetic and osteohistological variability be performed on caenagnathids, to facilitate more thorough assessments of their taxonomic validity and biodiversity.

In addition to general questions of ontogenetic status and taxonomic validity, the fragmentary nature of caenagnathids has somewhat impeded attempts to characterize their palaeobiology. One metric proposed as a proxy for mass-specific growth rate is osteocyte lacunar density (OLD) (Stein & Werner 2013). If the relationship between OLD and mass-specific growth rate is robust, then in-depth assessments of growth and ontogeny may be possible even with highly fragmentary material (i.e. lacking full transverse limb samples). However, other authors have suggested that high OLD in bones is a result of higher rates of remodelling (Reilly 2000; Hernandez et al. 2004), and possibly related to increased mechanical loading/stress (Hunter & Agnew 2016). Also, previous research on lacunar density in ornithomimids has found that OLD values can vary considerably within an individual skeleton and between individuals of the same taxon (Cullen et al. 2014), though it has remained unclear how prevalent this high degree of variation is among coelurosaurians more generally. A similar measure, osteocyte lacunar area (OLA), has also been proposed as a proxy for multiple organisinal features, such as genome size, growth rate and body size, though it remains unclear how broadly these relationships hold in a broader phylogenetic context, and to what extent multiple factors may interact or counteract in influencing lacunar area (Organ et al. 2007, 2009; Montanari et al. 2011).

The discovery of a fragmentary yet associated skeleton (ROM VP 65884) of a large-bodied caenagnathid from the Hell Creek Formation, tentatively referred to the genus Anzu wyliei represents one of only a few known from this well-sampled formation, and is the first record of this genus to be formally documented from Montana. In addition to morphological description and taxonomic identification, the fragmentary nature of the specimen is ideally suited for multi-element osteohistological sampling, as it does not warrant the same degree of curatorial concern/reticence often associated with ’sacrificing’ more complete fossil specimens (Padian & Lamm 2013). Multi-element osteohistological sampling of ROM VP 65884 is performed with the purpose of ascertaining the relative skeletal maturity of the specimen and documenting intra-skeletal patterns of variability in osteohistological traits, including vascularity, growth zone spacing/thickness, osteocyte lacunar density, and osteocyte lacunar area. These analyses will characterize the ontogeny of Anzu wyliei, provide insight into the use of size as a distinguishing feature in caenagnathid taxonomy, while also providing additional assessments of the utility of osteocyte lacunar density and area as a proxy for mass-specific growth in theropods.

### MATERIAL AND METHOD

**Specimen collection and preparation**

ROM VP 65884 was collected and freed from surrounding rock matrix using standard preparation tools and techniques (e.g. hammer/chisel, hand tools, burlap/plaster, saws and pneumatic pin vise, etc.) Skeletal elements were measured with digital calipers and digitally photographed with a Nikon D3100 DSLR camera.

**Taxonomic identification and phylogenetic analysis**

Fragmentary fossils can be difficult to assign taxonomically. In order to verify the caenagnathid affinity of ROM VP 65884 and identify the specimen as precisely as possible, we scored the specimen into the data matrix of Funston & Currie (2016) and compared the scoring to other oviraptorosaurian taxa (with a focus on the contemporary Anzu wyliei), as well as several outgroup theropods. The highly fragmentary nature of the specimen precludes reliability of the analysis for precise placement within Caenagnathidae, but it serves to demonstrate that the specimen is deeply nested within Caenagnathidae. Results of the character comparisons are presented below, and detailed methods and results for the phylogenetic analysis are presented in Cullen et al. (2020, appendices S1–S2).

**Osteohistological thin-section preparation**

Elements selected for thin-sectioning were chosen to represent as many major skeletal regions as possible, given...
the limitations of specimen completeness, and include a tibia, fibula, manual phalanx, rib and gastralia. Sectioning was performed as close to mid-shaft as possible for each limb element, given the relative differences in completion of each element. This was not the case for the sampled fragments of rib and gastrarium, and ascertaining exact position in these fragments was more difficult. Larger elements (tibia and manual phalanx) were stabilized using Technovit 5071 (Kulzer Technique), a reversible resin for surface embedding, and cut with a Buehler Isomet 1000 diamond wafer blade, prior to grinding using a Variable Speed Grinder Crystal Master Pro12. Specimens were then glued to plexiglass slides using Mercury M5T Cyanoacrylate (Mercury Adhesives LLC) thin viscosity adhesive. Small elements (fibula, rib, gastrarium) were embedded in Castolite AP, a polyester/acrylic resin mixed with methyl-ethyl-ketone peroxide catalyst. These specimens were cured for 24 h, then cut with using the Buehler Isomet 1000, and glued to plexiglass slides using cyanoacrylate (as above). All specimens were then trimmed using the Buehler Isomet saw and ground to optimal thickness using a Hillquist 1010 grinding cup, with 600 grit carbide powder and 1-micron aluminum oxide powder applied afterwards to achieve final thickness and polish. High resolution full-section images are available in Cullen et al. (2020, appendix S4).

Analysis of osteocyte lacunar density and area

Osteocyte lacunar density measurements between different bones and in different locations within the bone cortex (representing ontogenetic change; locations indicated by red squares on associated figures) of ROM VP 65884 were taken in order to: (1) quantify the degree of intra-skeletal variability present in osteocyte lacunar density and area in a caenagnathid and compare it to the range of variation known from previously sampled coelurosaurids; and (2) test if recorded osteocyte lacunar densities/areas in the tissues of ROM VP 65884 are more consistent with the interpretation of OLD as a proxy for mass-specific growth rate, or as a result of other factors (e.g. differential patterns of bone remodelling, mechanical loading/stress, etc.).

Osteocyte lacunar density (OLD) was counted using the method of Cullen et al. (2014), itself modified from the method of Stein & Werner (2013). Slides were viewed under plane-polarized light on a Nikon AZ100 using 240× magnification, and image data captured using NIS-Elements (Nikon). A Z-stack of 10 images was identified, aligned and merged in NIS-Elements to produce a two-dimensional image. A 250 μm × 250 μm field of vision on the XY-plane was selected, and the slide thickness at that location measured using NIS-Elements software. The refractive index of the resin (c. 1.6) (Rogers 1924; Padian & Lamm 2013) was accounted for when using slide thickness, alongside the length and width measurements, to calculate the volume of the sampled region of bone cortex. Osteocyte lacunae were manually counted from primary tissue within the Z-stacked field of vision, including those intersecting with the X–Y border. Counts were performed by two of the authors (TMC and DJS), and each performed their counts three times per thin section, in the same locations of the inner, middle and outer cortex of each specimen (with the exception of the gastralia, where primary tissue only remained in the outer cortex). This was done to minimize the effects of measurement error and control for possible individual biases. Regions of similar vascular space were selected for lacunar counts, though this was probably influenced to some extent by the broader scale vascular organization of the cortex and each micro-sampling count location. Primary tissue was measured in order to facilitate comparisons with data from earlier studies, and to focus investigations on factors influencing lacunar density/size during the primary growth period of the organism, rather than relating to later periods of bone remodelling. Osteocyte lacunar density (OLD) was calculated by dividing the number of osteocyte lacunae (OL) by the calculated three-dimensional volume of the Z-stacked sampling space. Lacunar density was computed from the measurements taken from the inner, middle and outer primary cortex of each sampled element, excluding the gastralia (where, as also noted above, only the outer cortex counts could be taken due to extensive secondary remodelling). Osteocyte lacunar area measurements were taken based on the method of Organ et al. (2007), with the long axis and short axis radii recorded for the lacunae in a given image. These were then used to calculate mean lacunar area (π × mean short-axis radius × mean long axis radius).

Institutional abbreviations. CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; CMN, Canadian Museum of Nature, Ottawa, Ontario, Canada; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; TMP, Royal Tyrrell Museum, Drumheller, Alberta, Canada; ZPAL, MgD-I, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

SYSTEMATIC PALAEOONTOLOGY

Suborder THEROPODA Marsh, 1881
Infraorder OVIRAPTOROSAURIA Barsbold, 1976
Family CAENAGNATHIDAE Sternberg, 1940
cf. Anzu wyliei Lamanna et al., 2014

Material. ROM VP 65884, a partial skeleton comprised of dorsal vertebral fragments, three nearly-complete caudal vertebrae, dorsal rib and gastralia fragments, the distal end of a left manual phalanx II-1, fragments of the left
pubis and left fibula, a distal tibia fragment, partial left metatarsals II–IV, an almost complete right metatarsal V, plus many unidentifiable bone fragments.

**Locality and horizon.** ROM VP 65884 was collected in 2012 by Jared Hudson, from Upper Cretaceous (late Maastrichtian) strata of the Hell Creek Formation on private deeded land in Section 6, Township 22 N, Range 42 E, Garfield County, Montana, USA. The nearly complete right foot was also collected, assembled into a display mount, and sold to a private collector, with the remainder of the material, which is described here, subsequently acquired by the ROM in 2013. Detailed locality information is on file at the Royal Ontario Museum.

**Remarks.** ROM VP 65884 can be assigned to Caenagnathidae based on the presence of the following derived characters from the phylogenetic analysis of Funston & Currie (2016): presence of lateral pneumatic fossae on the caudal centra (char. 113[1]); an anteroposteriorly flattened metatarsal III with a concave posterior surface (char. 205[1]); a prominent and deep concavity on posterior surface of the tarsometatarsus (char. 242[1]); sharp ‘cruciate’ ridges on both sides of the posterior surface of metatarsal III that form a chiasmata on the posterodistal surface (char. 243[1]); metatarsus with a straight metatarsal II and laterally directed metatarsal IV (char. 245[2]). The latter four derived character states are found only within Caenagnathidae in the data matrix of Funston & Currie (2016) (see Table 1; Cullen et al. 2020, appendix S1). In addition, ROM VP 65884 has an enclosed, shallow, oval-shaped fossa located proximally on the medial surface of the pubis, which has been argued by Sullivan et al. (2011) to characterize caenagnathids. Other features of the ROM specimen are also consistent with an oviraptorosaurian identification, most notably that the distal caudal vertebrae have a distinctive pygal morphology (Lamanna et al. 2014). See Figure 1 and Cullen et al. (2020, appendix S3) for specimen photographs.

ROM VP 65884 is a large oviraptorosaur from the same formation as the type series of *Anzu wyliei* (Lamanna et al. 2014), suggesting possible referral to this taxon. Only four characters from Funston & Currie (2016) can be scored for both ROM VP 65884 and *Anzu wyliei*, and these are scored identically for both OTUs (Table 1). Phylogenetic analysis of ROM VP 65884 based on the characters in Table 1 in the context of Funston & Currie (2016) places it within Caenagnathidae, but ROM VP 65884 does not form a sister taxon relationship with *Anzu wyliei*, despite the fact that it is scored identically to *A. wyliei* where overlapping material is known (see Cullen et al. 2020, appendices S1–S2, for full character comparison/discussion and phylogenetic analysis). This phylogenetic placement is probably due to ROM VP 65884 not preserving cranial elements, where most autapomorphic characters of *A. wyliei* are located (Lamanna et al. 2014). As a result of this fragmentary nature, we do not think phylogenetic analysis is adequate to establish the species-level identity of the specimen. Importantly, in addition to the preserved morphology being virtually identical to overlapping elements of *A. wyliei*, ROM VP 65884 is also consistent in size with *A. wyliei* (c. 3% difference in linear size, on average), one of the largest known North American oviraptorosaurs (see Table 2 for comparative measurements). Despite the limitations of the fragmentary available material, ROM VP 65884 can unequivocally be identified as a large caenagnathid oviraptorosaur, and we believe that there is enough morphological similarity to tentatively refer ROM VP 65884 to *Anzu wyliei*.

### ANATOMICAL DESCRIPTION

#### Axial skeleton

The preserved axial skeleton consists of fragments of dorsal vertebrae, three caudal vertebrae and several dorsal rib and gastralia fragments. Of the vertebral remains, only the relatively complete caudal vertebrae are described here. The three preserved caudals are all from the distal half of the caudal series based on comparisons with *Anzu wyliei* (Lamanna et al. 2014), and may be sequential around the prepygal–pygal transition. All of the centra are generally amphiplatyan, but with a slight a concavity on the anterior face of the centrum, and are wider than tall (Table 2). Each of the vertebrae also have a prominent midline sulcus on the ventral surface of the centrum. The anteriormost and largest caudal (Fig. 1, V-1) is proportionally the shortest anteroposteriorly of the preserved vertebrae with a centrum approximately as wide (30.8 mm) as it is long (31.1 mm). The transverse processes are situated on the anterior half of the centrum but are broken at their base on both sides and are incomplete distally. The cross-section of the base of the broken transverse processes is ovoid in shape. A partial neural spine is present and widens dorsally.
FIG. 1. Skeletal overview of ROM VP 65884. Abbreviations: fib., fibula; man. phal. II–1, first manual phalanx of digit 2; mt, metatarsal; V, vertebra. Scale bars represent 1 cm.
TABLE 2. Size comparison of select bones of ROM VP 65884 and *Anzu wyliei*.

| ROM VP 65884 | *Anzu wyliei* holotype (CM 78000) | *Anzu wyliei* CM 78001 |
|--------------|-------------------------------|------------------------|
| V-3 (pygal 1), anterior centrum width | 25.6 | 24.8 | – |
| V-3 (pygal 1), anterior centrum height | 13.5 | 12.0 | – |
| V-3 (pygal 1), centrum length | 35.2 | 33.9 | – |
| V-3 (pygal 1), width across transverse processes | 30.0 | 37.2 | – |
| V-2 (prepygal 1), anterior centrum width | 27.9 | 24.3 | – |
| V-2 (prepygal 1), anterior centrum height | 15.4 | 14.3 | – |
| V-2 (prepygal 1), centrum length | 31.4 | 33.2 | – |
| V-1 (prepygal 2), anterior centrum width | 30.2 | 26.1 | – |
| V-1 (prepygal 2), anterior centrum height | 18.1 | 16.0 | – |
| V-1 (prepygal 2), centrum length | 30.9 | 33.8 | – |
| Manus phalanx II-1, width across distal width | 26.2 (L) | 26.4 | – |
| Manus phalanx II-1, width of shaft | 18.3* (L) | 17.4 | – |
| Fibula, maximum diameter of fibula at apex of fibular crest | 33.4 (L) | 31.3 (L) | 32.2 (L) |
| Metatarsal V, length | 104.2+ (L) | – | 116.8 |
| Metatarsal V, anteroposterior depth of proximal end | 17.6 (L) | 16 | 20.7 |

+ length of incomplete element; * taken 40 mm from the distal end.

The middle posterior caudal vertebra (Fig. 1, V-2) has a preserved neural canal and a partial neural spine. The left transverse process is intact and is rectangular in shape, slightly narrowing dorsoventrally as it extends from the centrum. The base of the broken right transverse process has a rectangular cross-section. A large anteroposteriorly elongate pneumatic foramen is present on the lateral surface of the centrum beneath the base of each transverse process. A much smaller, round foramen is also present posterior to the base of each transverse process. The neural spine is incomplete distally. This vertebra appears to be positioned directly anterior to V-3 in this caudal series (i.e. prepygal 1). The most distal caudal (Fig. 1, V-3) appears to be the first ‘pygal’ (Lamanna et al. 2014). The complete centrum is highly elongate and the transverse processes are very weakly developed, longer then they project laterally, and are positioned in the middle of the centrum when viewed anteriorly. There are no chevron facets present on the anteroventral or posteroverentral regions of the centrum. The neural spine is incomplete distally along its entire length. The ventral sulcus of V-3 has a small foramen in the distal third of the centrum. The centrum tapers rapidly in diameter from its anterior face to approximately mid-length, posterior to which it maintains an essentially constant width. Measurements of the preserved caudal vertebrae are in Table 2. Comparisons of vertebral dimensions suggest that ROM VP 65884 is from an individual approximately the same size as *A. wyliei* (Table 2).

Several dorsal ribs are represented by their biramous rib heads, and other fragments of rib shaft. The most complete example has well preserved capitulum and tubercle, which are separated from each other by at least 51 mm. The size and configuration of the rib head suggest that this is from a posterior dorsal vertebra and it has an unusual, probably pathological, circular foramen located just distal to the confluence of the tubercle and capitulum. Numerous gastralia fragments are also preserved. Although most are fragmentary, one gastralia is substantially complete and measures 165 mm as preserved. Its medial end is flattened dorsoventrally into a rectangular plate that contacts the other belly ribs in the series. The lateral ramus is cylindrical and has a distinctive loosely helical shape.

**Appendicular skeleton**

The appendicular skeleton of ROM VP 65884 consists of partially preserved left manual phalanx II-1, left pubis, left fibula, distal tibia fragment, left metatarsals IV and right metatarsal V. Approximately one-quarter to one-third of the distal portion of manual phalanx II-1 is preserved and the transition between the shaft and distal condyles is abrupt (Fig. 1). Both condyles are rounded and symmetrical in lateral and dorsal views and the lateral condyle extends further posteroverventrally than does the medial condyle. Anteroposteriorly elongate collateral ligament pits are located ventral of the midpoint on both condyles; however, the medial pit is shallow while the lateral pit is well developed.

The left pubis is represented by two large and robust proximal fragments (Fig. 1). The proximal of the two pubis fragments is y-shaped in cross-section and a shallow, dorsoventrally elongate fossa is present on the posterior medial surface of the ischial peduncle, as has been described in other caenagnathids (Sullivan et al. 2011). The more distally positioned second fragment is derived from approximately the midshaft of the bone. A thin medial flange on the second fragment indicates the presence of a proximal apron connecting the pubes.

The femur could not be identified in the collection, but a significant portion of the left fibula is preserved, as are fragments of the tibia. The largest preserved piece of fibula is wide dorsally, reflecting the proximally enlarged fibular head, and tapers distally to a small-diameter shaft. The proximally-located iliofibularis tubercle projects anterolaterally (Fig. 1), and is virtually identical in morphology to that of *Anzu wyliei* (Lamanna et al. 2014).
OSTEOHISTOLOGICAL ANALYSIS

Osteohistological description

Tibia. Although only a fragment of the mid-shaft of the tibia could be sampled, it captures a full transect from endosteal to periosteal margin (Fig. 2A). However, since osteohistological description is limited to this transect, variability in bone texture and growth zone thickness/ circumference cannot be completely described. However, the sampled section shows a majority of bone cortex is primary tissue. Vascular pattern/density (sensu Francillon-Vieillot et al. 1990; Padian & Lamm 2013) ranges from reticular in portions of the cortex near the endosteal margin, grading to a mix of predominantly reticular and some plexiform in the inner third to half of the cortex (with a concomitant reduction in vascular density), to primarily plexiform with some laminar canals in the outer half of the cortex, particularly near the periosteal margin, by which point vascular density has noticeably decreased. Bone remodelling in the form of secondary osteons is generally limited (c. 25–30% of cortex) and are more prevalent towards the endosteal margin and in two broad diagonal (relative to the primary growth zones) bands that extend between the endosteal and periosteal margins. The endosteal margin is irregular, indicative of endosteal resorption (Horner et al. 1999). Primary bone is present at the periosteal margin, with no evidence of an outer circumferential layer (OCL)/external fundamental system (EFS) (Cormack & Ham 1987; Horner et al. 1999). Seven lines of arrested growth (LAGs) are visible, with the third (counting from the inner cortex) approximately marking the transition from primarily reticular to primarily plexiform vascular organization. The outermost LAG is located proximate to the periosteal margin, and variably developed (i.e. difficult to consistently trace circumferentially). Growth zone thickness varies, but in general decreases steadily going from the endosteal to periosteal margins. This overall thickness decrease is somewhat punctuated, with greater decreases occurring between the first zone (c. 30% relative thickness) and the second zone (c. 18% relative thickness), and between the third zone (c. 20% relative thickness) and the fourth zone (c. 10% relative thickness, with all subsequent zones being under 10% relative thickness) (Fig. 2A; Table 3).

Fibula. The bone cortex is predominantly primary tissue, although a large region (c. 40% of cortex) of secondary remodelling is present endosteally and across the medial side of the cortex (Fig. 2B). Vascular canal orientation transitions from reticular near the endosteal margin and in regions of the medial side of the cortex, to plexiform throughout most of the cortex, with some sections of laminar vascularization near the periosteal margin on the lateral side. Vascular density broadly decreases from inner to outer cortex, though this difference is more pronounced on the lateral side of the cortex. Eight LAGs are visible, with some towards the external surface on the lateral side difficult to discern. Primary bone is present at the periosteal margin and there is no evidence of an OCL/EFS. Growth zone thickness and vascularity decrease steadily towards the periosteal margin, with a similar punctuated pattern to that observed in the fibula (Table 3).

Manual phalanx. As with the other sampled limb bones, the majority of the bone cortex is primary tissue, with secondary tissue concentrated in two broad zones on the medial and ventrolateral sides of the section (Fig. 3A). Vascular orientation is primarily plexiform in the inner and mid cortex, though varies positionally with localized patches of reticular (inner medial and ventral cortex) and laminar (inner to mid dorsolateral cortex), grading into laminar orientation predominantly towards the periosteum. In isolated regions of the ventrolateral cortex, the vascular orientation
appears subradial, although this may be the result of intersections between elongated secondary osteons and reticular primary tissue. Vascular density appears to relatively decrease from endosteal to periosteal margin as organization increases, with a notable region of lower vascular density throughout the entirety of the dorsolateral cortex. Nine LAGs are visible in the section, though one LAG near the endosteal margin is not visible over much of the cortex due to medullary drift and remodelling, and three closely packed LAGs in the outer cortex probably represent a multiple LAG (triple in this case). As such, the count of discrete LAGs occurring in this section is considered to be seven. Primary bone is present at the periosteal margin, and an OCL/EFS in not developed. LAG spacing decreases consistently from endosteal to periosteal, with a steeper reduction in zone thickness only occurring before the externalmost zones (Table 3).

Gastralia. Secondary remodelling is indicated by secondary osteons present across the entirety of the inner cortex of the bone (Fig. 3B), with secondary osteons more densely clustered closer to the endosteal margin. A small amount of primary bone is visible near the periosteal margin, and may contain a LAG, although it is difficult to determine this for certain. In this region of primary tissue, vascular density is low and lamellar bone is present.

Rib. The tissue of the rib shaft fragment is highly remodelled, with secondary osteons comprising c. 70% of the cortical area. Where primary tissue remains, towards the external bone surface, it is primarily longitudinally vascularized (Fig. 3C). Vascular density is relatively high throughout the section, with some decrease from endosteal to periosteal margin on the medial side of the cortex. There does not appear to be an OCL/EFS, and primary tissue is present at the periosteal margin. An inner circumferential layer (ICL) is developed along almost the entirety of the endosteal margin. Six LAGs occur in the cortex; the precise extent and character of their distribution along the circumference of the cortex is difficult to discern given the high degree of secondary osteon. Nevertheless, where visible, growth zone spacing generally decreases steadily, with a major drop in zone thickness after the third LAG (Table 3).

Osteohistological trait variation

Lines of arrested growth. LAGs were identified in the tibia, pedal phalanx and rib. The gastralia was almost completely remodelled and preserved a probable growth mark in the outer cortex that may represent a LAG. Some variability exists in preserved LAG number between sampled elements, with 8–9 being the highest LAG count preserved. The total range of preserved LAGs preserved in limb elements (tibia, fibula, manual phalanx) varied from 7 to 8 (7, 8, 7, respectively), with the non-limb elements (rib and gastralia) preserving fewer LAGs, 6 and 0–1, respectively. In all sampled elements, growth zone spacing broadly

FIG. 2. Osteohistological thin-section of ROM VP 65884 tibia. A–B, magnified views of growth marks in cortex. C–E, sampling locations for osteocyte lacunar measurements. Scale bars represent: 5 mm (main image); 1 mm (A, B); 50 μm (C–E).
Table 3. Comparison of relative growth zone sizes for each sampled element.

| Element       | Growth zone    | Relative % of cortex |
|---------------|----------------|----------------------|
| Tibia         | Endosteal to LAG 1 | 29.53                |
|               | LAG 1 to LAG 2    | 17.74                |
|               | LAG 2 to LAG 3    | 19.58                |
|               | LAG 3 to LAG 4    | 10.55                |
|               | LAG 4 to LAG 5    | 4.69                 |
|               | LAG 5 to LAG 6    | 5.97                 |
|               | LAG 6 to LAG 7    | 7.36                 |
|               | LAG 7 to periosteal | 4.58                |
| Fibula        | Endosteal to LAG 1 | 31.22                |
|               | LAG 1 to LAG 2    | 11.21                |
|               | LAG 2 to LAG 3    | 13.52                |
|               | LAG 3 to LAG 4    | 10.81                |
|               | LAG 4 to LAG 5    | 13.07                |
|               | LAG 5 to LAG 6    | 5.54                 |
|               | LAG 6 to LAG 7    | 2.54                 |
| Manual Phalanx| Endosteal to LAG 1 | 23.14                |
| Rib           | Endosteal to LAG 1 | 29.67                |
|               | LAG 1 to LAG 2    | 24.28                |
|               | LAG 2 to LAG 3    | 17.39                |
|               | LAG 3 to LAG 4    | 17.53                |
|               | LAG 4 to LAG 5    | 15.69                |
|               | LAG 5 to LAG 6    | 14.89                |
|               | LAG 6 to LAG 7    | 13.06                |
| Rib           | LAG 7 to periosteal | 7.67                 |
|               | LAG 7 to periosteal | 4.87                |

decreases from endosteal to periosteal through the cortex. However, some differences do exist. For the tibia and fibula, the earlier growth zones are the largest, after which there is a considerable reduction in zone spacing, followed again later by an additional major drop in zone spacing, after which thin growth zones are present until the periosteal margin (Fig. 2; Table 3). The relative pattern of growth zone spacing in the phalanx is broadly similar, but with smaller drops in spacing early in the cortex, followed by several relatively similarly spaced zones, and then by a single major pattern shift to tightly spaced zones (Fig. 4A). While remodelling obscures the primary growth record in the gastrium (Fig. 5A), in the rib fragment there is a steady reduction in growth zone thickness going from endosteum to periosteum, with one major zone spacing drop after the third LAG (Fig. 5C).

Osteocyte lacunar density and area. Osteocyte lacunar density and area were calculated in all histologically sampled elements taken from ROM VP 65884 (Table 4), with sampling locations indicated by red squares over cortical regions of sampled elements in Figs 2–5. Given the degree of secondary remodelling present in the gastralia, only the OLD of the outer cortex could be measured. When OLD values are compared between and within elements (Fig. 6), no ontogenetic trend is evident based on cortex location sampled (i.e. along an endosteal–periosteal axis). However, OLD values differ between axial and appendicular elements in the sample. The overall mean OLD values of each limb element are similar in being between 44 000 and 52 000 OL/μm³ (and having a combined limb element mean OLD of 48 233 OL/μm³). The non-limb elements have very different OLD values (100 697 and 69 366 OL/μm³ for rib and gastralia, respectively), when compared to limb elements and when compared to each other. The overall mean OLD for all sampled elements is 62 952 OL/μm³, although given the highly divergent nature of the non-limb values, the limb mean OLD may need to be compared separately from non-limb OLD values. The range of variation in limb OLD values measured here is similar to those seen in other known small-medium coelurosaurs, such as ornithomimids, where an average range of c. 8000 OL/μm³ from highest to lowest lacunar density among sampled limb elements was measured across three individuals (Cullen et al. 2014). These new measurements from Anzu wyliei differ from previously sampled ornithomimids in having higher calculated mean limb element OLD (c. 48 000 OL/μm³ vs c. 36 000 OL/μm³). Although lacunar area varied between measurements, no distinct trend could be seen between elements or through ontogeny (i.e. along endosteal to periosteal transects in a given element) (Fig. 6).

Discussion

Taxonomic comparison

ROM VP 65884 can be identified as a member of Caenagnathidae based on the suite of derived characters identified above (see Table 1). Comparisons with the co-occurring taxon Anzu wyliei are more problematic due to the fragmentary state of ROM VP 65884. However, there are no conflicting morphological characteristics between ROM VP 65884 and Anzu wyliei that preclude assignment of ROM VP 65884 to the Anzu wyliei, though due to the lack of overlapping and diagnostic skeletal elements we here tentatively refer ROM VP 65884 as cf. Anzu wyliei. Also, ROM VP 65884 is clearly from a large caenagnathid, similar to or larger than known specimens of Anzu wyliei in most comparable elements (Table 2). The width of the pubic fossa is 33.5 mm, which is similar to the pubic fossa width of CM 78000 (34.7 mm). Comparisons with other caenagnathid pubic fossae yield smaller measurements. Chirotornotes pergracilis has a pubic fossa width of 15 mm and Ojoraptorsaurus boerei has a pubic fossa width of c. 13.6 mm. The minimum preserved length of the ROM VP 65884 metatarsals are close to the length of
the Caenagnathus collinsi metatarsals (Funston et al. 2015b). The first pygal is comparable to Anzu wyliei in size (Table 2).

Due to the potentially problematic nature of deriving taxonomic associations from relative sizes of skeletal elements, skeletochronological assessments were performed on ROM VP 65884 using data derived from osteohistological sampling. Despite its large size, the osteohistological data, particularly growth mark count, growth zone thicknesses, and lack of an OCL/EFS, indicate that ROM VP 65884 was not yet skeletally mature (Horner et al. 1999; Erickson et al. 2001; Hubner 2012). The lack of ossification between the metatarsals also supports the idea of an immature individual, as noted by Currie & Russell (1988). The presence of extensive secondary remodelling in the rib and gastralia fragments is not necessarily indicative of maturity in the whole organism, and is probably the result of allometry throughout the skeleton and/or localized stresses (Hubner 2012; Cullen et al. 2014). Despite not being a mature individual, ROM VP 65884 possesses some of the largest metatarsals of any North American caenagnathid, quite possibly larger than the larger variations of Caenagnathus collinsi, supporting our assignment of the specimen to Anzu wyliei.

Despite the fact that ROM VP 65884 is larger than the type series of Anzu wyliei, it appears to have been actively growing. If ROM VP 65884 represents Anzu wyliei, we predict that the specimens comprising the type series of A. wyliei (Lamanna et al. 2014) are probably also immature. Unfortunately, in units with multiple named caenagnathid taxa based on fragmentary specimens, such as the Campanian Dinosaur Park Formation of Alberta, size is frequently used to associate isolated elements or partial, but non-overlapping, skeletons to particular taxa (Currie & Russell 1988; Longrich et al. 2013; Funston et al. 2015a; Persons et al. 2015). These results strongly suggest that using size to refer various disassociated elements to particular taxa (e.g. Longrich et al. 2013; Bell et al. 2015; Funston et al. 2015a) is highly problematic, and calls into question the validity of this type of referral in caenagnathids, where relative maturity and osteohistology of the type materials is unknown, particularly in North America. Furthermore, it would not be surprising if some of the previously named taxa in fact represent ontogimorphs (sensu Goodwin & Evans 2016) of others, as has been hypothesized with numerous other taxa from the Upper Cretaceous of North America (e.g. Horner & Goodwin 2009).

FIG. 3. Osteohistological thin-section of ROM VP 65884 fibula. A, magnified view of growth marks in cortex. B–D, sampling locations for osteocyte lacunar measurements. Scale bars represent: 1 mm (main image); 0.5 mm (A); 50 μm (B–D).
Osteohistological variability

Five skeletal elements were sampled histologically (tibia, fibula, manual phalanx, rib and gastralia). Of these, the three limb bones are similar in their microstructure, exhibiting predominately fibrolamellar tissue (*sensu* Ricqlès 1975; Francillon-Vieillot *et al.* 1990), or a woven-parallel bone complex (*sensu* Prondvai *et al.* 2014; Stein & Prondvai 2014). They all exhibit a mixture of reticular, plexiform and laminar patterns of vascular orientation (with plexiform predominating), and relatively high vascular densities (Francillon-Vieillot *et al.* 1990; Padian & Lamm 2013). Generally, the osteohistological features of these limb bones are consistent with those of other medium to large-bodied coelurosaurs (Horner & Padian 2004; Cullen *et al.* 2014). The pattern of growth zone thickness/spacing is relatively consistent between limb elements (early zones of considerable thickness, followed by a drop in thickness, and steady decrease in thickness with each successive zone), and not as noticeably disjunct intra-skeletally as previously observed in limb samples of ornithomimids (Cullen *et al.* 2014). In that case the difference was most apparent when comparing upper hindlimb bones (femur, tibia, fibula) with lower hindlimb/foot bones (metatarsals, pedal phalanges), where steady thickness decrease existed in upper hind limb bones, but lower hind limb bones instead preserved consistent zone thickness throughout the cortex (Cullen *et al.* 2014). It is possible that such growth pattern differences are not as readily recorded in forelimb bones such as the manual phalanges. Given that this specimen has over twice the number of growth marks as those sampled ornithomimids, it is also possible that these intra-skeletal growth zone thickness differences generally disappear over the course of the organism’s age.

![Figure 4](image.png)
ontogeny. Other aspects of allometry may be a factor here as well, as the long slender hands of caenagnathids are characteristic for the group, and unique among most theropods, and thus may possess differences in growth pattern when compared to distal limb elements of other coelurosaurans. This may explain the lack of the first major spacing drop (seen in the tibia and fibula, but not the phalanx), and the presence of the second major spacing drop (seen in tibia, fibula, phalanx and rib). Though growth inferences from LAG spacing can be problematic (Cullen et al. 2014), such distinctive decreases in growth zone spacing pattern, as recorded in multiple sampled elements, may indicate changes in growth pattern during the life history of this animal, and, coupled with the triple-LAG present in the phalanx, may indicate possible periods of resource scarcity (Curtin et al. 2005).

Osteocyte lacunar density was sampled in multiple locations in the bone cortex of the sampled elements of

**FIG. 5.** Osteohistological thin-sections of ROM VP 65884. A, gastraliaum. B–F, rib: C, magnified view of growth marks in cortex; D–F, sampling locations for osteocyte lacunar measurements. Scale bars represent: 1 mm (A); 50 μm (inset in A); 2 mm (B); 0.5 mm (C); 50 μm (D–F).
**Table 4.** Measurements and calculations related to osteocyte lacunar (OL) density and area.

| Sampled element | Fibula | Tibia | Manual phalanx | Rib | Gastralia |
|-----------------|--------|-------|----------------|-----|-----------|
| Sampling location in cortex | Inner | Middle | Outer | Inner | Middle | Outer | Inner | Middle | Outer | Outer |
| **Length (μm)** | 250 | 250 | 250 | 250 | 250 | 250 | 250 | 250 | 250 | 250 |
| **Width (μm)** | 250 | 250 | 250 | 250 | 250 | 250 | 250 | 250 | 250 | 250 |
| **Measured Thickness (μm)** | 34.0 | 32.0 | 32.0 | 32.0 | 32.0 | 32.0 | 32.0 | 32.0 | 32.0 | 32.0 |
| **Thickness x 1.6 refractive index (μm)** | 54.4 | 51.2 | 51.2 | 51.2 | 51.2 | 51.2 | 51.2 | 48.0 | 48.0 | 48.0 |
| **Volume (μm³)** | $3 \times 10^6$ | $3 \times 10^6$ | $3 \times 10^6$ | $3 \times 10^6$ | $3 \times 10^6$ | $3 \times 10^6$ | $3 \times 10^6$ | $3 \times 10^6$ | $3 \times 10^6$ | $3 \times 10^6$ |
| **Volume (mm³)** | 0.0034 | 0.0032 | 0.0032 | 0.0032 | 0.0032 | 0.0032 | 0.0032 | 0.0032 | 0.0032 | 0.0032 |
| **Lacunae count 1a (# OL)** | 154 | 138 | 154 | 125 | 154 | 125 | 148 | 153 | 148 | 306 |
| **Lacunae count 1b (# OL)** | 161 | 149 | 163 | 130 | 157 | 159 | 153 | 158 | 153 | 325 |
| **Lacunae count 1c (# OL)** | 150 | 145 | 167 | 123 | 143 | 161 | 153 | 158 | 153 | 312 |
| **Lacunae count 2a (# OL)** | 170 | 140 | 163 | 149 | 150 | 142 | 150 | 145 | 150 | 305 |
| **Lacunae count 2b (# OL)** | 165 | 147 | 178 | 152 | 161 | 153 | 161 | 153 | 161 | 323 |
| **Lacunae count 2c (# OL)** | 170 | 148 | 169 | 158 | 152 | 145 | 152 | 145 | 152 | 322 |
| **Mean lacunae count (# OL)** | 162 | 145 | 166 | 140 | 152 | 152 | 152 | 152 | 152 | 316 |
| **Osteocyte lacunar density (OL/mm³)** | 47,577 | 45,184 | 50,605 | 51,803 | 43,607 | 45,497 | 47,478 | 50,756 | 51,590 | 105,237 |
| **Element mean lacunar density (OL/mm³)** | 47,789 | 46,969 | 49,941 | 100,697 | 69,366 |
| **Lacunar long-axis radius 1 (μm)** | 9.94 | 8.69 | 8.01 | 8.15 | 8.22 | 9.64 | 9.29 | 8.76 | 8.2 | 8.09 |
| **Lacunar short-axis radius 1 (μm)** | 3.16 | 3.01 | 3.15 | 3.33 | 3.03 | 3.63 | 3.26 | 3.15 | 2.59 | 3.53 |
| **Lacunar long-axis radius 2 (μm)** | 8.56 | 7.84 | 7.26 | 7.79 | 7.86 | 9.51 | 9.07 | 8.36 | 8.7 | 7.98 |
| **Lacunar short-axis radius 2 (μm)** | 2.48 | 3.31 | 3.07 | 2.85 | 2.73 | 3.03 | 3.25 | 3.52 | 3.1 | 3.44 |
| **Lacunar long-axis radius 3 (μm)** | 8.32 | 9.03 | 8.76 | 7.1 | 8.14 | 8.86 | 9.05 | 9.17 | 7.56 | 8.38 |
| **Lacunar short-axis radius 3 (μm)** | 2.73 | 3.14 | 3.25 | 3.44 | 3.01 | 3.07 | 3.52 | 3.37 | 2.86 | 3.37 |
| **Lacunar area (μm²)** | 78 | 84 | 79 | 77 | 74 | 95 | 96 | 92 | 73 | 88 |
| **Element mean lacunar area (μm²)** | 81 | 82 | 87 | 86 | 81 | 94 | 81 | 94 | 94 | 94 |
ROM VP 65884 (Fig. 6), in order to compare it with the lacunar density results of other theropods from Cullen et al. (2014) and Stein & Werner (2013), and to test whether these data support previous interpretations of lacunar density as a proxy for mass-specific growth rate. Osteocyte lacunar density (OLD) values in ROM VP 65884 are consistent with other dinosaur values presented in Stein & Werner (2013), and the OLD of the limb elements of ROM VP 65884 have a similarly high range of variation to the ornithomimids sampled in Cullen et al. (2014). However, the mean OLD values of ROM VP 65884 are higher than those of ornithomimids, moderately so when comparing limb element means, and extremely so when including the rib and gastralia values. While the functional implications of differing osteocyte lacunar densities are not fully resolved, a number of studies on extant mammals suggest that higher OLD may be related to increased bone re-modelling (Reilly 2000; Hernandez et al. 2004) and mechanical loading/stress (Hunter & Agnew 2016). The higher OLD recorded in the rib and gastralia of ROM VP 65884 may be consistent with the former interpretation, given the higher degree of remodelling present in these elements relative to the sampled limb bones, though regarding the latter interpretation

**FIG. 6.** Intra-skeletal variation in osteocyte lacunar density (A) and area (B) in ROM VP 65884.
there is no apparent reason why these non-weight-bearing elements would be receiving greater mechanical loading/stress when compared to limb elements. The lack of ontogenetic pattern in OLD when measuring across transects of the sampled bones also provides some support for the hypothesis that OLD is related to factors related to remodelling rates, and provides additional evidence against the hypothesis that OLD is a reliable proxy for mass-specific growth rate (Stein & Werner 2013; Cullen et al. 2014). Future intra-skeletal sampling in multiple locations longitudinally through a bone, rather than in multiple locations of the cortex at the mid-section or minimum circumference of a bone, may be useful in further testing OLD differences related to mechanical loadings/stress.

Similarly, osteocyte lacunar area (OLA) was sampled from the same locations in ROM VP 65884 as OLD measurements were taken, then calculated based on methods from previous investigations of lacunar size in dinosaurs (Organ et al. 2007, 2009; Montanari et al. 2011), with the purpose of assessing proposed relationships between lacunar size and various organismal features, and more directly to compare the measures and variation recorded in Anzu wyliei to those of other dinosaurs and tetrapods. Lacunar area recorded for ROM VP 65884 (Fig. 6) is broadly consistent with values recorded from related coelurosauras (e.g. tyrannosaurs and ornithomimids) (Rensberger & Martinez 2015). No ontogenetic trend was observed in lacunar area (e.g. in terms of consistent increase or decrease along an endosteal-periosteal transect), suggesting that at least in this taxon we have no evidence for a strong link between OLA and growth rate. While lacunar size varied between sampled elements, previous studies have found that similar levels of variability did not strongly impact resultant genome size estimations (Montanari et al. 2011). Nevertheless, some caution may be warranted with measuring lacunar size, as D’Emic & Benson (2013) noted that the method for calculating lacunar volume from 2-dimensional images of thin-sections may inaccurately capture actual lacunar shape, and so may in many situations underestimate the resultant volume. While this should not particularly impact measurements of lacunar area, it is worth consideration for future studies of lacunar density, area and volume.

CONCLUSION

Based on the suite of available morphological characters, element size and skeletochronological assessment, ROM VP 65884 is assigned to the caenagnathid Anzu wyliei. The lack of osteohistological indicators of skeletal maturity, relatively high vascularity, mostly disorganized vascular orientation, and growth zone thicknesses, indicate that this specimen was still actively growing and would probably have reached a larger overall body size than it was at death. Detailed osteocyte lacunar density/size measurements obtained from this specimen add to the growing body of evidence that lacunar density was not closely tied to mass-specific growth rates, but instead may be related to multiple others factors, including bone remodelling rate. Overall, our results suggest that caution be taken when using size as a primary cause for referral of disassociated elements to specific or new taxa, and stress the importance of performing osteohistological analyses and ontogenetic assessments on Upper Cretaceous dinosaur specimens whenever possible.

Acknowledgements. We thank D. Larson, K. Chiba, and M. Wosik of the Evans lab for laboratory assistance, discussion, and providing comments on early manuscript drafts. Additional thanks to Shino Sugimoto and Ian Morrison for specimen preparation. Scott Hartman is thanked for permitting the use of the Anzu silhouette image. We thank Sally Thomas and two anonymous referees for their helpful comments on an earlier draft of this paper.

DATA ARCHIVING STATEMENT

Data for this study (e.g. character argumentations, phylogenetic analyses, additional image plates of described skeletal elements, high resolution thin-section images) are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.v94m6q6s

Editor. Roger Benson

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