New data on small theropod dinosaurs from the Upper Jurassic Morrison Formation of Como Bluff, Wyoming, USA

Sebastian G. DALMAN[1]

Abstract. In 1879, Othniel C. Marsh and Arthur Lakes collected in the Upper Jurassic Morrison Formation Quarry 12 at Como Bluff, Wyoming, USA, several isolated axial and appendicular skeletal elements of small theropod dinosaurs. Since the discovery the specimens remained unnoticed for over a century. The skeletal remains of small theropods are rare at Como Bluff and throughout the Morrison Formation. Their bones are delicately constructed, so they are not as well-preserved as the bones of large-bodied theropods. The bones of small theropods described here were found mixed with isolated crocodile teeth and turtle shells. Comparison of the skeletal materials with other known theropods from the Morrison Formation reveals that some of the bones belong to a very small juvenile *Allosaurus fragilis* and *Torvosaurus tanneri* and also to a new ceratosaur taxon, here named *Fosterovenator churei*, whereas the other bones represent previously unidentified juvenile taxa of basal tetanuran and coelurid theropods. The discovery and description of these fossil materials is significant because they provide important information about the Upper Jurassic terrestrial fauna of Quarry 12, Como Bluff, Wyoming. The presence of previously unidentified theropod taxa in the Morrison Formation indicates that the diversity of basal tetanuran and coelurid theropods may have been much greater than previously expected. Although the fossil material here described is largely fragmentary, it is tenable that theropods of different clades co-existed in the same ecosystems at the same time and most likely competed for the same food sources.

INTRODUCTION

The Upper Jurassic deposits of the Morrison Formation at Como Bluff, Wyoming, yield large assemblages of fossil remains of small and large vertebrates dominated by large-bodied dinosaurs (Dodson *et al*., 1980; Foster, 2003, 2007). The dinosaurian fauna at Como Bluff is diverse and includes some of the largest terrestrial animals, sauropods such as *Camarasaurus* and *Diplodocus* (Foster, 2003, 2007). *Allosaurus fragilis* is the best known and the most common large theropod dinosaur found at Como Bluff and throughout the Morrison Formation and is considered as one of the top predators of the Upper Jurassic. At Como Bluff, *Allosaurus* co-

existed in the same ecosystem with other large-bodied theropods, the megalosaurids "*Brontoraptor*" and "*Edmarka rex*" (= *Torvosaurus*; Bakker *et al.*, 1992; Siegwarth *et al.*, 1997; Foster, 2003, 2007). The dinosaurian fauna at Como Bluff also includes small-bodied coelurid theropods, and the best known are *Coelurus fragilis* (Marsh, 1884), *Ornitholestes hermanii* (Osborn, 1903), and *Tanycolagreus topwilsoni* (Carpenter *et al.*, 2005a).

The paleogeographic distribution of *Allosaurus* (Turner, Peterson, 1999; Foster, 2003, 2007; Loewen, 2004, 2009) and *Torvosaurus* (Galton, Jensen, 1979; Jensen, 1985; Britt, 1991; Carrano *et al.*, 2012) is throughout the entire Morrison Formation. In other localities of the formation, *Allosaurus*

[1] Department of Geosciences, Fort Hays State University, 600 Park Street, Hays, KS 67601, USA; e-mail: sebastiandalman@yahoo.com:
Corresponding address: 104 Johnson Dr.1002 Chicopee, MA 01022, USA

and *Torvosaurus* co-existed with other medium-sized and large-bodied theropods, such as *Ceratosaurus nasicornis* (Marsh, 1884), *Stokesosaurus clevelandi* (Madsen, 1974), *Marshosaurus bicentesimus* (Madsen, 1976), *Elaphrosaurus* sp. (Galton, 1982), *Koparion douglassi* (Chure, 1994), *Saurophaganax maximus* (Chure, 1995), *Ceratosaurus dentisulcatus* (Madsen, Welles, 2000), and *Ceratosaurus magnicornis* (Madsen, Welles, 2000).

Allosaurus and *Torvosaurus* are represented by numerous well-preserved specimens consisting largely of adult individuals. However, juvenile specimens of *Allosaurus* are rare, whereas juveniles of *Torvosaurus* are unknown. The skeletal fossil remains of small-bodied coelurid theropods are also rare at Como Bluff and in other localities of the Morrison Formation (Foster, 2003, 2007; Carpenter *et al.*, 2005a, b). The carcasses of juveniles and other small-bodied theropods decomposed much faster than those of large-bodied theropods, and their remains were most likely scavenged by other theropods and by other small and large reptiles (*e.g.*, crocodiles), and their remains were either scattered around the area or were consumed entirely. Although specimens of juveniles of basal tetanuran and of small coelurid theropods are rare, they represent a very important component of the terrestrial fauna of the Upper Jurassic Morrison Formation, which was dominated by giant dinosaurs (Madsen, 1976; Foster, 2003, 2007).

Institutional abbreviations. BMNH, Natural History Museum, London, UK; BYUVP, Brigham Young University Vertebrate Paleontology, Provo, Utah, USA; SDSM, South Dakota School of Mines, Rapid City, South Dakota, USA; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA.

GEOLOGICAL BACKGROUND

The Morrison Formation is located in the western states of the United States: Arizona, Colorado, Montana, New Mexico, Oklahoma, South Dakota, Utah, and Wyoming (Cross, 1894; Foster, 2003, 2007). Radioisotopic dates provide an age between 155 to 147 Ma (Kimmeridgian/ Tithonian) for the Morrison Formation (Kowallis *et al.*, 1998; Litwin *et al.*, 1998). The formation is famous for the occurrence of a diverse vertebrate fauna consisting of crocodiles, dinosaurs, fish, sphenodontians, turtles, and mammals (Foster, 2003, 2007). The isolated skeletal fossil remains described here of juvenile *Allosaurus fragilis*, *Torvosaurus tanneri*, and *Fosterovenator churei* n. gen., n. sp., and unidentified basal tetanuran and coelurid theropods mixed with isolated crocodile teeth and turtle shells were found in the Morrison Formation at Quarry 12, Como Bluff, Wyoming.

Quarry 12 is located in the western part of Como Bluff and consists of a gray silty claystone bed in which the skeleton of *Stegosaurus ungulatus* (Marsh, 1879) was found (Foster, 2003). The dinosaurian fauna at Quarry 12 includes: *Allosaurus*, *Camarasaurus*, *Coelurus*, *Diplodocus*, and *Stegosaurus*. At other localities at Como Bluff the dinosaurian fauna is diverse and includes large megalosaurid theropods "*Edmarka rex*" (Bakker *et al.*, 1992) and "*Brontoraptor*" (Siegwarth *et al.*, 1997), which are most likely the sister taxa of *Torvosaurus tanneri*, and *Ceratosaurus* sp. (Foster, 2003, 2007; Carrano *et al.*, 2012).

SYSTEMATIC PALEONTOLOGY

Saurischia Seeley, 1887

Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

Carnosauria von Huene, 1920

Allosauridae Marsh, 1878

Allosaurus fragilis Marsh, 1877

Materials. – YPM VP 058258 right femur and proximal left tibia, YPM VP 058259 dorsal vertebra, YPM VP 058260 right lacrimal, right angular, left radius, and distal end of left fibula, YPM VP 058261 left ulna, YPM VP 058273 distal caudal vertebra, YPM VP 058275 distal end of right metatarsal M-III, YPM VP 058276 manual phalanx III-1, YPM VP 058277 ungual phalanx II-1.

Locality, horizon and age. – Quarry 12, Como Bluff, Wyoming, USA. The specimens were found in the Morrison Formation, Upper Jurassic (Kimmeridgian/ Tithonian).

Description:
Lacrimal. YPM VP 058260 is identified as a right lacrimal (Fig. 1). The bone is partially preserved, missing the entire proximal region, which in complete specimens includes the contact with maxilla, nasal, and prefrontal. In medial view a small portion of contact with the jugal is preserved. Overall length of the preserved bone fragment is 8.4 cm.

Angular. YPM VP 058260 is identified as a right angular (Fig. 1). The angular is partially preserved and consists of two isolated fragments, which articulate together. Overall length of both bone fragments in articulation is 14 cm. The complete angular was longer and most likely reached the length of approximately 20 cm when compared to known angular bones of subadult and adult examples of *Allosaurus*.
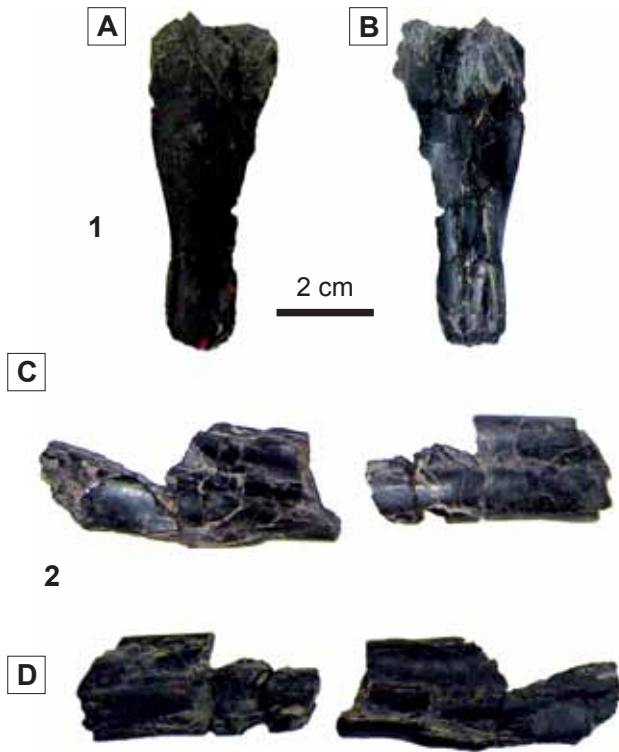
Fig. 1. *Allosaurus fragilis* YPM VP 058260, right lacrimal (1) and right angular (2) from the Upper Jurassic Morrison Formation, Quarry 12, Como Bluff, Wyoming

A, C. Lateral view. **B, D.** Medial view

Dorsal vertebra. YPM VP 058259 is identified as the centrum of dorsal vertebra (Fig. 2). The total length of the centrum is 6 cm; height of the intervertebral articulation is 5.3 cm and width 4.2 cm. The centrum is narrow waisted, and has a convex posterior face. Ventral to the suture for the neural arch the centrum is laterally depressed. The suture extends for the entire length of the centrum, and its height is 0.5 cm. The suture exhibits a clear break, which suggests that in life the neural arch was not fused to the centrum, which further indicates that the centrum belongs to a juvenile animal (Azuma, Currie, 2000). No pleurocoel is present, which indicates that the centrum most likely is from the sixth or the seventh vertebra in the dorsal series. In general, the pleurocoels in *Allosaurus* are present and well-developed on the first dorsal centrum, they gradually decrease in size on each consecutive dorsal vertebra and eventually they become absent on the sixth vertebra (Madsen, 1976). In dorsal view a long and narrow neural canal is fully exposed.

Caudal vertebra. YPM VP 058273 is identified as the distal caudal vertebra (Fig. 3). The vertebra preserves only the centrum and partial prezygapophyses. The centrum is amphicoelous and elongated. In general, the distal caudal vertebrae in *Allosaurus* and also in other non-avian theropods are much longer than tall (Madsen, 1976; Currie, Zhao, 1994). In articulated specimens of *Allosaurus* the nineteenth vertebral centrum in the caudal series becomes elongated and each consecutive vertebra that follows is progressively smaller and elongated. Although the prezygapophyses are only partially preserved, however, when complete they were elongated and extended beyond the vertebral centrum.
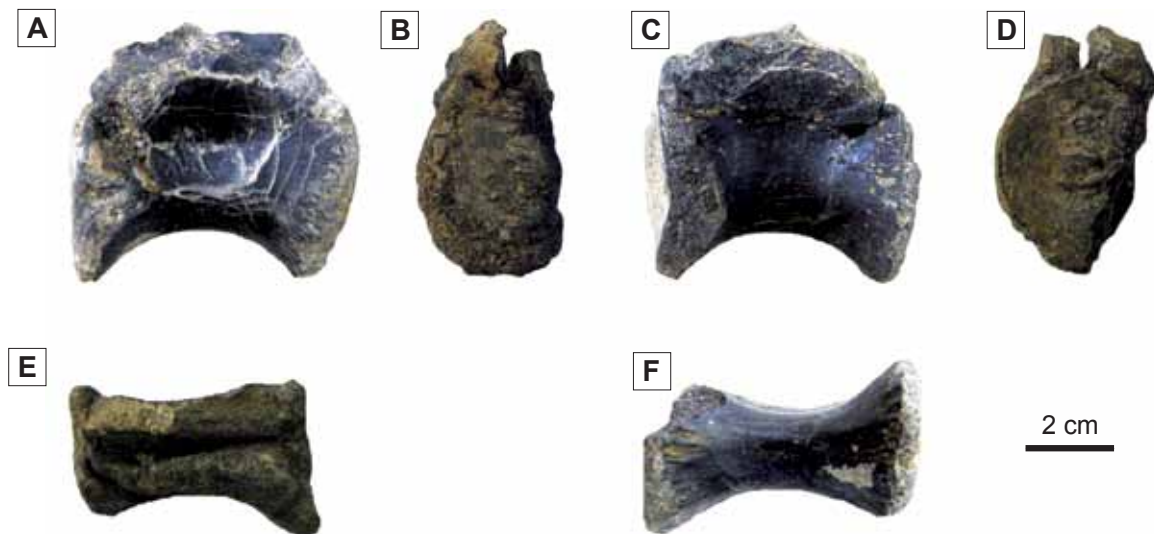

Fig. 2. *Allosaurus fragilis* YPM VP 058259, centrum of dorsal vertebra from Upper Jurassic Morrison Formation, Quarry 12, Como Bluff, Wyoming

A. Right lateral view. **B.** Anterior view. **C.** Left lateral view. **D.** Posterior view. **E.** Dorsal view. **F.** Ventral view
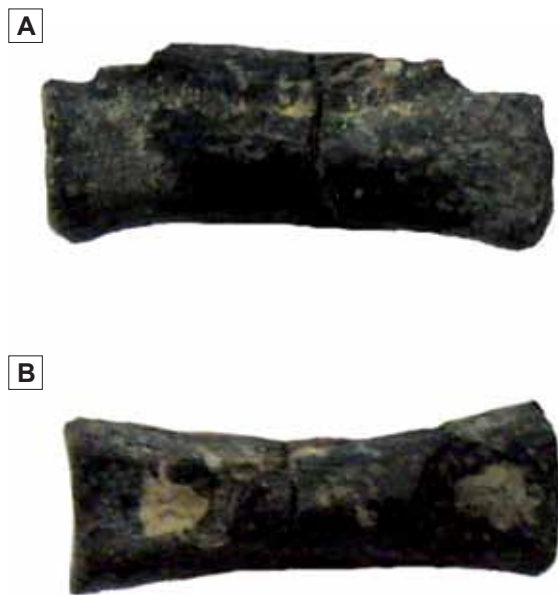
Fig. 3. *Allosaurus fragilis* YPM VP 058260, centrum of distal caudal vertebra (2) from Upper Jurassic Morrison Formation, Quarry 12, Como Bluff, Wyoming

A. Lateral view. **B.** Dorsal view

Radius. YPM VP 058260 is identified as the distal end of the left radius (Fig. 4). The length of the preserved bone fragment is 7.3 cm. The bone preserves a nearly complete distal articular surface and approximately half of the radial shaft, which is nearly straight. The distal end is slightly expanded and rounded in a way similar to that of adult *Allosaurus* (Madsen, 1976a). The articular surface is rugose and flattened.

Ulna. YPM VP 058261 is identified as a partial left ulna (Fig. 4). The bone consists of three isolated fragments, which, based on their overall morphology, belong to a single ulna. When the bone fragments are assembled together the ulna is slightly bowed laterally and closely resembles the ulnae of subadult and adult *Allosaurus*. Overall length of the preserved ulna fragment is 12.5 cm, and approximately 5 cm of the bone is missing when compared to well-preserved ulnae of *Allosaurus*.

Phalanges. YPM VP 058276 is identified based on overall morphology as the manual phalanx III-1 of the right manus (Fig. 5). The phalanx is missing the anterior end. The preserved phalangeal shaft is elongated and slightly mediolaterally compressed. The posterior end of the phalanx is deep and the proximal articular surface has two shallow grooves for the articulation with phalanx III-2.

YPM VP 058277 is identified as the manual ungual phalanx III of the right manus and is missing a small portion of the pointed anterior end (Fig. 5). The ungual is mediolaterally compressed. As in other *Allosaurus* specimens (Madsen, 1976a; Loewen, 2009), the ungual phalanx (YPM VP 058277) has a pronounced posterodistal curvature and is expanded ventrally. Nutrient grooves are well developed and are present on lateral and medial sides of the ungual phalanx.

Femur. YPM VP 058258 is identified as the right femur (Fig. 6). The femoral head is complete and well preserved, and its overall morphology is identical to that of subadult and adult examples of *Allosaurus*. The femoral head projects from the shaft at an approximate right angle, and the articular surface is rounded (Madsen, 1976). In both anterior and posterior views the anteroventral face of the femoral head forms a small hook-like structure. The lesser trochanter is partially preserved. However, as in other examples of *Allosaurus* and also in other large non-avian theropods such as *Acrocanthosaurus*, *Bahariasaurus*, *Ceratosaurus*, *Fukuiraptor*, *Gasosaurus*, *Sinraptor*, and *Yangchuanosaurus*, the lesser trochanter is large and plate-like and is separated from the femoral shaft by a deep slot (Azuma, Currie, 2000; Currie, Zhao, 1994; Rauhut, 2003; Currie, Azuma, 2006). The fourth trochanter, which is present in *Allosaurus* and in other non-avian theropods, is not preserved in YPM VP 058258 because the bone is broken and heavily damaged in this region. The femoral shaft is crushed and misshapen.

Tibia. YPM VP 058258 is identified as the proximal left tibia (Fig. 7). The bone is missing most of the shaft and is slightly compressed mediolaterally. The proximal articular end is well preserved and has an overall length of 5.5 cm. The width of the anterior region of the proximal articular end is 1.7 cm and the posterior region 2.5 cm. The medial condyle is ovoid shaped and in overall morphology is similar to that of subadult and adult examples of *Allosaurus*. The condyles are separated from each other by a deep and narrow intercondylar notch. The medial condyle is confluent with the cnemial crest, and the articular surface of the tibia is not inclined distolaterally. The lateral condyle is also ovoid shaped, but is slightly smaller and in lateral view is shorter than the medial condyle. In proximal view the lateral condyle is extended more distally and appears much longer than medial condyle. The lateral condyle is separated from the proximal end of the tibia by a well-developed crescentic concavity, the incisura tibialis (Madsen, 1976; Azuma, Currie, 1994; Madsen, Welles, 2000; Rauhut, 2003; Benson, 2009). Located on the anterior edge of the lateral condyle is a well-developed, distinct craniolateral projection a feature that is characteristic of basal tetanuran theropods (*e.g.*, *Allosaurus*, *Saurophaganax*, and *Torvosaurus*). The craniolateral projection is also present in neoceratosaurs (*e.g.*, *Ceratosaurus* and *Elaphrosaurus*), small coelurid theropods (*e.g.*, *Coelurus*,
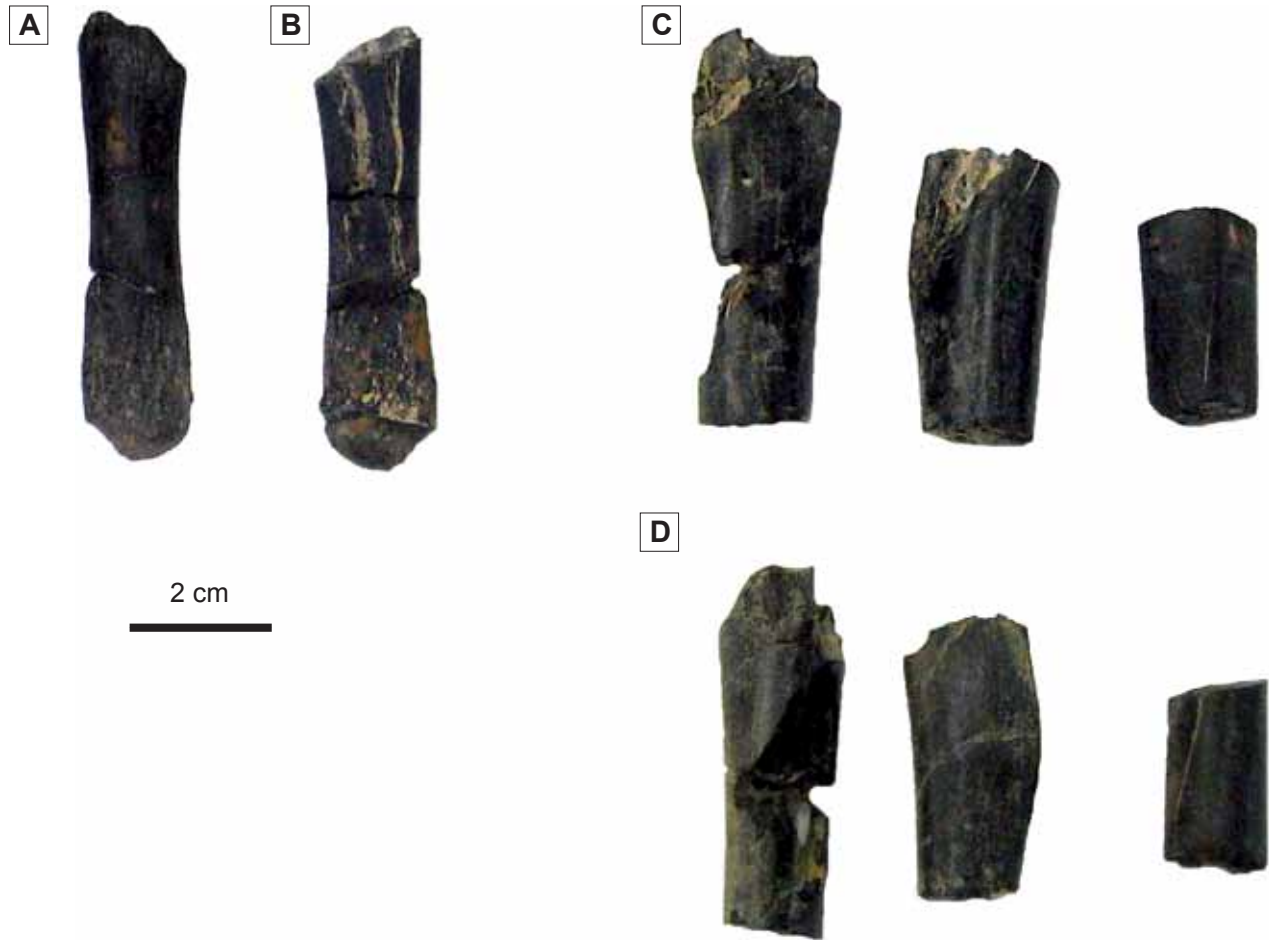
Fig. 4. *Allosaurus fragilis* YPM VP 058260, left distal radius in A, lateral and B, medial views and left ulna in C, lateral and D, medial views, from the Upper Jurassic Morrison Formation, Quarry 12, Como Bluff, Wyoming

Ornitholestes, and *Tanycolagreus*), and tyrannosaurids (*e.g.*, *Albertosaurus*, *Gorgosaurus*, *Lythronax*, *Tarbosaurus*, and *Tyrannosaurus*).

The cnemial crest in YPM VP 058258 arises from the anterior surface of the tibia's shaft and is curved anteroproximolaterally, as in other large-bodied, non-avian theropods (Benson, 2009). On the lateral surface of the cnemial crest is a poorly-developed anteroproximally inclined ridge. The cnemial crest is elongated and narrowed transversely.

Fibula. YPM VP 058260 is identified as the distal end of a left fibula (Fig. 8). The bone is small and only partially preserved. The overall morphology of the preserved bone fragment is nearly identical to the fibula of adult *Allosaurus fragilis*. In general, the distal end of the fibula of *Allosaurus* is small and crescentic, which is evident in YPM VP 058260.

Metatarsal. YPM VP 058275 is identified as the distal end of the right metatarsal III (Fig. 9). The metatarsal preserves a small portion of the shaft. Overall length of the preserved bone fragment is 3 cm. The distal articular surface in YPM VP 058275 is round but not strongly expanded transversely, and the characteristic ginglymus that is present in subadult and adult *Allosaurus* is only slightly developed. It is tenable that these undeveloped features in YPM VP 058275 represent ontogenetic variations.

In anterior view just above the articular surface is a large hyper extensor pit also known as the insertion site for M. extensor digitorum longus (Carrano, 2007). In posterior view, a large fossa (flexor pit) separates the medial and lateral condyles. Both condyles are round and well developed. The collateral ligament pits are large and of equal depths and sizes.

Fig. 5. *Allosaurus fragilis* **YPM VP 058276, right manual phalanx III-1 (top), and right manual ungual phalanx II (bottom) from the Upper Jurassic Morrison Formation, Quarry 12, Como Bluff, Wyoming**

A. Dorsal view. **B.** Ventral view. **C.** Lateral view. **D.** Medial view. **E.** Posterior view
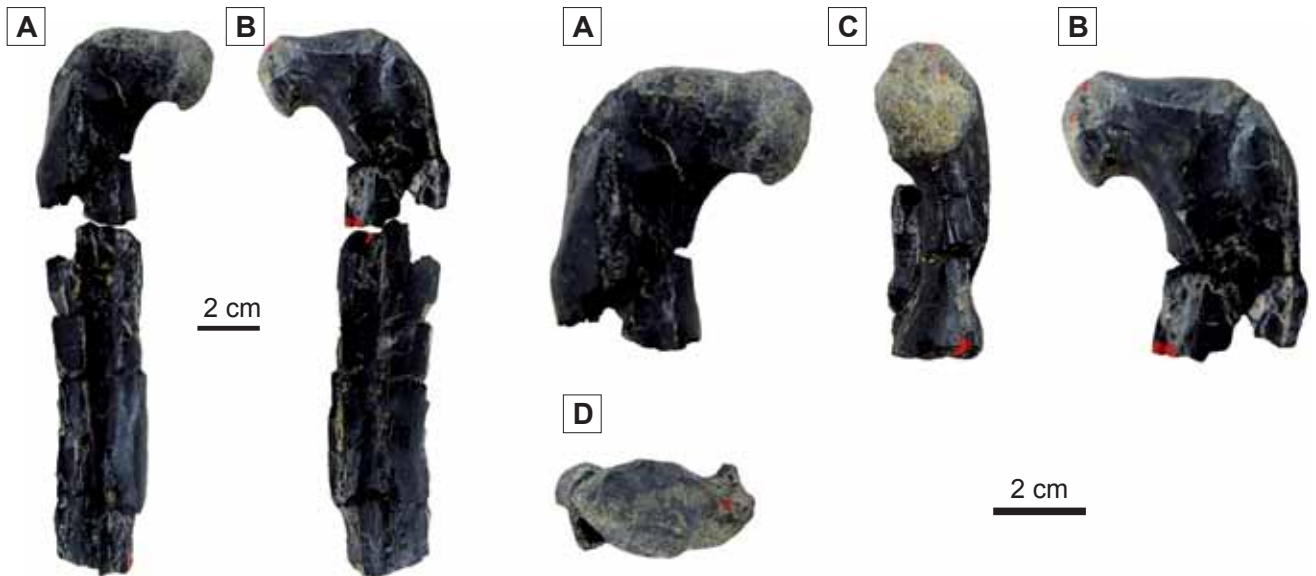

Fig. 6. *Allosaurus fragilis* **YPM VP 058258, right femur from the Upper Jurassic Morrison Formation, Quarry 12, Como Bluff, Wyoming**

A. Anterior view. **B.** Posterior view. **C.** Medial view. **D.** Dorsal view. Complete fossil (left) and close-up (right)
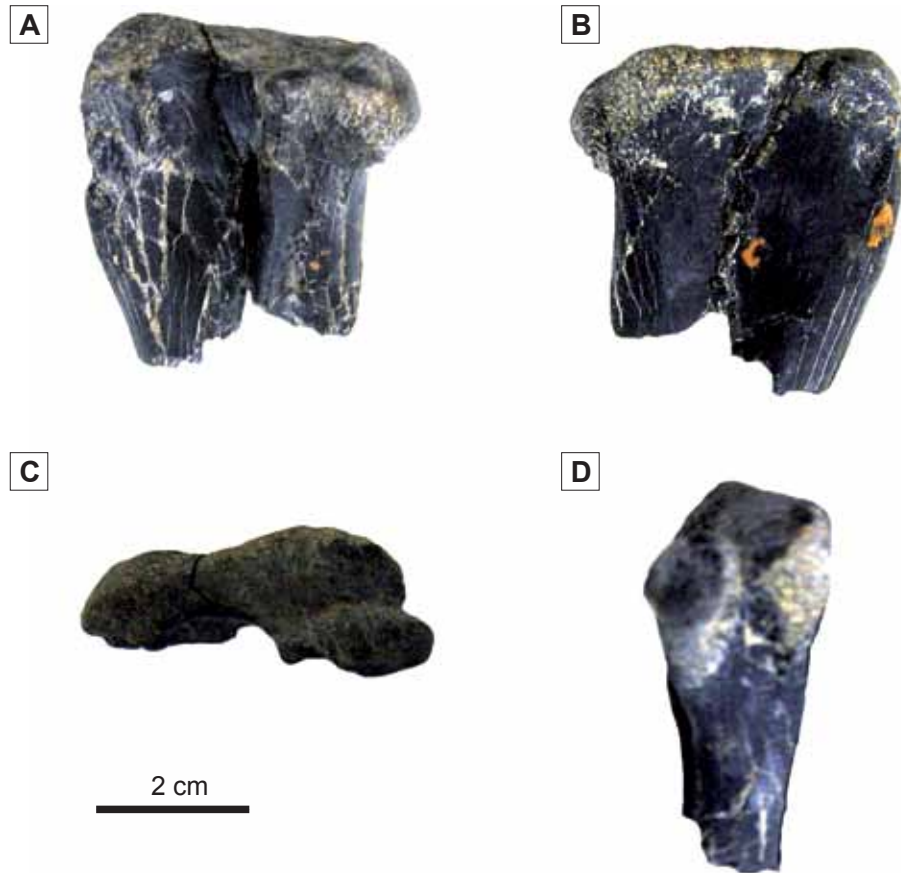
Fig. 7. *Allosaurus fragilis* **YPM VP 058258, proximal left tibia from the Upper Jurassic Morrison Formation, Quarry 12, Como Bluff, Wyoming**

A. Lateral view. **B.** Medial view. **C.** Dorsal view. **D.** Posterior view

Ceratosauridae Marsh, 1884

Fosterovenator n. gen.

Etymology: The generic name honors John R. Foster in recognition of his contributions to the study of the vertebrate fauna of the Morrison Formation; "*venator*" in Greek meaning "hunter."
Holotype: YPM VP 058267A, B, C, a nearly complete right tibia with co-ossified astragalus.
Paratype: YPM VP 058267D, complete right fibula of a much larger individual.
Diagnosis: As for the genus and only species.

Fosterovenator churei n. sp.

Etymology: The species name honors Daniel J. Chure in recognition of his contributions to the study of the vertebrate fauna of the Morrison Formation.
Type locality, horizon and age: Quarry 12, Como Bluff, Wyoming, USA. The specimens were found in the Morrison Formation Upper Jurassic (Kimmeridgian/ Tithonian).
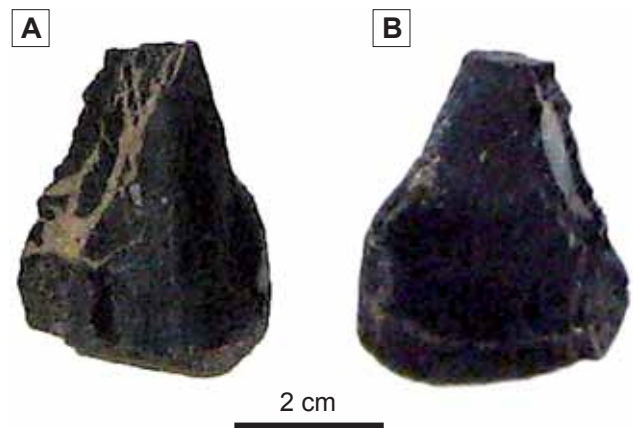

Fig. 8. *Allosaurus fragilis* **YPM VP 058260, distal end of a left fibula from the Upper Jurassic Morrison Formation, Quarry 12, Como Bluff, Wyoming**
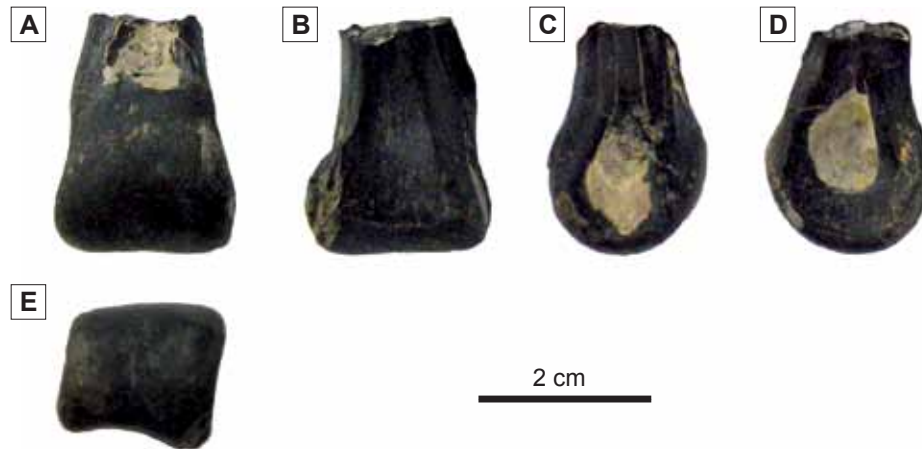
A. Lateral view. **B.** Medial view

Fig. 9. ***Allosaurus fragilis*** **YPM VP 058275, right distal metatarsal M-III from the Upper Jurassic Morrison Formation, Quarry 12, Como Bluff, Wyoming**
A. Anterior view. **B.** Posterior view. **C.** Lateral. **D.** Medial view. **E.** Distal articular surface

Diagnosis: Small-bodied (juvenile) theropod dinosaur known only from partially preserved tibia with co-ossified astragalus and complete fibula of slightly larger individual. Tibia condyles are round, whereas the medial is larger than the lateral; intercondylar notch is deep and "V" – shaped; lateral condyle is strongly removed from the posterior and of the main body of proximal tibia. Fibula shaft with uniform anteroposterior width throughout most of its length; distal end of fibula anteroposterior width 90% of the width of the proximal fibular head.

Description:

Tibia. YPM VP 058267A is a nearly complete right tibia that is missing a portion of the distal shaft (Fig. 10). The tibia has a well-developed cnemial crest on the proximal end, which is visible in all aspects. In proximal view the cnemial crest is wide transversely and has a blunt anterior end. The cnemial crest arises from the anterior surface of the tibia's shaft and is curved anteroproximolaterally as in other non-avian theropods (Benson *et al.*, 2009). On the lateral surface of the cnemial crest is a well-developed, anteroproximally inclined ridge. The medial and lateral condyles are large. In proximal view the medial condyle is round and appears larger than the lateral condyle. In distal view, the medial condyle is approximately at the same height as the lateral condyle. However, proximally the medial condyle is slightly more elevated than the lateral condyle, and the articular surface of the tibia is inclined distolaterally, which can be seen in medial and lateral views. The lateral condyle is slightly smaller but in proximal view it is also round. The condyle is positioned at the posterior margin of the tibia and is separated from the proximal end by a characteristic "C"-shaped concavity, the incisura tibialis, which is present in all basal tetanuran, neoceratosaur, and other non-avian theropods

(Madsen, 1976; Azuma, Currie, 1994; Madsen, Welles, 2000; Chure, 2001; Carrano, Sampson, 2008; Benson, 2009; Carrano *et al.*, 2012). A well-developed craniolateral projection is located on the anterior edge of the lateral condyle. In proximal view the medial condyle is confluent with the cnemial crest, and the medial margin of the tibia is convex. The condyles are separated from each other by a distinct, "V"-shaped intercondylar notch.

The lateral and posterior surfaces of the tibia's shaft are heavily damaged, which prevents the identification of other morphological features. However, based on overall morphology the YPM VP 058267A tibia clearly belongs to a basal tetanuran theropod that differs from all other known taxa from the Morrison Formation by a strongly inclined anterior articular surface and by the "C"-shaped incisura tibialis. In medial view the YPM VP 058267D tibia closely resembles the tibia of YPM VP 058267A, which is a small bone and most likely belongs to a juvenile individual. Therefore, some of the morphological features may represent ontogenetic variation. In medial view, the (YPM VP 058267A) tibia closely resembles the tibia of some basal tetanuran theropods such as *Neovenator* and *Sinraptor*, but also those of small abelisauroid theropods. YPM VP058267A is a small bone and most likely belongs to a juvenile individual. Therefore, some of the morphological features may represent ontogenetic variation.

YPM VP 058267B is a partial distal end of a right tibia with a co-ossified astragalus (Fig. 10). As in other tetanuran and neoceratosaur theropods (Madsen, 1976; Madsen, Welles, 2000; Carrano, Sampson, 2008; Benson, 2009, 2010; Carrano *et al.*, 2012), the distal end of the tibia of (YPM VP 058267B) in anterior and posterior view is expanded mediolaterally. Although the lateral face in YPM VP 058267B
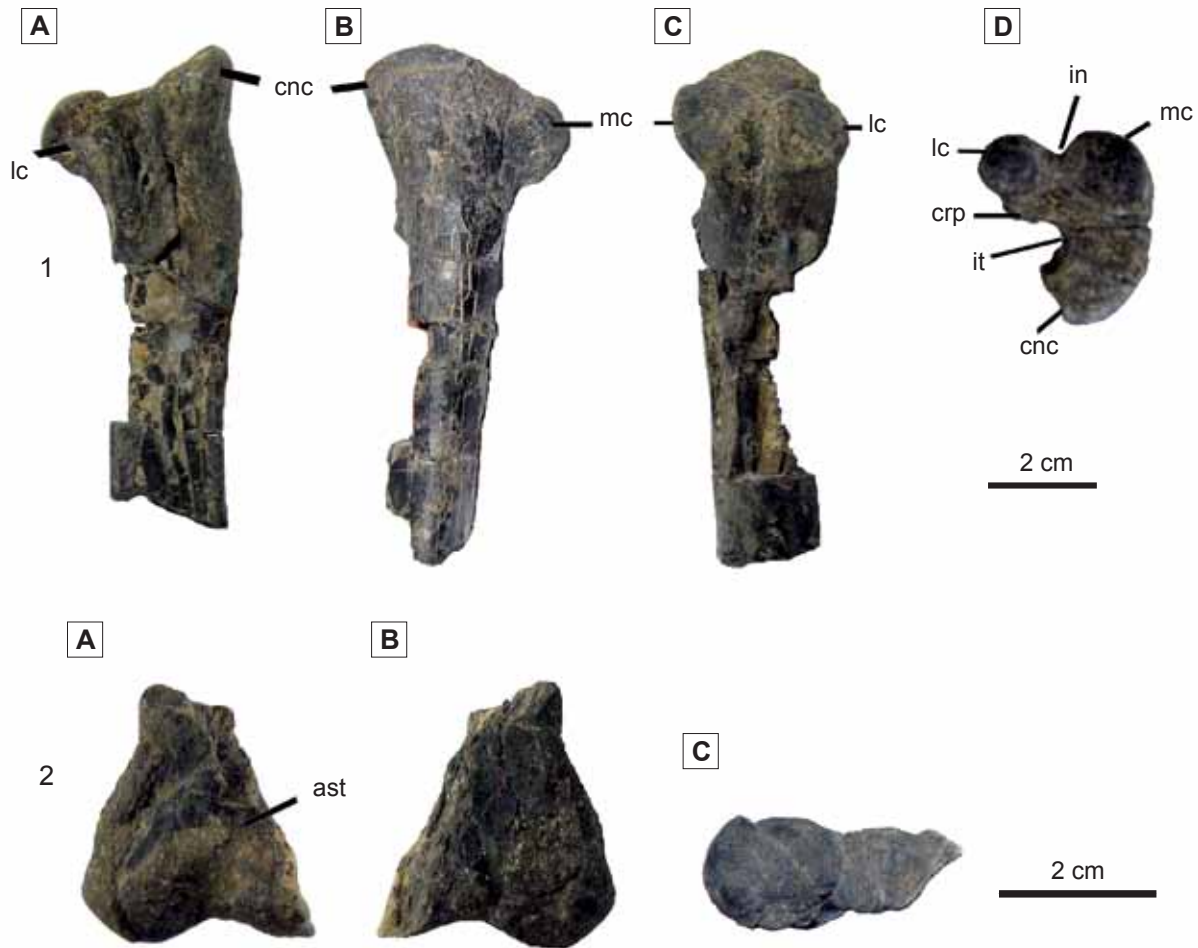
Fig. 10. *Fosterovenator churei* **YPM VP 058267D proximal right tibia (1) in A, lateral view, B, medial view, C, posterior view, D, dorsal view, and distal tibia with co-ossified astragalus (2) in A, lateral, B, medial, and C, ventral view**

Abbreviations: ast – astragalus, cnc – cnemial crest, crp – craniolateral projection, in – intercondylar notch; it – incisura tibialis, lc – lateral condyle, mc – medial condyle

is not preserved, the distal end of the tibia exhibits a slight asymmetry. The anteromedial buttress is well developed. It is bluntly rounded, and a nearly vertical ridge is located on the medial side of the distal tibia. A similar condition is also present in noasaurid and megaraptoran theropods, whereas in allosaurids and carcharodontosaurids the ridge is oblique, reduced, and rounded (Carrano *et al.*, 2012).

Astragalus. The astragalus of *Fosterovenator churei* is nearly complete and co-ossified with the distal end of the tibia of YPM VP 058267C (Fig. 10). The ascending process is long and extends to the distal portion of the tibia's shaft. The lateral side of the astragalus is not preserved. Therefore, it is difficult to determine whether the ascending process of the astragalus was more laterally oriented as in *Torvosaurus tanneri* (Britt, 1991), *Allosaurus fragilis* (Madsen, 1993), and

Coelurus fragilis (Carpenter *et al.*, 2005a) or extended the entire width of the astragalus as in *Ceratosaurus magnicornis* (Madsen, Welles, 2000) and *Tanycolagreus topwilsoni* (Carpenter *et al.*, 2005b). Although the ascending process is incomplete it is very likely that it projected much higher than in *Allosaurus*, *Coelurus*, and *Torvosaurus*.

In anterior and posterior views the ventral border of the astragalus of *Fosterovenator churei* is much more strongly concave than in *Allosaurus*, *Ceratosaurus*, *Coelurus*, *Tanycolagreus*, and *Torvosaurus*.

Fibula. YPM VP 058267D is an isolated complete right fibula (Fig. 11). The bone consists of several broken fragments, which perfectly articulate with one another. Overall length of the bone is 27.5 cm. The fibular head is nearly straight in proximal view and has a length of

Fig. 11. *Fosterovenator churei* YPM VP 058267D, right fibula from the Upper Jurassic Morrison Formation, Quarry 12, Como Bluff, Wyoming

A. Lateral view. **B.** Medial view. **C.** Proximal view. **D.** Distal view

4.6 cm and width of 1.5 cm. The size of the fibular head relative to the width of the proximal tibia is <75 %. The articular surface is concave for most of its length and convex at the anterior end, which slightly slopes down posteriorly. The lateral surface of the fibular head is convex, and, as in other theropods, the head is flared anteroposteriorly beyond the shaft. The posterior end of the fibular head in lateral and medial views projects slightly more beyond the shaft than the anterior end.

As in other non-avian theropods the medial surface of the fibular head is rugose. Two distinct fossae are present on the medial surface of the fibular head. The anteriormost fossa is a shallow crescentic structure, which is proximo-distally oriented and has parallel striae on its surface. The depth of the anteriormost fossa is approximately 0.4 cm. The posteriormost fossa is shallow and slightly smaller

than the anteriormost fossa and its surface has also parallel striae.

The lateral surface of the shaft is convex, and the medial surface is flat and is D-shaped in cross-section. The medial surface has a shallow, elongated groove in the middle that extends through most of the shaft's length. A similar groove is also present in other non-avian theropods such as in the majority of abelisauroids, allosauroids, megalosauroids, and tyrannosauroids. However, in these taxa the groove does not extend through most of the length of the fibular shaft.

Although the fibular shaft of *Fosterovenator churei* (YPM VP 058267D) is complete, the anterior and posterior edges are distorted, and the tibial flange that is present in basal tetanuran and neoceratosaur theropods is not preserved in this specimen. However, it is tenable that in a complete fibula the position of the tibial flange in *F. churei* (YPM VP 058267) was ventral to the fibular head, because the bone surface directly below the site where the fibular flange should be is smooth.

The proximal end of the shaft for most of its length has a uniform width, but near the distal end the shaft is slightly narrowed. The distal end of the fibula is expanded anteroposteriorly, and the distal articular surface has a distinct triangular shape. The anteroposterior width of the distal articular end is 4 cm.

Megalosauroidea Fitzinger, 1843

Megalosauridae Fitzinger, 1843

Torvosaurus tanneri Galton et Jensen, 1979

Material. – YPM VP 058269 a nearly complete left tibia that is missing the distal end.

Type locality, horizon and age. – Quarry 12, Como Bluff, Wyoming, USA. The specimen was found in the Morrison Formation, Upper Jurassic (Kimmeridgian/Tithonian).

Description:
Tibia. YPM VP 058269 is a nearly complete left tibia that is missing the distal end (Fig. 12). This specimen is well preserved. The medial condyle is extensive, short, and wide transversely. The condyles are separated from each other by a deep intercondylar notch. The medial condyle is confluent with the cnemial crest, its proximal end is at the same height as the lateral condyle and the articular surface of the tibia is not inclined distolaterally. The lateral condyle is slightly smaller, and in proximal view it is more centered than posteriorly oriented, as in other theropods. The condyle is separated from the proximal end by a characteristic "C"-shaped concavity, the incisura tibialis (Madsen, 1993; Azuma, Currie, 2000; Hutt *et al.*, 1996; Hutt, 1999; Madsen, Welles,
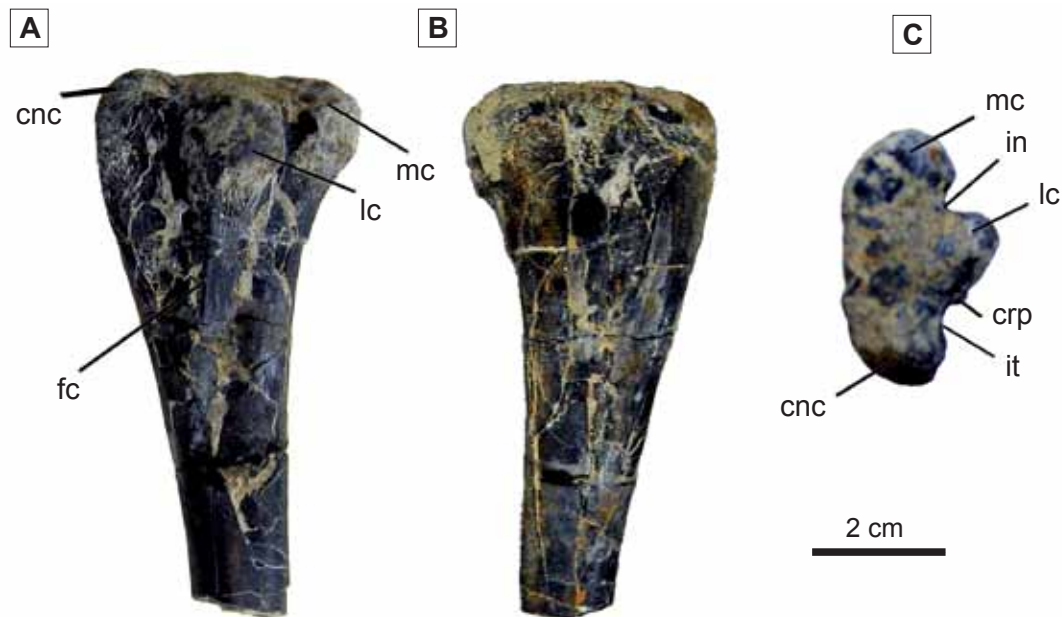
Fig. 12. *Torvosaurus tanneri* **YPM VP 058269, left tibia from the Upper Jurassic Morrison Formation, Quarry 12, Como Bluff, Wyoming**

A. Lateral view. **B.** Medial view. **C.** Dorsal view. **Abbreviations:** cnc – cnemial crest, crp – craniolateral projection, fc – fibular crest, in – intercondylar notch, it – incisura tibialis, lc – lateral condyle, mc – medial condyle

2000; Rauhut, 2003; Brusatte *et al.*, 2008; Benson, 2009). However, the incisura tibialis in YPM VP 058269 is not extensively crescentic as in the tibia of *Fosterovenator churei* (YPM VP 058267A). A well-developed craniolateral projection is located on the anterior edge of the lateral condyle. In medial and lateral views the tibia (YPM VP058269) closely resembles the tibiae of *Torvosaurus tanneri* (BYUVP 2016) (Britt, 1991), *Allosaurus fragilis* (Madsen, 1993) from the Cleveland-Lloyd Quarry, Utah, USA, and a theropod tibia (BMNH 39496) (Benson, 2010) from the Blue Lias of Charmouth, Dorset, United Kingdom. In all these taxa and in YPM VP058269 the cnemial crest arises from the anterior surface of the tibia's shaft and is curved anteroproximolaterally, as in other non-avian theropods (Benson, 2009). Further, the proximal end of medial condyle in these taxa is approximately at the same height as the lateral condyle, and the articular surface of the tibia is not inclined distolaterally.

On the lateral surface of the cnemial crest in (YPM VP 058269) is a poorly-developed anteroproximally inclined ridge. In medial and lateral views the cnemial crest is extremely short, and in proximal view the crest is wide transversely. A nearly identical condition is also present in the tibia of *Torvosaurus tanneri* (BYUVP 2016) (Britt, 1991). The lateral condyle in *T. tanneri* (BYUVP 2016) is slightly

centered in similar way as in (YPM VP 058269). However, the intercondylar notch that separates the condyles is deeper in (YPM VP 058269) than in *T. tanneri* (BYUVP 2016). It is very likely that this morphological feature represents an ontogenetic variation, given that YPM VP 058269 belongs to a juvenile animal. The striking similarity of YPM VP 058269 to that of *T. tanneri* (BYUVP 2016) suggests that it most likely represents a juvenile of this taxon.

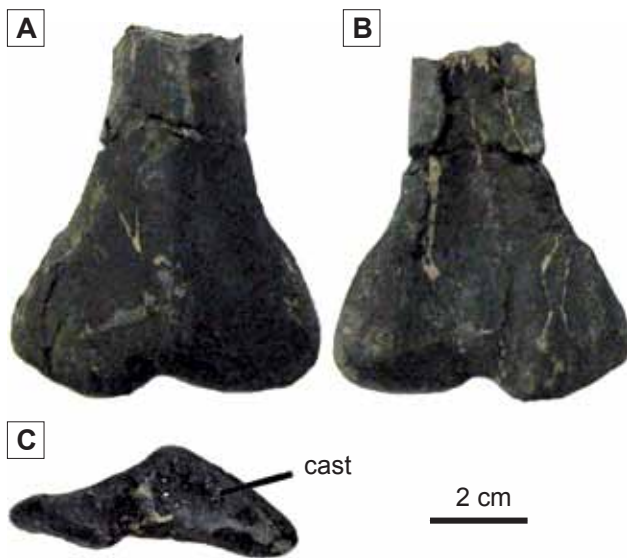**Carnosauria** Huene, 1920

Allosauroidea Currie et Zhao, 1993

Gen. et sp. indet.

Material. – YPM VP 058268 right distal end of tibia.

Type locality, horizon and age. – Quarry 12, Como Bluff, Wyoming, USA. The specimen was found in the Morrison Formation, Upper Jurassic (Kimmeridgian/Tithonian).

Description:
Tibia. YPM VP 058268 is the right distal tibia including part of the shaft (Fig. 13). The anterior face of the tibia is slightly crushed, and the posterior face is intact. The preserved fragment of the tibia's shaft is flattened and straight.

Fig. 13. Allosauroidea indet. YPM VP 058268, right distal end of tibia from the Upper Jurassic Morrison Formation, Quarry 12, Como Bluff, Wyoming

A. Lateral view. **B.** Medial view. **C.** Distal view. **Abbreviations:** cast – contact for astragalus

As in other tetanuran and neoceratosaur theropods (Britt, 1991; Madsen, 1993; Benson, 2009, 2010), the tibia (YPM VP 058268) gradually expands both medially and laterally towards its distal end and in distal view has a triangular outline. The anterior face has a well-defined, large and uneven depression for the ascending process of the astragalus. The distal surface of the tibia has a gentle depression for articulation with a corresponding eminence of the astragalus (Madsen, 1993; Benson, 2009, 2010). The suprastragalar buttress is well defined in YPM VP 058268. It is a ridge or step-like, which is proximolaterally oriented in overall morphology, and thus, resembles that of other tetanuran theropods (Madsen, 1976a; Benson, 2009, 2010).

The distal surface of the YPM VP058268 tibia closely resembles that of *Allosaurus fragilis* (Madsen, 1993). However, in anterior and posterior views the distal end of YPM VP 058268 is more symmetrical than that of *A. fragilis* and also of other basal tetanurans such as *Torvosaurus tanneri* (Britt, 1991), *Magnosaurus nethercombensis* (Benson, 2009), and *Megalosaurus bucklandii* (Benson, 2009). A significant asymmetry of the distal end of the tibia is also present in neoceratosaur theropods (Madsen, Welles, 2000). The YPM VP 058268 tibia is further distinguished from basal coelurid theropods by having a significantly more expanded distal end. The characteristically shaped distal surface for the articulation with the corresponding eminence of

the astragalus suggests that (YPM VP 058268) belongs to a juvenile tetanuran theropod and most likely represents a previously unrecognized taxon.

Coelurosauria von Huene, 1914

Coelurosauridae indet.

Material. – YPM VP (uncatalogued), left proximal humerus.

Type locality, horizon and age. – Quarry 12, Como Bluff, Wyoming. The specimen was found in the Morrison Formation, Upper Jurassic (Kimmeridgian/ Tithonian).

Description:
Humerus. YPM VP (uncatalogued) is identified as a proximal left humerus (Fig. 14). The length of the preserved bone fragment is approximately 4 cm. If complete the humerus would be slightly longer than that of *Coelurus fragilis* and *Ornitholestes hermanii*. That of *C. fragilis* is 11.9 cm and of *O. hermanii* is 12.4 cm. Therefore, the humerus (YPM VP uncatalogued) could have reached a length of 13 cm. A small portion of the proximal humeral shaft is preserved, which appears to be flat, but not markedly, as in *Coelurus*. The humeral head of YPM VP uncatalogued is slightly eroded. However, as in *Ornitholestes* (Carpenter *et al.*, 2005b), the humeral head is low and most likely was confluent with the deltopectoral and bicipital crests.

DISCUSSION

Skeletal fossil remains of small and juvenile theropods are rare in the Morrison Formation (Foster, Chure, 2006; Hunt, Lucas, 2006). They consist largely of isolated bones and teeth. Several taxa of small-bodied theropods are well-recognized in the Morrison Formation, including *Coelurus fragilis*, *Elaphrosaurus* sp., *Koparion douglassi*, *Marshosaurus bicentesimus*, *Ornitholestes hermanii*, *Stokesosaurus clevelandi*, *Tanycolagreus topwilsoni*, and Coeluridae indet. (NMMNH P-26093) (Madsen, 1974, 1976; Galton, 1980; Chure, 1994; Foster, Chure, 2000; Foster, 2003, 2007; Carpenter *et al.*, 2005a, b; Hunt, Lucas, 2006; Benson, 2008; Brusatte, Benson, 2013). During the past three decades numerous isolated bones identified as belonging to dromaeosaurid and troodontid theropods were found in the Dry Mesa Quarry, Colorado, Quarry 9 at Como Bluff, Wyoming, and in east-central Wyoming (Ostrom, 1980; Jensen, 1981; Jensen, Padian, 1989; Bakker, 1998; Carpenter *et al.*, 2005a; Hartman *et al.*, 2005). YPM VP (uncatalogued), a right proximal humerus from Quarry 12, Como Bluff, Wyoming, is
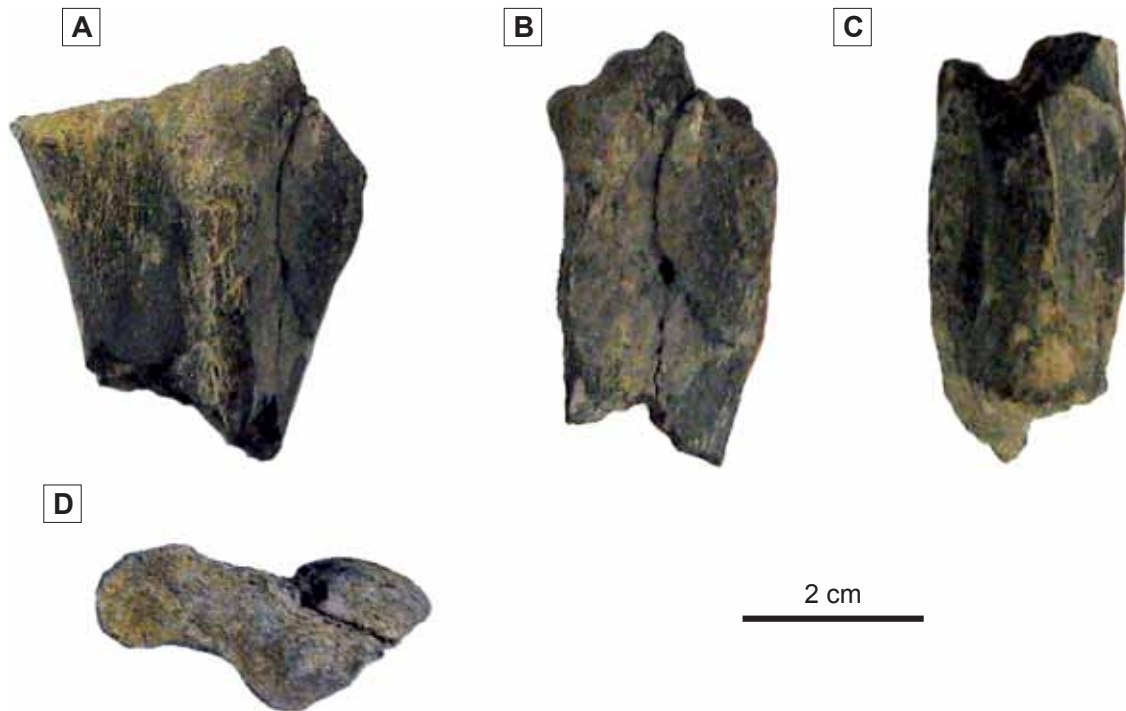
Fig. 14. Coeluridae indet. YPM VP (uncatalogued), proximal left humerus from the Upper Jurassic Morrison Formation, Quarry 12, Como Bluff, Wyoming

A. Anterior view. **B.** Lateral view. **C.** Medial view. **D.** Cross-section of the proximal articular end

morphologically distinct from *Coelurus*, *Ornitholestes*, and *Tanycolagreus*, and suggests the presence of another small-bodied theropod, which adds to the diversity of coelurid theropods in the Morrison Formation. The discovery of new diagnostic skeletal materials suggests that coelurid diversity during the Late Jurassic in North America was much greater than previously suggested (Hunt, Lucas, 2006). It is very likely that new specimens of small-bodied coelurid theropods will be discovered in the near feature at the other Morrison Formation localities.

During the Late Jurassic the North American coelurid theropods first evolved at small-body size and lived in the shadows of the large-bodied basal tetanurans *Allosaurus* and *Torvosaurus* and the neoceratosaurian *Ceratosaurus*, with which they shared the same ecosystems. They most likely hunted smaller prey but occasionally may have fed on large carcasses of sauropods and other dinosaurs (Bakker, 1986, 1998). Isolated teeth of small theropods assigned to coelurid theropods are found in the macrovertebrate sites in the Morrison Formation mixed with the bones of large herbivorous dinosaurs (Bakker, 1998).

Allosaurus is the most common large-bodied basal tetanuran theropod from the Upper Jurassic Morrison Forma-

tion, which is largely represented by subadult and adult examples. The genus had a wide paleogeographic distribution across the Morrison Formation (Foster, 2003, 2007). Four species are known in the Morrison Formation, *Allosaurus atrox*, *A. fragilis*, *A. jimmadseni*, and *A. lucasi* (Foster, 2003, 2007; Dalman, 2014 – this volume). The genus is also present in Portugal and is referred to a new species *A. europaeus* by Mateus *et al*. (2006). However, other workers (Malafaia *et al*., 2007) suggested that *A. europaeus* is morphologically more similar to *A. fragilis*, and thus, may belong to this taxon. Other materials from Portugal of *Allosaurus* such as a partial pelvis and hind limb were referred to *A. fragilis* (Pérez-Moreno *et al*., 1999), and a juvenile maxilla from Guimarota to *Allosaurus* sp. (Rauhut, Fechner, 2005).

Although small juveniles of *Allosaurus* are rare in the Morrison Formation they are known from several localities within the formation such as the Dry Mesa Quarry in Colorado, Cleveland-Lloyd Quarry in Emery County, Utah, and the Black Hills in northeastern Wyoming (Foster, Chure, 2006). These specimens are mostly isolated bones consisting of axial and appendicular elements. It has been observed that the population sample of *Allosaurus* from the Cleveland-Lloyd Dinosaur Quarry in Utah does not show radical

ontogenetic change in the postcranial skeleton, especially of the hind limb morphology, which is identical to that of large adults (Madsen, 1993; Foster, Chure, 2006; Hunt, Lucas, 2006). This observation is supported by a nearly complete specimen of a small juvenile *Allosaurus* sp., (SDSM 30510) (Foster, Chure, 2006) from the Black Hills of Wyoming and the isolated cranial, axial and appendicular elements here described from Quarry 12.

Torvosaurus is another large-bodied Upper Jurassic theropod, based on several incomplete specimens, which were found at various localities in the Morrison Formation, suggesting a wide paleogeographic distribution of this important taxon (Carrano *et al.*, 2012). The incomplete materials originally referred to *Edmarka rex* (Bakker *et al.*, 1992) and "*Brontoraptor*" (Siegwarth *et al.*, 1997) from Como Bluff, Wyoming, are most likely junior synonyms of *Torvosaurus* (Holtz *et al.*, 2004; Carrano *et al.*, 2012). However, both need much detailed osteological description to determine the validity of this assumption. Isolated skeletal materials of *Torvosaurus* are known from the Early Tithonian of Casal do Bicho and the Lourinhã Formation of Portugal (Mateus, Antunes, 2000). Recently, re-description by Hendrickx and Mateus (2014) of the fossil materials from Portugal referred the material to new species, *Torvosaurus gurneyi*, and suggests a much wider paleogeographic distribution of the genus during the Late Jurassic. Both the North American and Portuguese *Torvosaurus* specimens represent fully grown adults, and no juveniles of this genus were previously reported from either locality. The proximal left tibia (YPM VP 058269) identified here as *Torvosaurus tanneri* from Como Bluff, Wyoming, thus represents the first occurrence of a juvenile of this taxon in the Morrison Formation. YPM VP 058269 is morphologically identical to adult examples of *T. tanneri* (Britt, 1991), and, as in adults, the lateral condyle is more centered and the cnemial crest is short and transversely wide. However, in YPM VP 058269 the intercondylar notch that separates the condyles in the posterior region of the tibia is deeper than in adult *Torvosaurus* and has a characteristic triangular shape. It is tenable that this characteristic morphology represents an ontogenetic variation.

Fosterovenator churei (YPM VP 058267) is identified as a ceratosaurid theropod, which based on its overall morphology is more closely related to *Elaphrosaurus* than to *Ceratosaurus*. The proximal end of the tibia of *Fosterovenator* also resembles a right tibia of a small theropod from the Morrison Formation of the Garden Park, Colorado, which was originally referred to *Elaphrosaurus* by Chure (2001). However, Carrano and Sampson (2008) suggested that the Garden Park right tibia exhibits a greater resemblance to isolated Tendaguru abelisauroid tibiae (Rauhut, 2005) than to *Elaphrosaurus*. The tibia of *Fosterovenator* is also morpho-

logically similar to that of Tendaguru abelisauroid tibiae (Rauhut, 2005). Therefore, based on this evidence both the *Fosterovenator* and the Garden Park "*Elaphrosaurus*" (Chure, 2001) most likely represent the first occurrence of basal Late Jurassic abelisauroids in the Northern Hemisphere. However, more complete specimens are needed to determine the validity of this assumption.

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