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A caenagnathid oviraptorosaur metatarsal from the Mesaverde Formation (Campanian) of Wyoming, USA

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Abstract: A well-preserved left theropod metatarsal I from the Campanian Mesaverde Formation of Wyoming is described and identified as belonging to a caenagnathid, representing the first occurrence of this clade from the formation. The specimen is unique in being relatively small, but featuring a suite of characters (triangular shaft, relatively minimal constriction between the shaft and the distal condyle, spherical distal condyle) that are seen in larger-bodied caenagnathids such as *Anzu wyliei* and "*Macrophalangia canadensis*". This suggests that the previously-observed differences in metatarsal I morphology between small and large caenagnathids are not solely the result of allometry, but may represent phylogenetically informative variation. This new specimen lends some support to the hypothesis that "*Macrophalangia canadensis*" does not represent a large *Chirostenotes pergracilis*. Furthermore, the specimen is important in establishing the presence of caenagnathids within the Mesaverde Formation fauna, in which theropods are rare.

INTRODUCTION

Caenagnathidae is a group of edentulous theropods that is nested within the clade Oviraptorosauria, and their fossil remains have been reported from Cretaceous strata of western North America and Asia (e.g., Sullivan et al., 2011; Longrich et al. 2013; Lamanna et al. 2014; Funston and Currie 2016; Funston 2020). Derived oviraptorosaurs, including caenagnathids, are unique among theropods in the possession of beaked jaws, prominent cranial crests, feathered wings and pygostyle-like terminal caudal vertebrae, indicating a somewhat bird-like paleobiology (e.g., Longrich et al. 2013; Lamanna et al. 2014; Funston and Currie 2016). While several caenagnathids like *Elmisaurus* or *Gigantoraptor* have been found in Asia, most known caenagnathids are from North America, including *Anzu*, *Apatoraptor*, *Caenagnathus*, *Chirostenotes*, and *Citipes* (e.g., Lamanna et al. 2014; Yu et al. 2018; Funston 2020). This pattern possibly reflects marginalization of caenagnathids in Asia by other oviraptorosaur groups (Funston et al. 2021).

Significant new discoveries made in recent years have substantially increased our knowledge of North American caenagnathids, especially in terms of their anatomy (e.g., Funston et al. 2015, 2016), ecology (e.g., Funston and Currie 2014, 2018; Rhodes et al. 2020) and taxonomy (e.g., Lamanna et al. 2014; Funston et al. 2015; Funston 2020). However, much remains unresolved about the paleogeographic distribution and especially the taxonomy of these dinosaurs, partly because of their fragmentary fossil record (Lamanna et al. 2014) and the fact that the vast majority of their fossils have been reported from the northern part of the continent (Longrich et al. 2013; Funston 2020). A good example of this is the case of "*Macrophalangia canadensis*", a taxon erected based upon an isolated pes (Sternberg 1932; Currie and Russell 1988). Initially thought to be an ornithomimid (Sternberg 1932), this taxon was synonymized by Currie and Russell (1988) with *Chirostenotes pergracilis*, a conclusion followed by many subsequent studies (e.g., Sues 1997; Currie 2005; Funston et al. 2015; Funston and Currie 2020; Funston 2020). However, Longrich et al. (2013) suggested "*Macrophalangia canadensis*" may instead have been conspecific with *Caenagnathus collinsi*, mainly because of its large size and robustness compared to other specimens (e.g., TMP 1979.020.0001) of *Chirostenotes pergracilis*. While Lamanna et al. (2014) agreed with Longrich et al. (2013) that "*Macrophalangia canadensis*" could be distinct from *Chirostenotes*, these authors hesitated to refer "*Macrophalangia canadensis*" to either *Caenagnathus* or *Chirostenotes* due to the non-overlapping nature of the holotypes of these taxa. Funston et al. (2015) considered the holotype of "*Macrophalangia canadensis*" identical to a distal portion of the hindlimb of *Chirostenotes pergracilis*

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in all respects other than the size, and regarded the claim of Longrich et al. (2013) as doubtful. However, upon reexamination of the material, Funston (2020) recognized additional differences between the "*Macrophalangia canadensis*" holotype and TMP 1979.020.0001, such as the shapes of the shafts of metatarsals I (triangular in medial view vs. diamond-shaped in medial view) and V (straight vs. curved), and the length of pedal phalanx I-1 (longer than vs. equal in length to MT I). Nonetheless, he retained "*Macrophalangia canadensis*" as a junior synonym of *Chirostenotes pergracilis*, partly because little is known about ontogenetic changes in pedal elements of caenagnathids. Indeed, the robustness of the metatarsals in other coelurosaurian theropods has a demonstrated relationship with size and ontogeny, and only limited taxonomic significance (e.g., Holtz 1995; Currie 2003). However, it cannot be denied that additional fossils need to be recovered and described to determine whether this is the case for caenagnathids as well.

The Campanian Mesaverde Formation exposed in the Wind River and Bighorn basins of Wyoming has produced numerous vertebrate microfossils throughout forty-five localities (Demar and Breithaupt 2006, 2008). Two distinct paleocommunities are present in the Wind River and Bighorn basins, the former containing a continental fauna, and the latter a shallow marine one (Demar and Breithaupt 2006, 2008). The most abundant vertebrate fossils from the Mesaverde Formation exposed in the Wind River Basin are those of mammals and freshwater vertebrates (Demar and Breithaupt 2008), which have been the subject of many faunal studies (Lillegraven and McKenna 1986; Case 1987). Dinosaur fossils are much less common compared to these taxa, often very fragmentary, and typically not identifiable beyond the "family" level. While Demar and Breithaupt (2006) referred some theropod teeth to *Daspletosaurus* and *Saurornitholestes*, the referral of small, unserrated tyrannosaurid premaxillary teeth to *Daspletosaurus* is no longer justified (Yun 2021a), and the teeth of several other dromaeosaurids (e.g., *Atrociraptor*) are virtually indistinguishable from those of *Saurornitholestes* (Currie and Varricchio 2004). Consequently, the generic assignments made by Demar and Breithaupt (2006) are doubtful. Nevertheless, any additional dinosaurian material from this locality would be significant in further characterizing the scarcely known dinosaurian fauna of the Mesaverde Formation.

Here we describe an isolated theropod metatarsal I from the Mesaverde Formation exposed in the Wind River Basin of Wyoming, which we identify as that of a caenagnathid. In addition to being the first caenagnathid bone from this formation, the specimen is unique in being slightly smaller than the only known metatarsal I definitely referable to *Chirostenotes* (part of TMP 1979.020.0001), while also exhibiting characters that are more reminiscent of larger caenagnathids like *Anzu* or "*Macrophalangia*" (Funston 2020). This offers an opportunity to test the hypothesis that reported differences in metatarsal I morphology between "*Macrophalangia*" and *Chirostenotes* are merely allometric in nature.

Institutional Abbreviations: AMNH, American Museum of Natural History, New York, USA; BDM, Badlands Dinosaur Museum, North Dakota, USA; CM, Carnegie Museum of Natural History, Pennsylvania, USA; CMN, Canadian Museum of Nature, Ontario, Canada; MPC-D, Institute of Paleontology, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; NMMNH, New Mexico Museum of Natural History and Science, New Mexico, USA; ROM, Royal Ontario Museum, Toronto, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Alberta, Canada; UW, Scientific Collections at The University of Wyoming, Wyoming, USA; YPM, Yale Peabody Museum, New Haven, USA.

Material and Methods: The specimen, UW 44439 (Figs. 1, 2), is a nearly complete left metatarsal I. Unfortunately, due to travel restrictions imposed during the COVID-19 pandemic, this study had to be conducted using a high-quality cast and scan of the original specimen, which is housed at the Collection of Fossil Vertebrates in the Department of Geology and Geophysics of the University of Wyoming. The cast was made from a 3D scan using a David Structured Light Scanner SLS-3, which was generated by museum collection manager Dr. Laura A. Vietti. Figure 1 was generated from images provided by Dr. Vietti, taken with a Keyence VHX-5000 Digitizing station that automatically adjusted overexposed areas in the photograph (e.g., the specimen label). Anatomical comparisons with other theropods were made through an extensive review of the literature, prior direct observations of numerous specimens made by GFF, 3D images, and photographs supplied by other researchers. The anatomical nomenclature used in this study follows Carr (2005), Fowler et al. (2011), Hattori (2016) and Funston (2020).

Geological Setting: UW 44439 was collected at Fales Rocks Locality (UW V-81006), which is stratigraphically located within the lower part of the unnamed middle member of the Mesaverde Formation of the southeastern part of the Wind River Basin, Wyoming, USA (Demar and Breithaupt 2006). This member is composed of lenticular sandstones, yellow-gray claystones and organic-rich shales that are interpreted as sediments mainly derived from the rising of the Rocky Mountains during the middle Campanian (Demar and Breithaupt 2006). The sedimentology of Fales Rocks Locality indicates that this member originated in a meander belt depositional system with point-bar and floodplain deposits (Demar and Breithaupt

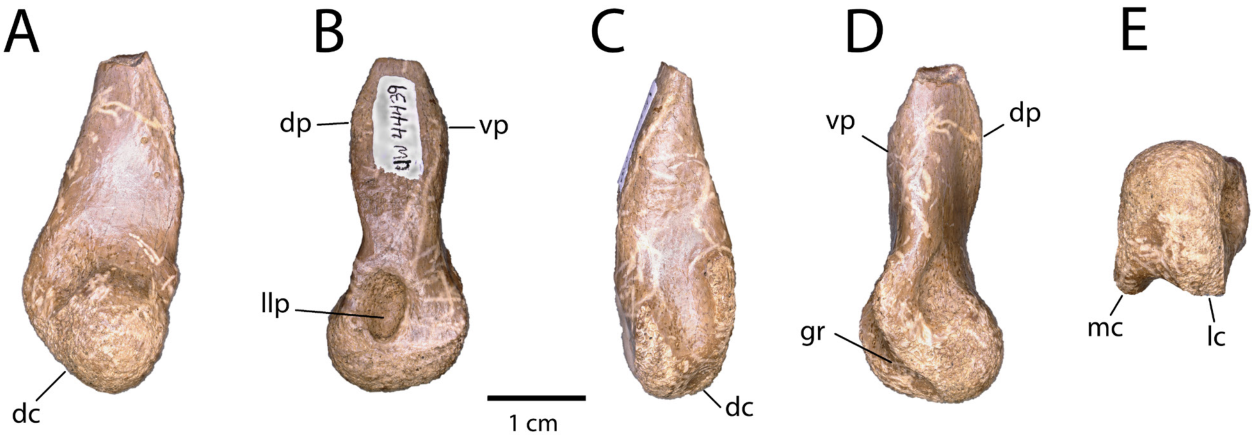

Figure 1. UW 44439, a left metatarsal I of Caenagnathidae indet., in A, dorsal view; B, lateral view; C, ventral view; D, medial view; E, distal view. Abbreviations: dc, distal condyle; dp, dorsal prominence; gr, groove; lc, lateral hemicondyle; llp, lateral ligament pit; mc, medial hemicondyle; vp, ventral prominence. Images are courtesy of Collection of Fossil Vertebrates, Department of Geology and Geophysics of the University of Wyoming.

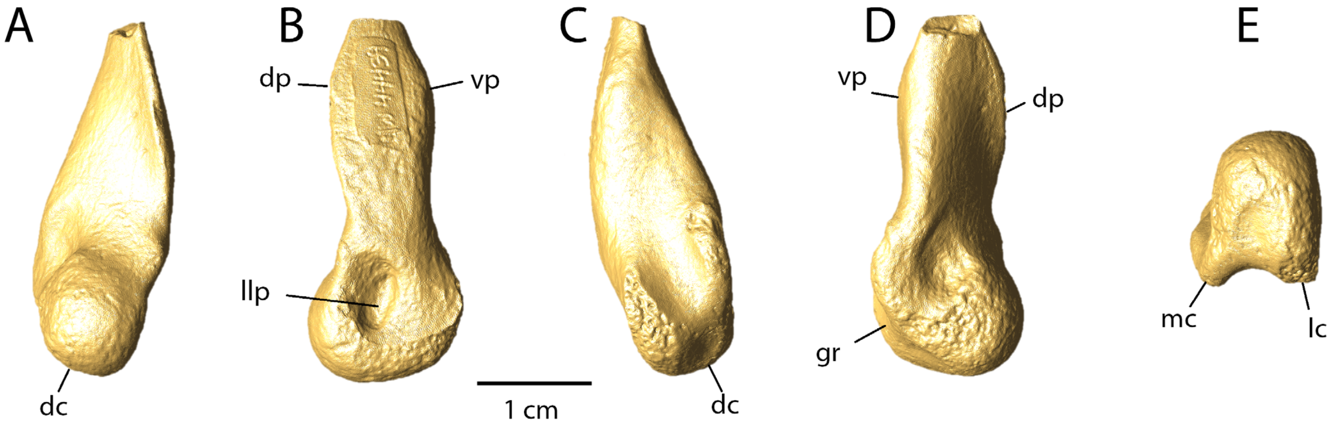

Figure 2. 3D model of UW 44439, a left metatarsal I of Caenagnathidae indet., in A, dorsal view; B, lateral view; C, ventral view; D, medial view; E, distal view. Abbreviations: dc, distal condyle; dp, dorsal prominence; gr, groove; lc, lateral hemicondyle; llp, lateral ligament pit; mc, medial hemicondyle; vp, ventral prominence. The model is courtesy of Collection of Fossil Vertebrates, Department of Geology and Geophysics of the University of Wyoming.

2006). Fossils found within this site include freshwater fishes, amphibians, squamates, turtles, champsosaurs, crocodilians, pterosaurs and dinosaurs, and the presence of crocodilians and trionychid turtles indicate a subtropical climate and an environment reminiscent of the modern lowlands of coastal Alabama, Florida, Georgia, Louisiana and Mississippi (Demar and Breithaupt 2006, 2008). The Wallace Creek Tongue of the Cody Shale, which directly underlies the unnamed middle member of the Mesaverde Formation, is probably correlative with the *Baculites gregoryensis* ammonite zone (Demar and Breithaupt 2006). According to Fowler (2017), the age of the base of this zone is estimated to be either 78.34 Ma or 77.59 Ma, so it is reasonable to assume that the strata exposed at the Fales Rocks Locality are slightly younger (Demar and Breithaupt 2006). In summary, the age of Fales Rocks Locality is probably middle to late Campanian.

SYSTEMATIC PALAEONTOLOGY

MANIRAPTORA Gauthier, 1986
PENNARAPTORA Foth et al., 2014
OVIRAPTOROSAURIA Barsbold, 1976
CAENAGNATHIDAE Sternberg, 1940
CAENAGNATHIDAE indet.

Material: UW 44439, a nearly complete left metatarsal I lacking its proximal-most portion (Figs. 1, 2).

Horizon and Age: Upper Cretaceous (Campanian) Mesaverde Formation, Wyoming, USA.

Comparative Description: UW 44439 is a nearly complete left metatarsal I, missing only the proximal-most part of the bone and with some slightly abraded areas on the distal articulation surface. The specimen measures 28 mm proximodistally, 11 mm dorsoventrally, and 9 mm mediolaterally at the distal articulation surface. Scaling from the holotype of *Anzu wyliei* (CM 78000) based on the distal width of the corresponding bone, the original proximodistal length of UW 44439 is estimated at approximately 32.7 mm.

The short shaft of the metatarsal is nearly straight, but the distal end is kinked medially like in other caenagnathids, including *Microvenator celer* (AMNH 3041), *Anzu* (BDM uncatalogued specimen, CM 78000), *Chirostenotes* and CMN 8538 ("*Macrophalangia*", Currie and Russell 1988: fig. 13). The shaft is transversely broad immediately proximal to the distal condyle (10 mm), but tapers proximally, resulting in a thick teardrop-shape in dorsal view that very closely resembles the corresponding elements of *Anzu* (BDM uncatalogued specimen) and CMN 8538 (Currie and Russell 1988: fig. 13). This contrasts with *Chirostenotes* (Currie and Russell 1988: fig. 13) and *Microvenator* (AMNH 3041), in which metatarsal I is more rod-like because the lateral margin of the constricted part of the metatarsal shaft, separating the articulation surface for metatarsal II from the distal condyle, is elongated (Fig. 3G–J). In *Anzu* (BDM uncatalogued specimen) and UW 44439, this margin is relatively short. The medial margin of the metatarsal in UW44439 is relatively straight, as in other caenagnathids such as *Microvenator* (AMNH 3041), *Anzu* (BDM uncatalogued specimen, CM 78000), *Chirostenotes* (TMP 1979.020.0001), and CMN 8538 (Currie and Russell 1988: fig. 13). This contributes to the thickened teardrop shape of the metatarsal in dorsal view. In contrast, the medial margin of the metatarsal in oviraptorids (e.g., *Citipati* and *Oksoko*) is concave, making the overall shape of the shaft appear more transversely compressed (Hattori 2016: fig. 6; Funston et al. 2020a).

The shaft of UW 44439 tapers in dorsoventral thickness towards its proximal end, resulting in a triangular shape in lateral or medial view, which is similar to *Anzu* (BDM uncatalogued specimen; Fig. 3K, L), *Microvenator* (AMNH 3041; Fig. 3G, J) and CMN 8538 (Funston 2020; Fig. 3A, D). In contrast, the shaft is distinctly diamond-shaped in medial and lateral views in *Chirostenotes* (Funston 2020; Fig. 3E, F), as the result of enlarged flanges (the dorsal and ventral prominences of Hattori 2016) extending from the dorsal and ventral margins of the shaft, and a more constricted "neck" distal to these features. In UW 44439, the ventral surface of the shaft is convex, tapering dorsoventrally proximal to a slight ventral prominence much smaller than that of *Chirostenotes*.

A small tubercle is present on the dorsolateral edge of the bone between the articulation surface for metatarsal II and the distal condyle. Proximal to this tubercle there is a pronounced ridge that extends along the craniolateral margin, which demarcates the teardrop-shaped articulation surface for metatarsal II. In *Anzu* (BDM uncatalogued specimen) this ridge is thicker and more rugose. The articulation surface for metatarsal II on the lateral surface of the bone is slightly convex and teardrop-shaped. This surface is separated from the distal condyle by a constricted "neck" that is most obvious in lateral or medial view. The degree of constriction appears to be similar to that of *Anzu* (BDM uncatalogued specimen) but slightly less than that of *Chirostenotes* (Currie and Russell 1988: fig. 13; Funston 2020). Such constriction is minimal in *Microvenator* (AMNH 3041) and CMN 8538 (Currie and Russell 1988: fig. 13; Fig. 3A–D, G–J).

The lateral collateral ligament pit is deep, kidney-shaped and dorsally positioned, similar to *Chirostenotes* (Currie and Russell 1988: fig. 13; Funston 2020: fig. 12) and *Anzu* (BDM uncatalogued specimen). In CMN 8538, the pit is more proximally positioned, situated within the slightly constricted "neck" between the condyle and the shaft (Currie and Russell 1988: fig. 13). In *Microvenator* (AMNH 3041), the pit is rounded and much larger (Fig. 3G). The medial collateral ligament pit is less clearly defined, and manifests as a deep, proximally-tapering depression without distinct borders, but is more circular than the lateral pit. In *Anzu* (BDM uncatalogued specimen), *Chirostenotes* (TMP 1979.020.0001), and CMN 8538, a distinct, small medial collateral ligament pit is present and positioned ventrally. Neither a pit nor a depression is present in *Microvenator* (AMNH 3041).

The distal articulation surface (= distal condyle) is more or less spherical, as is the case in CMN 8538 (Currie and Russell 1988: fig. 13) and *Anzu* (BDM uncatalogued specimen) but there is a ventral sulcus that separates the condyle into two small hemicondyles, which is most apparent in distal view. A very shallow groove extends from this sulcus proximally, but this is not as well-developed as the ginglymoid condition of *Chirostenotes* (Funston 2020) and some other theropods like dromaeosaurids (Fowler et al. 2011; Hattori 2016). The lateral hemicondyle is mediolaterally broader, and extends farther distally, than the medial one. These condyles are oriented sub-vertically, like *Anzu* (BDM uncatalogued specimen) but differing from *Microvenator* (AMNH 3041), which has dorsoventrally elongated hemicondyles that strongly flare medially and laterally. The lateral margin of the distal articulation surface is nearly straight, but the medial one is slightly concave, like *Anzu* (BDM uncatalogued specimen), *Chirostenotes* (TMP 1979.020.0001), and CMN 8538 (Currie and Russell 1988: fig. 13). In

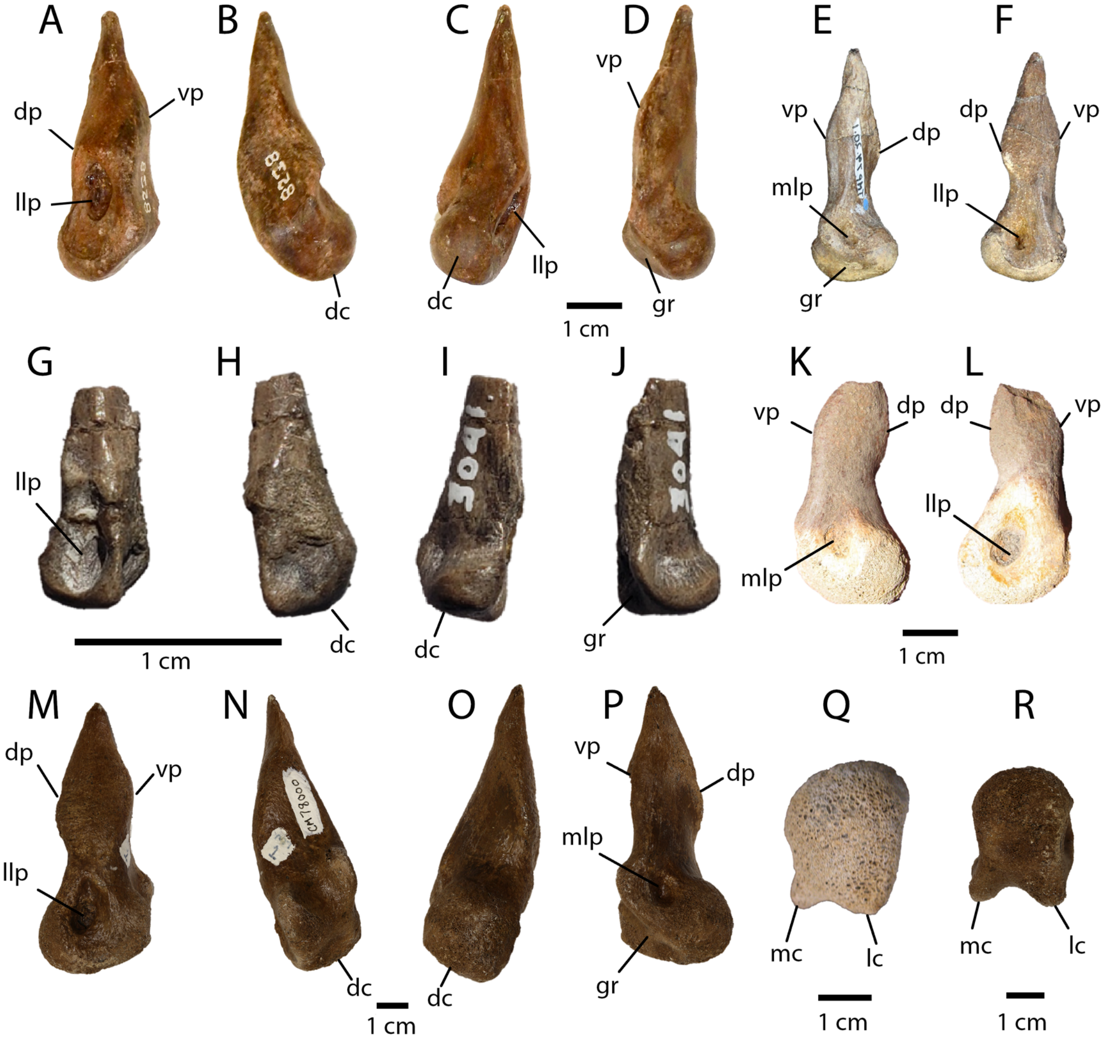

Figure 3. Comparison of metatarsal I morphology among caenagnathid theropods from North America. A–D, CMN 8538 "*Macrophalangia canadensis*" (mirrored) in A, lateral; B, ventral; C , dorsal; and D, medial views. E–F, TMP 1979.020.0001 *Chirostenotes pergracilis* (mirrored, from Funston, 2020), in E, medial and F, lateral views. G–J, AMNH 3041 *Microvenator celer* in G, lateral; H, ventral; I, dorsal; and J, medial views. K, L, Q, BDM uncatalogued specimen *Anzu wyliei* in K, medial; L, lateral and Q, distal views. M–P, R, CM 78000 *Anzu wyliei* in M, lateral; N, ventral; O, dorsal; P, medial and R, distal views. Abbreviations: dc, distal condyle; dp, dorsal prominence; gr, groove; lc, lateral hemicondyle; llp, lateral ligament pit; mc, medial hemicondyle; mlp, medial ligament pit; vp, ventral prominence. G-J are courtesy of the Division of Paleontology, American Museum of Natural History. K, L and Q, courtesy of Badlands Dinosaur Museum. M-P and R, courtesy of Section of Vertebrate Paleontology, Carnegie Museum of Natural History.

Microvenator (AMNH 3041), both margins are concave. In dorsal view, the distal margin of the metatarsal of UW 44439 is semicircular (Figs. 1, 2), rather than sinuous as in *Chirostenotes* (Currie and Russell 1988: fig. 13), or straight as in in *Microvenator* (AMNH 3041; Fig. 3I).

DISCUSSION

Taxonomic Referral: The Campanian-Maastrichtian strata of Laurasia have yielded numerous theropods that possibly retained a first pedal digit, including at least some members of each of the following groups: Alvarezsauridae, Avialae, Dromaeosauridae, Ornithomimosauria, Oviraptorosauria, Therizinosauria, Troodontidae, and Tyrannosauridae. However, UW 44439 differs morphologically from the first metatarsals of most of these taxa, so its potential identity can be narrowed down.

The first metatarsals of alvarezsaurs are distinct from UW 44439 in having a nearly straight, rod-like shaft and lacking a constricted "neck" (e.g., Perle et al. 1994: fig. 18c; Turner et al. 2009; Nesbitt et al. 2011: fig. 3b). Likewise, the rod-like shafts of dromaeosaurid first metatarsals differ starkly from UW 44439. UW 44439 also lacks the strongly ginglymoid distal articulation surface seen in dromaeosaurids, which is formed by a prominent groove separating medial and lateral hemicondyles (e.g., Fowler et al. 2011; Hattori 2016). Derived ornithomimids, which dominated Campanian-Maastrichtian ornithomimosaur faunas in western North America (e.g., Hattori 2016), lacked a hallux with only a few possible exceptions (Longrich 2008; Serrano-Brañas et al. 2020). All known first metatarsals in basal ornithomimosaurs (e.g., *Beishanlong*, *Garudimimus*) have a mediolaterally constricted shaft, and a pronounced concavity at the distal end formed by a sulcus separating the two distal hemicondyles, which nonetheless is less well-developed than in the ginglymoid condyles of dromaeosaurids. Furthermore, they lack a constricted "neck" between the distal condyle and the shaft (Kobayashi and Barsbold 2005: fig. 16; Makovicky et al. 2010: fig. 3). The presence of therizinosaurs in the Campanian-Maastrichtian of western North America is no longer supported (e.g., Russell and Manabe 2002; Cullen et al. 2021) but UW 44439 nevertheless differs from metatarsal I of therizinosaurs in being proximodistally short with a tapered proximal part, which is the typical theropod condition (Hattori 2016). The first metatarsal of therizinosaurs tends to be much more proximodistally elongated, and the midshaft and proximal part are mediolaterally "pinched" but dorsoventrally broad (e.g., Zhang et al. 2001; Hedrick et al. 2015). Like UW 44439, metatarsal I of troodontids and basal avialans has a ball-like distal articulation surface (e.g., Chiappe 1992; Mayr et al. 2007; Fowler et al. 2011; Zhang et al. 2013; Hattori 2016). However, first metatarsals of these clades differ from UW 44439 in possessing extremely dorsoventrally flattened shafts ("J"-shaped sensu Chiappe 1992) and mediolaterally sloping, nearly straight distal margins in dorsal view (e.g., Chiappe 1992; Fowler et al. 2011: fig. 9; Lefèvre et al., 2014; Hattori, 2016: fig. 10). UW 44439 can be distinguished from tyrannosauroid first metatarsals by the orientation of the articular surface for metatarsal II. This surface faces directly laterally in UW 44439, such that it is perpendicular to the flexor–extensor plane of the distal condyle. In contrast, in tyrannosauroids this surface is inclined towards the flexor aspect of the metatarsal, giving the articular facet a lateroventral orientation (Hattori 2016). Additionally, tyrannosauroids typically have a pronounced, triangular flange on the dorsolateral surface of metatarsal I (Carr 2005; Hattori 2016: fig. 4) and this feature is absent in UW 44439. Lastly, the distal articulation surface of metatarsal I of Tyrannosauroidea is sub-triangular and slightly ginglymoid (Hattori, 2016: fig. 4), which differs strikingly from the spherical condyle in UW 44439. As the aforementioned tyrannosauroid metatarsal I features are present even in small juvenile individuals of this clade (NMMNH P-25049, TMP 2000.054.0001), UW 44439 is unlikely to pertain to a juvenile tyrannosauroid.

Although the metatarsal I of UW 44439 can be clearly distinguished from most theropods, several features allow for its referral to Oviraptorosauria, and more specifically Caenagnathidae. Among oviraptorosaurs, avimimids lose the first metatarsal (Vickers-Rich et al. 2002; Osmólska et al. 2004), but all other clades, including caudipterygids, oviraptorids, and caenagnathids, are characterized by much larger dorsal and ventral prominences of the metatarsal I shaft than other theropods, which result in a diamond- or teardrop-shaped outline in medial or lateral view (Makovicky and Sues 1998; Zhou and Wang 2000; Balanoff and Norell 2012; Hattori 2016; Norell et al. 2018; Funston 2020). These dorsal and ventral prominences are situated near the midpoint of the metatarsal, and they comprise tab- or flange-like excursions of the dorsal and ventral margins of the metatarsal, distal to which the metatarsal is constricted into a "neck". In caudipterygids, the dorsal and ventral prominences are roughly equal in size and grade smoothly into the proximal end of the shaft, making the proximal end of the metatarsal triangular in medial view (Zhou and Wang 2000). Oviraptorids and caenagnathids diverge in morphology. In oviraptorids, the ventral prominence becomes even more pronounced, forming a tab-like process (Hattori 2016; Funston et al. 2018). The dorsal prominence either retains the plesiomorphic shape (e.g., MPC-D 100/42, the "Zamyn Khondt Oviraptorid", *Khaan mckennai*), becomes reduced (e.g., *Oksoko avarsan*, *Rinchenia mongoliensis*), or hypertrophies into a second tab-like process (e.g., *Citipati osmolskae*, *Heyuannia yanshini*) (Balanoff and Norell 2012; Hattori 2016; Funston et al. 2018, 2020a). Caenagnathids, in contrast, tend to have reduced dorsal and ventral prominences compared to other oviraptorosaurs, although the prominences remain larger than in other theropods. In *Chirostenotes pergracilis* (TMP 1979.020.0001), the dorsal prominence is enlarged compared to other caenagnathids (Fig. 3E, F; Currie and Russell 1988; Funston 2020), but not to the degree seen in some oviraptorids (e.g., *Citipati osmolskae*), and in the basal oviraptorosaurs *Caudipteryx dongi* (Zhou and Wang 2000) and *Similicaudipteryx* (He et al. 2008). These large prominences in *Chirostenotes pergracilis* augment the appearance of the constricted "neck" of metatarsal I (Fig. 3E, F). In other caenagnathids, including *Anzu wyliei* and CMN 8538 ("*Macrophalangia*"), metatarsal I has dorsal and ventral prominences that manifest as rugose ridges, and thus appears to have a less constricted "neck" (Fig. 3A–D, M–P). These caenagnathids also have a less transversely constricted shaft, resulting in a teardrop-shaped outline in dorsal or ventral view, as well as in medial or lateral view (Fig. 3A–D, M–P), whereas in other theropods, the shaft of metatarsal I is rod-like and transversely constricted (Hattori 2016).

UW 44439 exhibits the enlarged dorsal and ventral prominences characteristic of oviraptorosaurs (Figs. 1, 2), supporting its referral to this clade. Furthermore, the proportional sizes of these prominences compared to the rest of the metatarsal are congruent with the condition in caenagnathids. Within Caenagnathidae, UW 44439 is particularly similar to *Anzu wyliei* and CMN 8538, and contrasts in several features with *Chirostenotes pergracilis*. In UW 44439, the metatarsal is teardrop-shaped in extensor (dorsal) view, owing to the proximally-tapering shaft and a rounded distal condyle (Figs. 1, 2). This morphology is nearly identical to those of *Anzu* (BDM uncatalogued specimen, CM 78000) and CMN 8538 ("*Macrophalangia*"; Currie and Russell 1988: fig. 13). However, the distal condyle of TMP 1979.020.0001 is less spherical, making the outline of the metatarsal I more angular. Furthermore, the distal articulation surface of UW 44439 is nearly spherical in dorsal view and this is similar to CMN 8538 and *Anzu*, but contrasts with most other theropods (Currie and Russell 1988: fig. 13; Hattori 2016; Funston 2020).

As UW 44439 shows a combination of features that distinguish it from other contemporaneous theropods and ally it with oviraptorosaurs, particularly caenagnathids, referring it to Caenagnathidae indet. is the most parsimonious option. Within Caenagnathidae, it shares affinities with *Anzu wyliei* and the enigmatic CMN 8538 ("*Macrophalangia*"). However, because the taxonomy of caenagnathids remains problematic, it is unclear how diagnostic metatarsal I is within the clade. In any case, UW 44439 cannot be referred with confidence to a particular genus.

Metatarsal I Variation in Caenagnathids: UW 44439 highlights several characters that appear to vary interspecifically within Caenagnathidae. In particular, the morphology of the dorsal and ventral prominences, the transverse thickness of the shaft, and the presence of a ginglymoid distal condyle all appear to be significant sources of variation. Although very few examples of caenagnathid first metatarsals exist, the metatarsal I of TMP 1979.020.0001 (*Chirostenotes pergracilis*) appears to be unique in its plesiomorphic retention of enlarged dorsal and ventral prominences and a thick shaft (Funston 2020; Fig. 3E, F). Additionally, the distal condyle of the metatarsal I of TMP 1979.020.0001 is strongly ginglymoid compared to other caenagnathids (Funston 2020). CMN 8538, the holotype of "*Macrophalangia*" (Parks 1932), which is usually synonymized with *Chirostenotes pergracilis* (Currie and Russell 1988; Sues 1997; Varricchio 2001; Funston 2020), also preserves a metatarsal I. The absence in CMN 8538 of the distinct metatarsal I characters of TMP 1979.020.0001 (Fig. 3A–D) raises the question of whether the synonymy of these two taxa is appropriate. Longrich et al. (2013) appeared to refer CMN 8538 (erroneously labelled CMN 2367 in their study) to *Caenagnathus collinsi* on the basis of size and robustness, but preferred to retain the genus *Caenagnathus* ("*Macrophalangia*" would have priority). Funston (2020) also discussed the possibility that CMN 8538 represented *Caenagnathus collinsi*, highlighting features of the first pedal digit and fifth metatarsal, but retained it within *Chirostenotes pergracilis* because ontogenetic change in body size is poorly understood in these taxa. Thus, it was unclear whether the differences in morphology were simply the result of allometry, or if they indicated a taxonomic distinction between these specimens. However, UW 44439 shows that the distinct features of metatarsal I in CMN 8538 are present in an individual of similar size to TMP 1979.020.0001, eliminating allometry as the sole explanation for the differences in morphology between these specimens. Nonetheless, it is unclear whether the variation in metatarsal I could be attributed to relative maturity, as the ontogenetic stages of CMN 8538 and TMP 1979.020.0001 are unknown. Indeed, no ontogenetic series of metatarsal I are known for oviraptorosaurs, so it is unclear whether features like the dorsal and ventral prominences could become better developed with maturity, regardless of whether they change allometrically. Determining the ontogenetic status of CMN 8538 may help to resolve its identity within Caenagnathidae: if this specimen is of similar ontogenetic status to other specimens of *Chirostenotes*, the differences in morphology and overall size would likely indicate it pertains to a different taxon. However, if it were more mature than other specimens of *Chirostenotes*, the taxonomy would remain ambiguous but the results could illuminate several aspects of the ontogeny of caenagnathid pedes.

Interestingly, in *Microvenator celer* (AMNH 3041), typically recognized as the basal-most caenagnathid (Funston 2020), metatarsal I lacks the pronounced dorsal and ventral prominences of the shaft (Fig. 3G–J) seen in outgroups of Caenagnathidae such as Caudipterygidae or Oviraptoridae (Zhou and Wang 2000; Hattori 2016). Although this is tentative given that there are only a few examples of caenagnathid first metatarsals, the condition in *Microvenator* may suggest a less constricted shaft of metatarsal I distinguishes caenagnathids from other oviraptorosaurs. Additionally, while not spherical as in CMN 8538 and *Anzu*, the distal condyle of metatarsal I of *Microvenator* forms a single continuous unit (Fig. 3I), distinctly different from the ginglymoid condition seen in *Chirostenotes* and some oviraptorids (e.g., *Citipati*, Hattori 2016). In *Caudipteryx dongi* and *Similicaudipteryx*, some of the basal-most oviraptorosaurs (e.g., Lamanna et al. 2014; Hartman et al. 2020; Funston 2020; Funston et al. 2020a), the distal end of metatarsal I is described as having a "well developed ball shape" (Zhou and Wang 2000:118; He et al. 2008:183), indicating the condition in these taxa is bulbous rather than ginglymoid as well. This implies that metatarsal I possessed a condylar distal articulation surface in ancestral oviraptorosaurs, and that the ginglymoid condition in *Chirostenotes* and some oviraptorids (Hattori 2016; Funston 2020) is derived and convergently acquired.

Implications for Caenagnathid Fossil Record: While caenagnathid oviraptorosaurs are relatively well represented in the Cretaceous fossil record of western North America (e.g., Sullivan et al. 2011; Longrich et al. 2013; Lamanna et al. 2014; Funston and Currie 2016; Funston 2020), records from Wyoming are exceptionally rare. This is odd, considering that caenagnathids are known from contemporaneous terrestrial strata throughout the adjacent areas of the USA and Canada (Funston 2020). So far, the only formally reported example is an isolated cervical vertebra (USNM 546292) collected from the Cloverly Formation of Wyoming, briefly described by Oreska et al. (2013). While Oreska et al. (2013) referred USNM 546292 to *Microvenator celer* presumably based on stratigraphic position, this specimen was not figured, nor was this referral based on similarities with the holotype of *Microvenator celer* (AMNH 3041). Instead, Oreska et al. (2013) noted similarities with *Chirostenotes*, for which definitive cervical vertebrae were not known until 2020 (Funston and Currie 2020). It is likely that their comparisons were drawn with ROM 43250, referred by Sues (1997) to *Chirostenotes* but later transferred to the new genus *Epichirostenotes* (Sullivan et al. 2011), as they cited Sues (1997) as the source. In any case, because the specimen is unfigured and its affinities are ambiguous, the best approach is to treat this specimen as an indeterminate caenagnathid until it can be re-examined. Ostrom (1970) tentatively referred an isolated theropod tooth (YPM 5366) from the Cloverly Formation of Wyoming to *Microvenator celer*, but this is almost certainly incorrect because the holotype preserves an edentulous dentary (Makovicky and Sues 1998), and all available evidence suggests that most caenagnathids were edentulous throughout their lifespan (Funston et al. 2020b; but see Wang et al. 2018). Breithaupt (1994) included "*Chirostenotes*" in his faunal list for the Lance Formation of Wyoming in reviewing the dinosaur diversity of the state, but did not state to which specimen he was referring, nor why the specimen could be said to represent a caenagnathid. This is important, as some caenagnathid skeletal elements might be confused with those of ornithomimids, and vice versa (Funston 2020). For these reasons, we consider the specimens reported by Ostrom (1970) and Breithaupt (1994) as unreliable records of caenagnathids from Wyoming. Therefore, UW 44439 is important in being the second record of Caenagnathidae from Wyoming, the first record from the Mesaverde Formation, and the first reliable record from the Late Cretaceous. It is also possible that UW 44439 represents the first example of a derived caenagnathid from Wyoming, as the only previous definite record may represent the basal-most caenagnathid *Microvenator*. This assertion is supported by the age of the specimen as well as its similarity to *Anzu* in overall morphology, but must be considered tentative because the material is very fragmentary and has not been subjected to a phylogenetic analysis. It is unclear why caenagnathid remains are so rare in Wyoming despite their rich Late Cretaceous diversity in other parts of North America. However, it is known that caenagnathids were rare components of the faunae to which they belonged (Funston et al. 2018; Funston 2020) and this tendency may explain their rarity in Wyoming. It is also possible that caenagnathid fossils have been frequently collected in this state, but remain undescribed or unidentified in collections. Nonetheless, description of these specimens remains important, as even fragmentary fossils could be important for paleofaunal surveys or reconstructions of the fossil record (e.g., Maganuco 2004; Yun 2021b).

While the newly described specimen appears to show affinities with *Anzu* and CMN 8538, little else is known about the caenagnathids of the Mesaverde Formation. However, some tentative inferences regarding the habitat of this caenagnathid theropod within the Mesaverde paleoecosystem can be made on the basis of the currently known fauna of the formation and the presumed ecological niches of other caenagnathids. Currie and Russell (1988) suggested that caenagnathids like *Chirostenotes* may have been adapted for fluvial systems, wading and feeding on freshwater organisms. Their hypothesis was based on their elongated fore- and hindlimbs, and has been tentatively supported by some subsequent studies showing that these adaptations were widespread in caenagnathids (e.g., Lamanna et al. 2014; Funston and Currie 2020; Rhodes et al. 2020). The Wind River Basin of the Mesaverde Formation is a freshwater fluvial system, and its fauna was dominated by various freshwater vertebrates like amphibians, bony fishes, cartilaginous fishes and turtles (Demar and Breithaupt 2006, 2008). Therefore, although tentative, it appears likely that the caenagnathid taxon from the Mesaverde Formation was similar to other caenagnathids in inhabiting fluvial ecosystems.

CONCLUSIONS

UW 44439 is a left metatarsal I of a caenagnathid theropod, and represents the first record of this clade from the Mesaverde Formation (Campanian) of Wyoming. Interestingly, despite its relatively small size comparable to that of metatarsal I of *Chirostenotes pergracilis* (TMP

1979.020.0001), the specimen features a unique combination of characters (spherical distal condyle, only slightly constricted "neck" between the shaft and the distal condyle, triangular shaft) that is more reminiscent of the condition seen in larger caenagnathids, like *Anzu wyliei* or "*Macrophalangia canadensis*" (CMN 8538). This raises questions as to whether known variation in first metatarsals of caenagnathids is the result of allometry, ontogeny, taxonomy, or a combination of these factors. Nonetheless, our findings indicate that metatarsal I is distinctive in caenagnathids and other oviraptorosaurs, which may be useful for identifying isolated elements from the Late Cretaceous of North America.

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