

Osteology of a large allosauroid theropod from the Upper Jurassic (Tithonian) Morrison Formation of Colorado, USA

Sebastian G. DALMAN¹

Key words: dinosaur, Theropoda, Allosauridae, Morrison Formation, Upper Jurassic, Colorado.

Abstract. Two partial skeletons of allosaurid theropods belonging to an adult and a juvenile from the Upper Jurassic (Tithonian) Morrison Formation of McElmo Canyon in Montezuma County, southwestern Colorado, were discovered in 1953 by the late Joseph T. Gregory and David Techter. The adult specimen consists of several isolated cranial and postcranial skeletal elements that are exceptionally well-preserved and include the left premaxilla, maxilla, dentary, teeth, quadratojugal, two caudal vertebrae, pubic peduncle, ischium, proximal tibia, a nearly complete left foot, and several isolated teeth, whereas the juvenile specimen is represented by the distal portion of the right dentary and a fragmentary splenial. The specimens represent a new species of *Allosaurus*, here named *Allosaurus lucasi*, which differs from *Allosaurus fragilis* by having a relatively short premaxilla and robust quadratojugal with short jugal process and a short quadratojugal process of the quadratojugal that is at the same level as the rostral quadratojugal ramus. The presence of a new species of *Allosaurus* in the Tithonian of North America provides further evidence of the taxonomic and morphological diversity of the Allosauridae clade and their continuous evolutionary success, which extended to the Cretaceous.

INTRODUCTION

During the Late Jurassic in North America, *Allosaurus* was the numerically dominant large-bodied theropod, which shared the same ecosystems with other large-bodied theropods such as *Torvosaurus tanneri* (Galton, Jensen, 1979; Jensen, 1985; Britt, 1991), *Ceratosaurus dentisulcatus*, *C. magnicornis*, *C. nasicornis*, and *Saurophaganax maximus* (Gilmore, 1920; Chure, 1995; Madsen, Welles, 2000; Foster, 2003, 2007). Numerous skeletal remains of *Allosaurus* are found throughout the entire Morrison Formation in modern day Colorado, Montana, New Mexico, Oklahoma, South Dakota, Utah, and Wyoming.

The most complete and the best known species of *Allosaurus* are *Allosaurus atrox* (formerly *Creosaurus atrox*; Marsh, 1878), *A. fragilis* (Madsen, 1993), and *A. jimmadseni* (Chure, 2000). The Allosauridae clade includes some of the

largest predators that lived during the Late Jurassic and Cretaceous. Their remains are also known from Asia, Africa, and Europe (Pérez-Moreno *et al.*, 1999; Madsen, Welles, 2000; Naish, 2003; Mateus, 2006; Mateus *et al.*, 2006). I add to knowledge of North American Late Jurassic allosaurid diversity two specimens, here named *Allosaurus lucasi* sp. nov., representing adult and juvenile individuals, that were discovered in 1953 by the late Joseph T. Gregory and David Techter in McElmo Canyon in Montezuma County, Colorado, near the top of the Upper Jurassic Morrison Formation (Tithonian). The specimens were found in a hard conglomeratic matrix, which still encases some of the bones. The adult specimen consists of several cranial and postcranial elements, some of which are fragmentary and others, such as the left pes, are nearly complete, whereas the juvenile is known only from a fragmentary right distal dentary and partial splenial. The presence of a new species of *Allosaurus* in

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

the Tithonian of North America provides further evidence of the taxonomic and morphological diversity of the Allosauridae clade and their continuous evolutionary success, which extended to the Cretaceous. In this paper, YPM refers to the Yale Peabody Museum of Natural History.

GEOLOGICAL BACKGROUND

Field notes (July 20 to July 23, 1953) of Joseph T. Gregory of the Yale Peabody Museum of Natural History, New Haven, Connecticut, USA, indicate that the allosaurid specimens described here (YPM VP 57589 and YPM VP 57726) were collected west of Cortez in southwestern Colorado at

McElmo Canyon from the top of the Morrison Formation (Fig. 1). The lithology at the site is largely a conglomerate with a mix of fine-grained sandstone indicating a fluvial environment. The uppermost sediments in McElmo Canyon where the allosaurids were collected are included in the Brushy Basin Member of the Morrison Formation. Kowallis *et al.* (1998) reported that sanidine ages from the Brushy Basin Member in southwestern Colorado range from 150.33 ± 0.27 Ma to 147.82 ± 0.63 Ma, which indicate an age of Kimmeridgian to Tithonian. Bralower *et al.* (1990), Harland *et al.* (1990), Obradovich (1993), O'Sullivan (1997), and Turner and Peterson (2004) also indicated that the Brushy Basin Member in southwestern Colorado is Kimmeridgian to Early Tithonian in age. The age of the Morrison Forma-

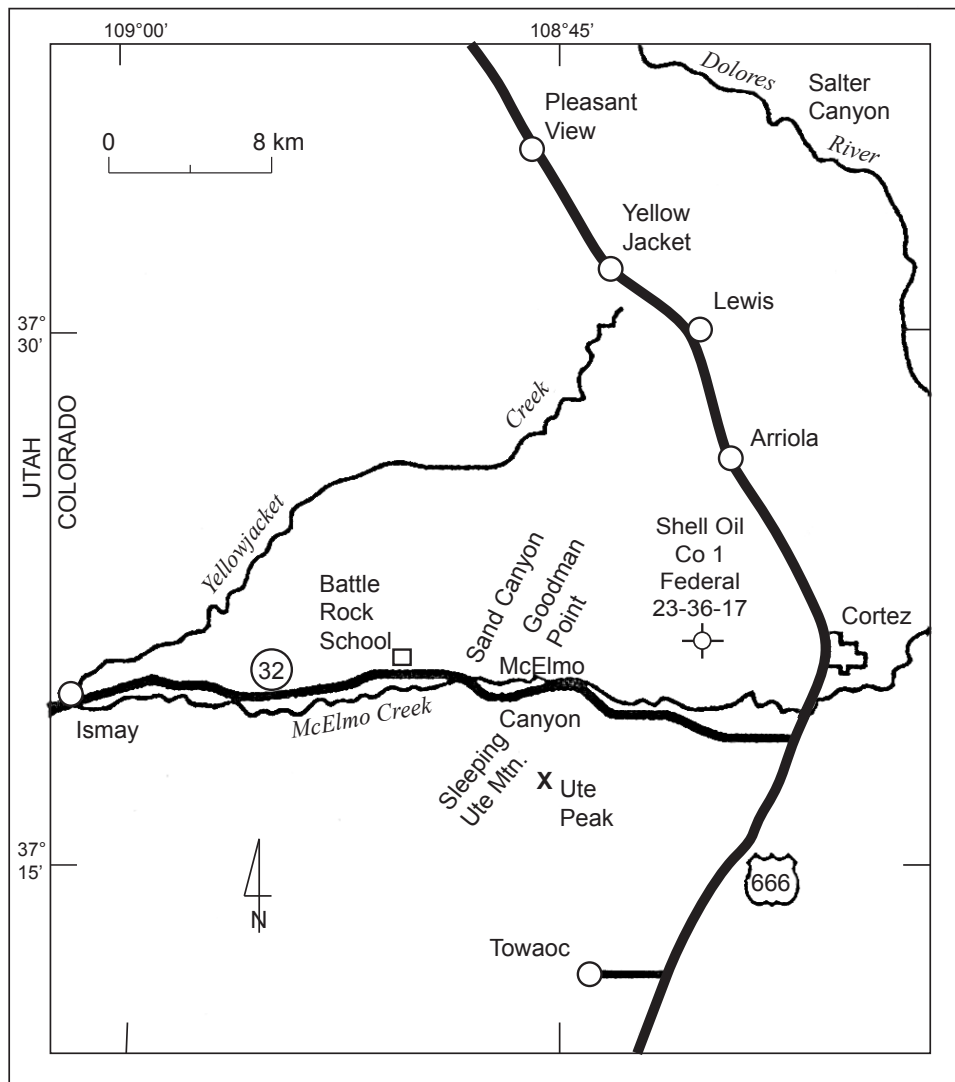


Fig. 1. Map of southern Colorado, USA showing the location of McElmo Canyon in which the *Allosaurus lucasi* sp. nov. (YPM VP 57589) was found (modified from O'Sullivan, 1997)

tion is similar to the Solnhofen Limestone in Germany, the Lourinhã and Alcobaça formations in Portugal, and the Tendaguru Formation in Tanzania (Mateus *et al.*, 2006; Foster, 2007).

SYSTEMATIC PALEONTOLOGY

Saurischia Seeley, 1887

Theropoda Marsh, 1881

Tetanurae Gauthier, 1986

Carnosauria von Huene, 1920

Allosauridae Marsh, 1878

Allosaurus lucasi sp. nov.

Holotype: YPM VP 57589, partial skeleton of an adult consisting of cranial, dental, and postcranial elements.

Included species: The type material is only known from type species *Allosaurus lucasi* sp. nov.

Included specimens: YPM VP 57726, posterior end of the right dentary and part of the right splenial belonging to a juvenile.

Etymology: The species name honors Spencer G. Lucas in recognition of his extensive contributions to vertebrate paleontology.

Type locality, horizon and age: McElmo Canyon, Montezuma County, Colorado, USA; Brushy Basin Member of the Morrison Formation Upper Jurassic (Tithonian).

Diagnosis: Large-bodied allosauroid theropod with the following autapomorphies: strongly reduced length of premaxilla; short and deep maxilla; quadratojugal with reduced jugal process and quadrate process; the ventral margins of the rostral quadratojugal ramus and the quadrate process of the quadratojugal form a single line; lateral condyle of the tibia strongly removed posteriorly, whereas in *Allosaurus fragilis* and *Saurophaganax maximus* the condyle is more centered and occupies almost half the length of the tibial head.

Remarks. – All specimens described here were found together at the same locality. They exhibit the same morphology, which suggests that they belong to the same species, but to theropods of different sizes and age groups.

DESCRIPTION AND COMPARISONS

The type specimen of *Allosaurus lucasi* (YPM VP 57589) consists of well-preserved but fragmentary cranial and postcranial skeletal elements.

CRANIAL SKELETON

Premaxilla. The left premaxilla of *Allosaurus lucasi* is well-preserved (Fig. 2). It is approximately 11 cm long and 11 cm high. In several basal tetanuran theropods such as

Allosaurus, *Monolophosaurus*, *Neovenator*, and *Sinraptor*, the premaxilla is longer than tall not including the nasal process (Currie, Zhao, 1993; Zhao, Currie, 1993; Brusatte *et al.*, 2008a, b, 2010; Eddy, Clarke, 2011) (Fig. 3). As in other examples of *Allosaurus*, there are five teeth in the premaxilla of *A. lucasi*. The number of premaxillary teeth in basal and more derived allosauroid theropods vary and is five in *A. fragilis*, *A. jimmadseni*, and four in *Sinraptor dongi*, whereas in derived allosauroids, the carcharodontosaurid theropods such as *Acrocanthosaurus atokensis* and *Carcharodontosaurus saharicus*, the premaxillary tooth count is four, and most likely it was the same in less complete taxa for which the premaxillae are unknown such as *C. iguidensis*, *Eocarcharia dinops*, *Giganotosaurus carolinii*, *Kelmaysaurus petrolicus*, *Mapusaurus rosea*, *Shaochilong maortuensis*, and *Tyrannotitan chubutensis*.

In *Allosaurus lucasi* the medial side of the bone is cemented to the conglomeratic matrix; covering most of the important features. However, in the future the specimen will be better prepared to reveal these features. The body of the premaxilla is slightly trapezoidal. The anteroventral margin of the premaxilla is inclined vertically and forms a low-angle snout, whereas the posterior margin is slightly angled posteriorly. The premaxillary angle that is formed between the ventral and anterior margins is 55° in *A. lucasi*, whereas in *A. fragilis* and *Ceratosaurus magnicornis* and *Torvosaurus tanneri* the premaxillary angle is slightly higher (Britt, 1991; Madsen, Welles, 2000). *Allosaurus*, *Ceratosaurus*, and *Torvosaurus* are distinguished from each other based on various premaxillary angle measurements (Britt, 1991). The alveoli for the premaxillary teeth are slightly elliptical in shape. The length of each of the alveoli is 2 cm. The angle, as measured between the symphysis and the center of the

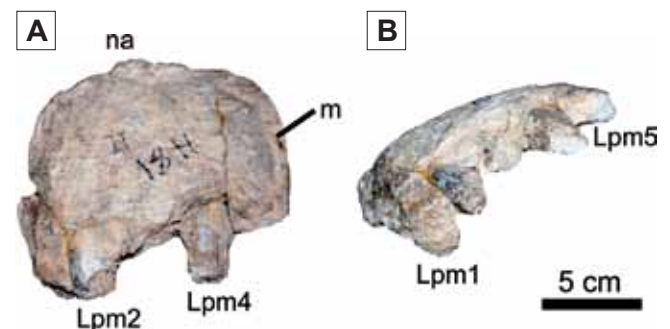


Fig. 2. Left premaxilla of *Allosaurus lucasi* sp. nov. (YPM VP 57589) from the Morrison Formation (Tithonian), McElmo Canyon, Montezuma County, Colorado, USA

A. Lateral view. **B.** Ventral view showing the premaxillary tooth row and partially preserved teeth. **Abbreviations:** m – maxilla contact; na – bony naris; Lpm1 to Lpm5 – premaxillary teeth

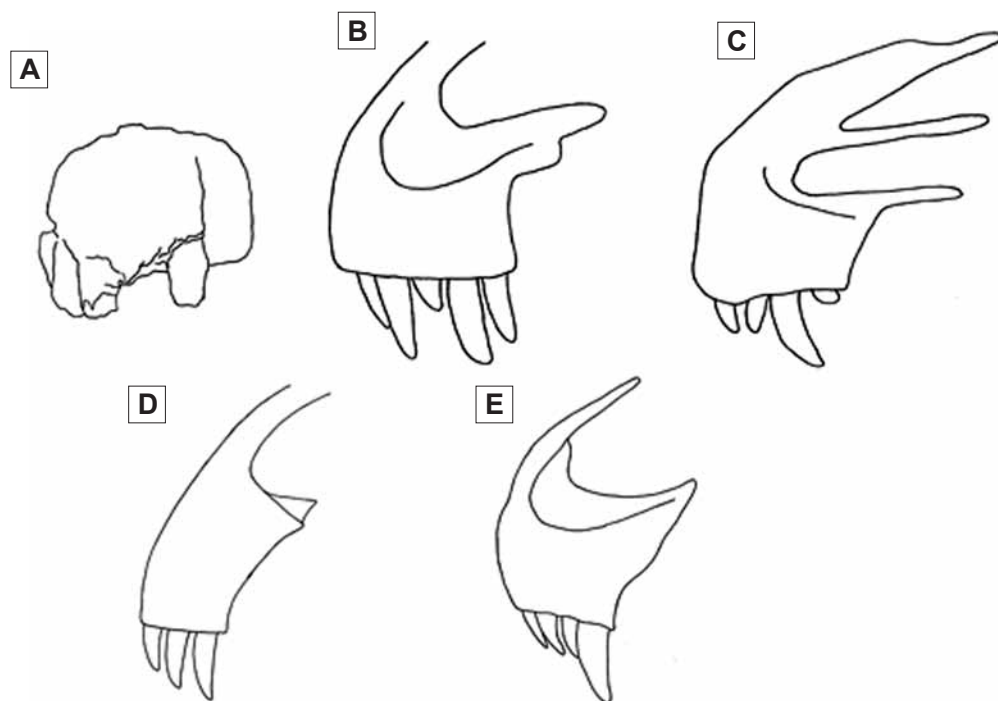


Fig. 3. Comparison of premaxillae of the Jurassic and Cretaceous basal tetanuran theropods

A. *Allosaurus lucasi*. **B.** *Allosaurus fragilis*. **C.** *Monolophosaurus jiangi*. **D.** *Neovenator salerii*. **E.** *Sinraptor dongi*. Premaxillae in lateral view. Fig B after Madsen (1993); Fig. C after Zhao, Currie (1993); Fig. D after Brusatte *et al.* (2008a); Fig. E after Currie, Zhao (1994). Not to scale

most anterior and most distal alveoli, is 20° in *A. lucasi*, whereas in *A. fragilis* the angle is between 25° and 30° . The consequence of this small angle in *A. lucasi* is that the snout is relatively narrow. Similar conditions are also present in other large theropods such as *Acrocanthosaurus*, *Carcharodontosaurus*, and *Giganotosaurus* (Currie, Carpenter, 2000; Eddy, Clarke, 2011).

The lateral surface of the premaxillary body of *Allosaurus lucasi* is smooth and lacks any type of ornamentation. Additionally, there is no evidence of the neurovascular foramina due to extensive weathering of the lateral surface of the bone.

Maxilla. The left maxilla of *Allosaurus lucasi* is partially preserved, missing most of the posterior portion (Fig. 4). The body of the preserved maxilla is triangular, and its length is approximately 17.7 cm. However, when compared to other large-bodied non-avian theropods (*e.g.*, *Acrocanthosaurus*, *Allosaurus*, and *Torvosaurus*) the original length of the maxilla of *A. lucasi* would have been approximately 35.4 cm, whereas the entire length of the skull would have been approximately 77.5 cm. These estimates are based on the length proportions of other large-bodied theropods such as *Acrocanthosaurus atokensis* and *Allosaurus fragilis*.

The maxilla is thick anteriorly and becomes thinner towards the posterior end, and it is slightly convex with a slight upturn in the anterior one-third, which is similar to that of *Torvosaurus tanneri* (Britt, 1991) (Fig. 5). The premaxilla-maxilla contact is not very clear; however, under closer examination it is discernible. The body of the maxilla in *Allosaurus lucasi* is relatively deep in the anterior region. It shows some similarities to the maxilla of *Acrocanthosaurus*. As in *Acrocanthosaurus*, the subnarial foramen in *A. lucasi* is absent, but it is present in *A. fragilis*. The subnarial foramen is also absent in other allosauroid theropods such as *Carcharodontosaurus*, *Giganotosaurus*, *Neovenator*, *Shaochilong*, and *Sinraptor*, but also in the abelisaurid theropods such as *Aucasaurus*, *Carnotaurus*, *Ekrixinatosaurus*, *Eoabelisaurus*, *Indosuchus*, *Majungasaurus*, and *Rugops*.

Basal tetanurans in general possess a distinctly shaped triangular anterior ascending ramus and a dorsal anterodorsal process that contacts the nasal (Brusatte *et al.*, 2010b). In *Allosaurus lucasi* only the base of the ascending ramus is preserved.

The tooth row in *Allosaurus lucasi* is not well-preserved, even though some partial teeth are preserved. Therefore, the exact maxillary tooth count cannot be determined at present. The number of the maxillary tooth count in basal allosauroid

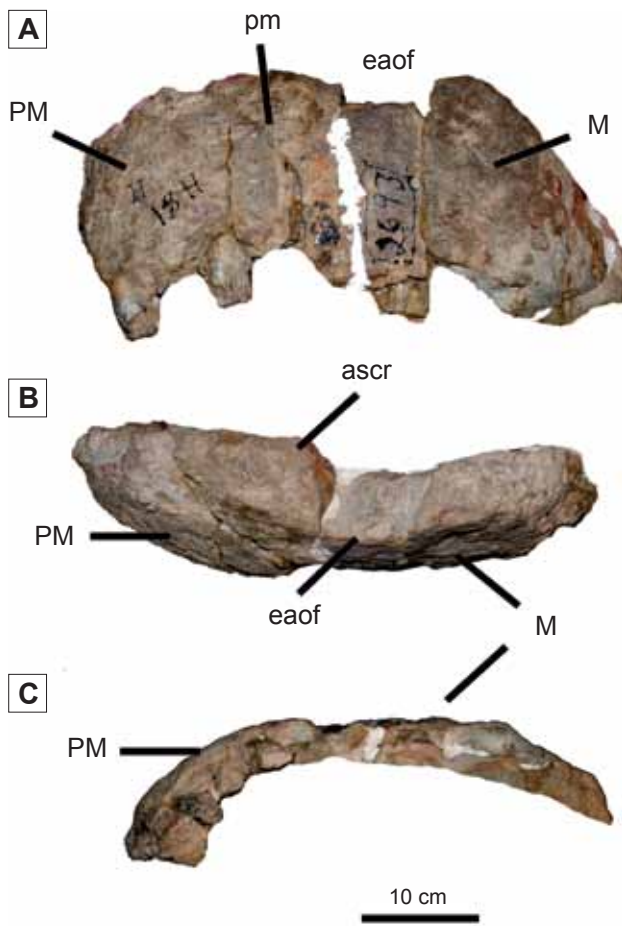


Fig. 4. Left premaxilla and maxilla of *Allosaurus lucasi* sp. nov. (YPM VP 57589) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA

A. Lateral view. B. Dorsal view. C. Ventral view showing the maxillary tooth row and partially preserved teeth. **Abbreviations:** ascr – ascending ramus of maxilla; eaof – margin of external antorbital fenestra; M – maxilla; PM – premaxilla; pm – premaxillary contact

theropods is variable: 16 in *A. jimadseni*, and 15 in *A. fragilis* and *Sinraptor dongi*. In carcharodontosaurid theropods the maxillary tooth count is 15 in *Acrocanthosaurus atokensis* and *Eocarcharia dinops*, 14 in *Carcharodontosaurus saharicus*, and 12 in *Giganotosaurus carolinii*, *Mapusaurus rosea*, and *Shaochilong maortuensis*. It is possible that the variation in tooth count in these taxa represents an ontogenetic variation.

The sandstone matrix on which the maxilla of *Allosaurus lucasi* rests contains a mix of bones from the skull, which include two partially preserved alveoli and a single preserved root of a tooth. Some of the flat bones exposed on the surface of the matrix are either parts of the maxilla or some other skull bones.

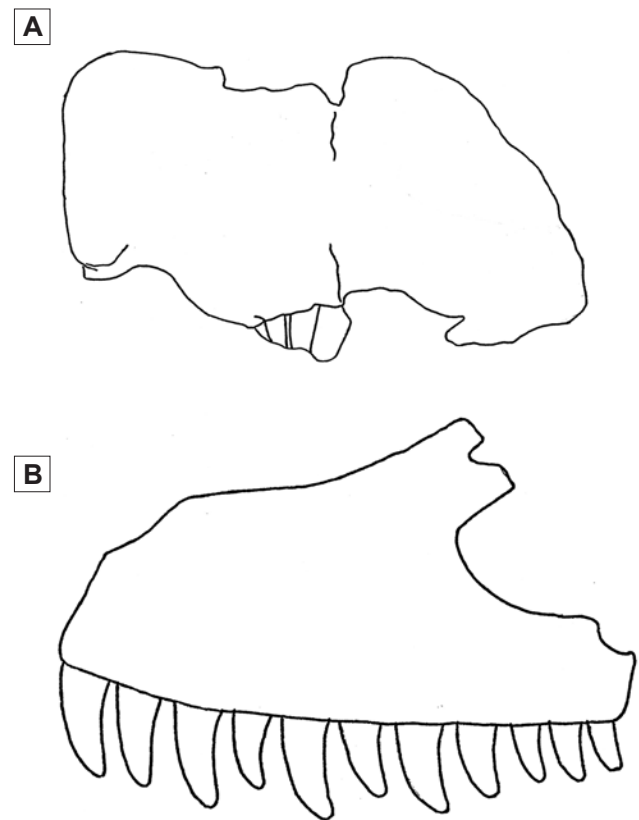


Fig. 5. Comparison of the maxillae of *Allosaurus lucasi* sp. nov. (YPM VP 57589) from the Morrison Formation (Tithonian) of McElmo Canyon, Montezuma County, Colorado, and *Torvosaurus tanneri* (BYUVP 9122; Britt, 1991) from the Morrison Formation (Tithonian) Dry Mesa Quarry, Colorado, USA. (*Torvosaurus tanneri* maxilla after Britt, 1991)

Not to scale

Quadratojugal. The left quadratojugal of *Allosaurus lucasi* is well preserved (Fig. 6). As in other theropods the bone is L-shaped and possesses a relatively short rostral quadratojugal ramus. The bone is split in half vertically, and the two parts are mirror images of each other encased in hard sandstone matrix.

The length of the preserved quadratojugal is 16 cm, and its height is 14.5 cm. The jugal process of the quadratojugal is broken off and missing; however, when reconstructed the jugal process of *A. lucasi* appears much shorter than that of *A. atrox*, *A. fragilis* and *A. jimadseni*. The angle between the dorsal quadratojugal ramus and the rostral quadratojugal ramus in *A. lucasi* is approximately 90°, whereas in *Allosaurus*

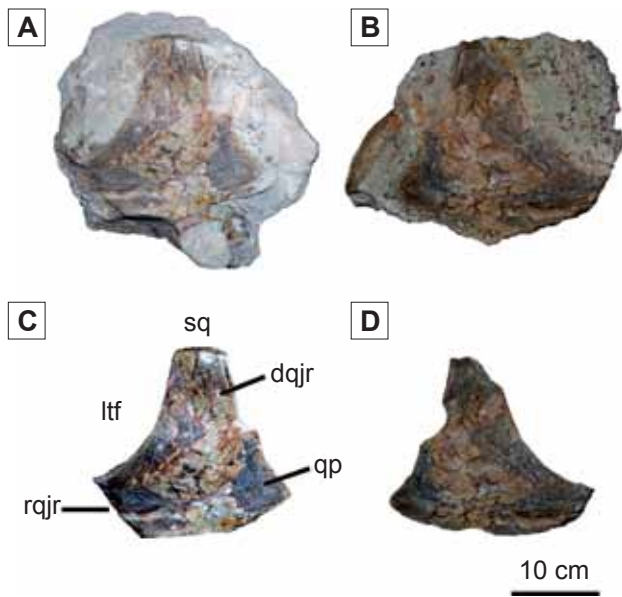


Fig. 6. Left quadratojugal of *Allosaurus lucasi* sp. nov. (YPM VP 57589) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA

A and **B.** Two halves of the quadratojugal in sandstone matrix; **C** and **D.** Two halves of the quadratojugal (digitally removed matrix). **Abbreviations:** dqjr – dorsal quadratojugal ramus; ltf – laterotemporal fenestra; qp – quadrate process of quadratojugal; rqjr – rostral quadratojugal ramus; sq – squamosal contact

the angle is 75°. The dorsal quadratojugal ramus in *A. lucasi* is relatively straight, whereas in *Allosaurus* it is bent forward. Similar conditions to that of *A. lucasi* are observable in the reconstructed skull of *Torvosaurus tanneri* (Britt, 1991). However, the quadratojugal of *T. tanneri* has yet to be collected; therefore, the reconstruction and its position in the skull is based on another bone, the quadrate (Britt, 1991). The rostral ramus in *A. lucasi* is deepest caudally and tapers rostrally. Taxonomic variation is in large part associated with the relative shape and size of the dorsal and the rostral rami (Sampson, Witmer, 2007). Within basal theropods the contact between the quadratojugal and squamosal is variable (Sampson, Witmer, 2007). The dorsal ramus in *Herrerasaurus*, for example, is twice the width of the rostral ramus and does not have a clear connection with the squamosal (Sereño, Novas, 1993). However, taxa such as *Ceratosaurus* and *Eoraptor* have both rami relatively slender and narrow quadratojugal-squamosal contact (Sampson, Witmer, 2007). In contrast, in albertosaurine (e.g., *Albertosaurus* and *Gorgosaurus*) and in tyrannosaurine tyrannosaurids (e.g., *Daspletosaurus*, *Tarbosaurus*, and *Tyrannosaurus*) the dorsal rami are extensively expanded, and have a broad, rostrally projected contact for the squamosal, which form a large latero-

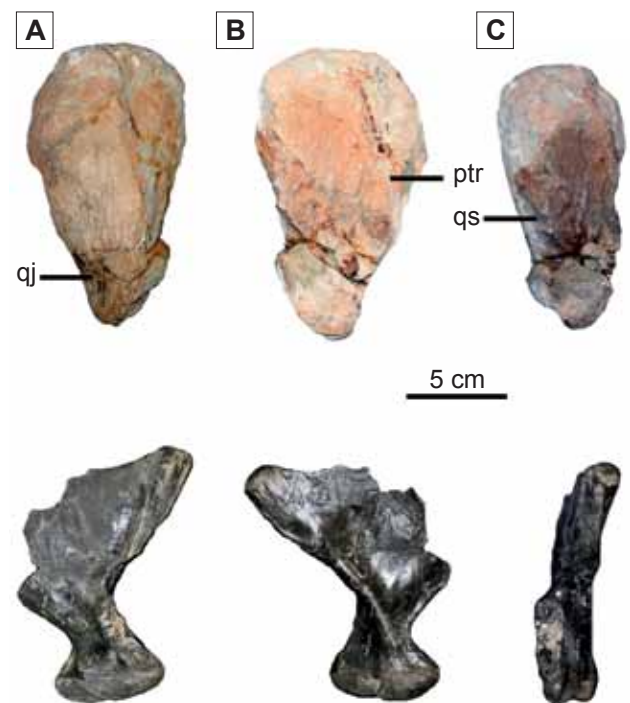


Fig. 7. Left quadrate of *Allosaurus lucasi* sp. nov. (YPM VP 57589) (above) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA compared with the left quadrate of *Allosaurus fragilis* (YPM VP 14554) (below)

A. Lateral. **B.** Medial. **C.** Rostral views. **Abbreviations:** ptr – pterygoid ramus of quadrate; qj – quadratojugal contact; qs – quadrate shaft

temporal fenestra (Carr, 1999; Carr, Williamson, 2004; Sampson, Witmer, 2007). As in *Allosaurus fragilis* (Madsen, 1993), the squamosal contact in *A. lucasi* is similarly broad, and the laterotemporal fenestra in both taxa may have been also of similar shape.

The length of the quadrate process of the quadratojugal in *A. lucasi* is 4.5 cm, and the height is 6 cm. The process is broader ventrally and forms a triangular slot for the contact with the quadrate. The dorsal quadratojugal ramus is approximately 13 cm tall. The process is broader ventrally and narrower dorsally, as in other theropods. The ventral side of the rostral quadratojugal ramus is in line with the quadrate process of the quadratojugal. A similar condition is also present in *A. jimmadseni* (Chure, 2000).

Quadrate. The left quadrate of *Allosaurus lucasi* is incomplete, however, several features, which are not well-preserved, can be recognized, including the pterygoid flange, pterygoid ramus, quadratojugal contact, quadrate shaft, and quadratojugal ramus of quadrate (Fig. 7). The bone is split in half and filled with hard sandstone matrix. The height of the bone is 13 cm. The pterygoid flange is incomplete; however,

it appears when reconstructed that it was anteroposteriorly long. As in other large-bodied theropods (Currie, Zhao, 1993; Madsen, 1993; Currie, 2006) the ventral margin of the pterygoid flange in *A. lucasi* was most likely curled medially. Most of the anterior and posterior sides of the lateral and medial surfaces are missing, including parts of the pterygoid process. The surface of the lateral side is smooth and lacks any ornamentation. The medial surface exhibits shallow sculpting in the form of parallel lines. These parallel lines represent muscle scars for the attachment of the posterior M. adductor mandibulae (Molnar, 2008).

The quadrate of *Allosaurus lucasi* is relatively tall, as in other medium- and large-bodied theropods, including *Ceratosaurus* and *Sinraptor* (Currie, Zhao, 1993; Madsen, Welles, 2000; Rauhut, 2003; Currie, 2006), and most abelisaurids (Bonaparte, Novas, 1985; Bonaparte *et al.*, 1990; Coria *et al.*, 2002; Sampson, Witmer, 2007; Canale *et al.*, 2008; Pol, Rauhut, 2012). Although, the quadrate condyle for the articulation with the quadrate contact on the quadrate process of the quadratojugal and for the articulation with the lower jaw is missing, the posterior end of the bone appears to be very slender, whereas in *A. fragilis* the structure is robust. In medial view the quadrate of *A. lucasi* is morphologically similar to that of *Sinraptor dongi* (Currie, Zhao, 1993). A distinct feature observed in allosauroid theropods (*e.g.*, *Acrocanthosaurus*, *Allosaurus*, *Giganotosaurus*, *Mapusaurus*, *Saurophaganax*, *Shaochilong*, and *Sinraptor*) is the presence of a quadratic foramen (Currie, Zhao, 1993; Chure, 1995; Coria, Salgado, 1995; Coria, Currie, 2006; Brusatte, Sereno, 2008; Eddy, 2008; Brusatte *et al.*, 2009, 2010; Eddy, Clarke, 2011). Because of the poor preservation of the bone it is unclear whether the quadrate of *A. lucasi* possessed the quadratic foramen. Other non-avian theropods such as *Ceratosaurus*, *Coelophysis*, and abelisaurids, including *Torvosaurus* all lack quadratic foramina (Currie, 2006).

Dentaries. There are two partially preserved right dentaries referred to *Allosaurus lucasi*. One dentary belongs to an adult (YPM VP 57589), whereas the other smaller dentary (YPM VP 57726) most likely represents a juvenile of *A. lucasi* (Fig. 8). According to the field notes of Gregory and Techter and their map of the specimen *in situ* (Fig. 9), these two dentaries were found in close proximity to each other and exhibit similar morphology. Therefore, it is tenable to suggest they belong to the same species.

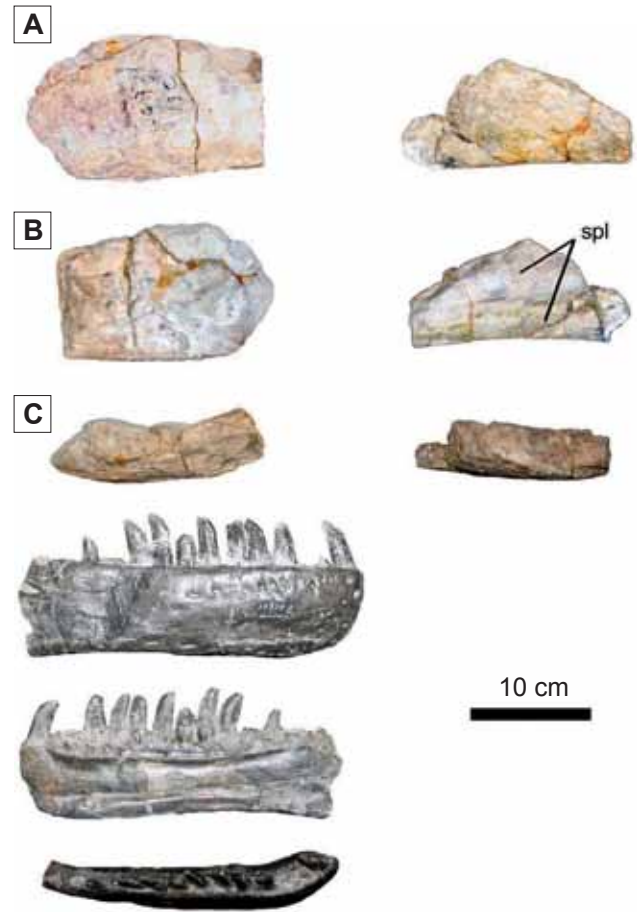


Fig. 8. Dentaries of an adult of *Allosaurus lucasi* sp. nov. (YPM VP 57589; on the left) and juvenile (YPM VP 57726; on the right) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA compared with the right dentary of *Allosaurus fragilis* (YPM VP 14554-8; on the left below)

A. Lateral. B. Medial. C. Occlusal views; spl – splenial contact

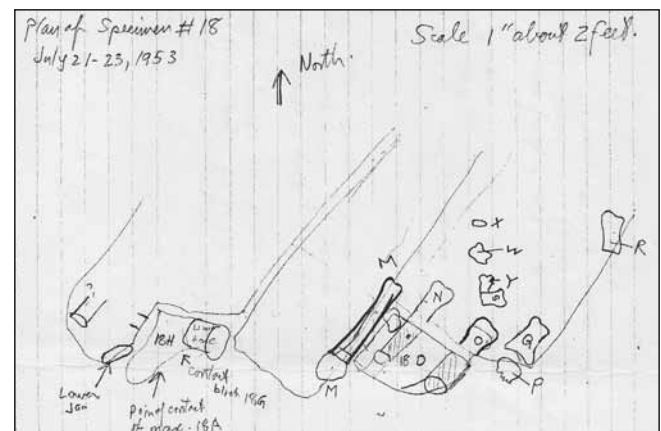


Fig. 9. Field map of the bones of *Allosaurus lucasi* sp. nov. (YPM VP 57589 and YPM VP 57726) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA (after Gregory and Techter 1953, Yale Peabody Museum of Natural History Archives)



Fig. 10. Splenial of juvenile of *Allosaurus lucasi* sp. nov. (YPM VP 57726) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA

A. Lateral. B. Medial

Dentary 1. A partial right dentary belongs to the holotype of *Allosaurus lucasi* (YPM VP 57589). The length of the preserved dentary fragment is 15 cm long and its depth is 9 cm. The bone, in cross section, preserves a single unerupted tooth. The tooth is split in half, exposing its cross section. The lateral surface of the bone is smooth and featureless, whereas the medial surface is heavily eroded and filled with hard sandstone matrix. The interdental plates are fused. The height of the interdental plate measured from the top of the splenial contact is approximately 2.5 cm. The splenial contact is a convex structure with an overall height of 3 cm and contacts the splenial medially.

Dentary 2. A partially preserved distal end of the right dentary of *Allosaurus lucasi* (YPM VP 57726) belongs to a juvenile. The dentary preserves five alveoli, containing five partially preserved teeth. The alveoli are elliptical in shape. The lateral surface of the bone is smooth and featureless and is similar to the dentary of an adult of *A. lucasi*. As in other theropods the dentary contacts the splenial medially. However, the splenial contact is much deeper than it is in other species of *Allosaurus*; it narrows anteriorly, widens posteriorly, and forms a V-shaped structure. The posteroventral portion of the dentary is much thinner than the anterior portion.

Splenial. A small elongated bone fragment identified as the right splenial (YPM VP 57726) most likely belongs to the juvenile individual (Fig. 10). The medial side of the bone has a shallow groove in the middle, which closely resembles the splenial contact. The ventral side of the bone has uniform thickness. When compared to the splenial of other large-bodied theropods the bone fragment (YPM VP 57726) most likely represents the anterior end of the splenial, as half way towards the posterior end the bone narrows uniformly and resembles that of other *Allosaurus*.

Teeth. YPM VP 57589 is a single well-preserved premaxillary tooth with root (Fig. 11). In lingual view, the tooth is convex. Most likely it is the fifth premaxillary tooth of the right premaxilla and resembles the premaxillary teeth of *Allosaurus fragilis*. Both anterior and posterior carinae are heavily eroded, and thus cannot provide important information on denticle density. The rostral carina of the premaxillary tooth in *A. lucasi* is oriented more medially, which is similar to that of *A. fragilis*. In labial view, the rostral side of the tooth has great convexity, whereas in the caudal side the tooth is flattened. The premaxillary tooth of *A. lucasi* possesses a moderate curvature. The angle of the curvature in labial and lingual views is 20°, and is similar to *A. fragilis*.



Fig. 11. Isolated premaxillary tooth of *Allosaurus lucasi* sp. nov. (YPM VP 57589) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA

A. Labial. B. Lingual views

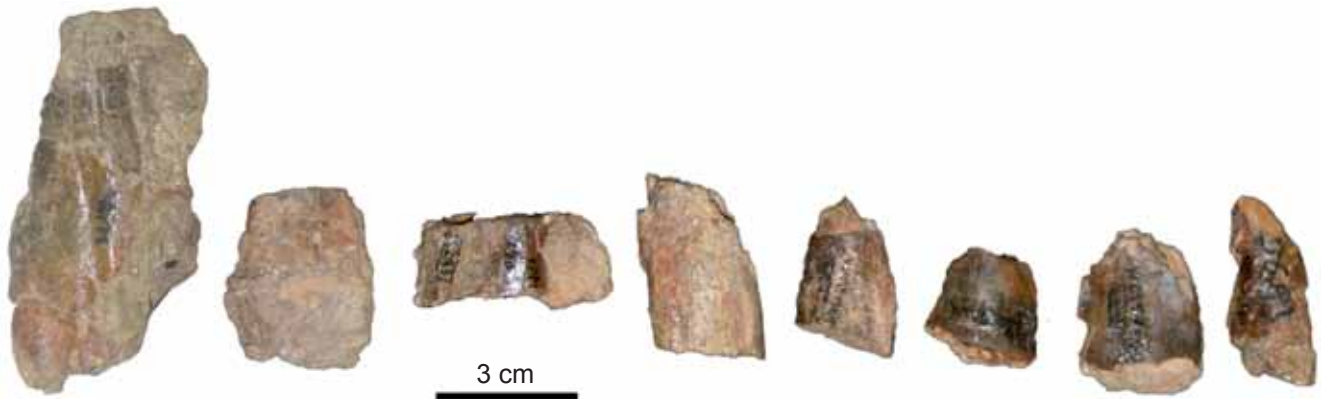


Fig. 12. Isolated lateral teeth of *Allosaurus lucasi* sp. nov. (YPM VP 57589) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA

Several isolated lateral teeth are partially preserved (Fig. 12). All teeth are laterally compressed and curved distally and are either from the maxilla or dentary. Some of the teeth preserved in the matrix on the left premaxilla and maxilla lie are large, and resemble those of *Allosaurus fragilis*. The degree of curvature can be determined in some teeth of *A. lucasi*. Sereno *et al.* (1998) suggested that tooth crowns with significant curvature are plesiomorphic in Theropoda, whereas teeth that lack curvature or with reduced curvature are considered the derived state and, therefore, a synapomorphy of Spinosaurinae. Smith (2007) suggested that this character represents a useful phylogenetic feature in theropods. The maxillary teeth of *A. lucasi* possess moderate curvatures. The anterior carina is oriented more on the lingual side, and the posterior carina is oriented on the labial side, which is similar to that of *A. fragilis* and to most other non-avian theropods.

The denticles on each lateral tooth are minute and similar to those of other allosauroid theropods such as *Acrocanthosaurus*, *Allosaurus*, and *Sinraptor*. However, not all the teeth preserve denticles due to their poor preservation. Therefore, the denticle densities and morphology cannot be determined at present for any of the teeth.

AXIAL SKELETON

Caudal vertebrae. Two caudal vertebral centra are known for *Allosaurus lucasi* (Fig. 13). Both centra are complete and exceptionally well-preserved. The larger centrum resembles the 19th vertebra in the caudal series of *A. fragilis*

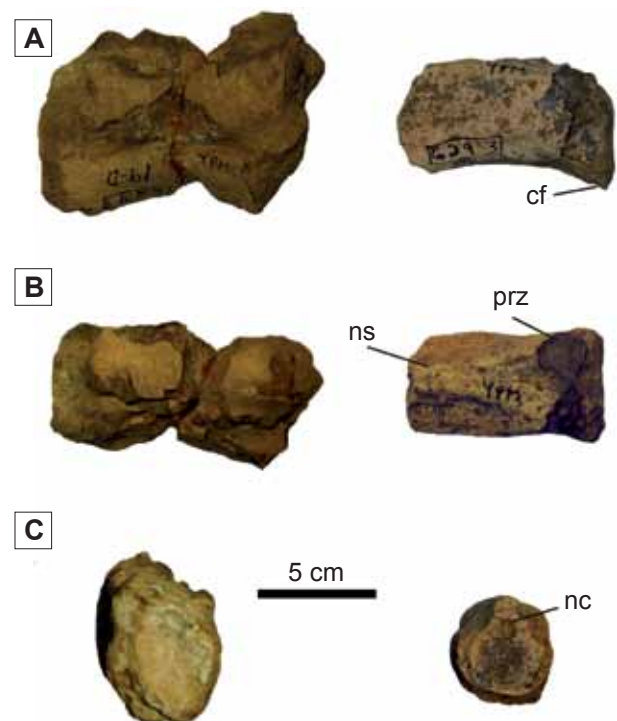


Fig. 13. Distal caudal vertebrae of *Allosaurus lucasi* sp. nov. (YPM VP 57589) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA

A. Right lateral. B. Dorsal. C. Cranial views. **Abbreviations:** cf – chevron facet; nc – neural canal; ns – neural spine; prz – prezygapophysis

(Madsen, 1993), and the smaller centrum is most likely the 25th or 28th in the caudal series (Madsen, 1993). As in *A. fragilis* and *A. jimmadseni* (Madsen, 1993; Chure, 2000), the caudal centra of *A. lucasi* are amphicoelous. In *A. fragilis* there are approximately 50 caudal vertebrae that form the tail, but the total number is variable (Madsen, 1993). It is tenable that *A. lucasi* had a similar number of caudal vertebrae in the tail. However, at present it cannot be determined for certain because only two caudal centra are known.

APPENDICULAR SKELETON

Ilium. The YPM material includes the left pubic peduncle of the ilium of *Allosaurus lucasi* (Fig. 14). The anteroposterior length is 15 cm, height is 11 cm, and transverse width is 7 cm. The neck of the pubic peduncle is slender. The lateral surface of the bone is partially preserved, and the medial surface is heavily eroded. The articular surface for the

contact with the pubis is slightly convex and ends with a small protruding structure, which extends throughout the entire anteroposterior length of the bone. This characteristic structure is unknown in *Allosaurus atrox*, *A. fragilis*, *A. jimmadseni*, *Torvosaurus tanneri*, and in other known theropods. In *A. fragilis*, the pubic peduncle is longer and less robust, whereas in *T. tanneri* it is transversely wide. The posterior region of the bone in *A. lucasi* is slightly concave, whereas in *A. atrox*, *A. fragilis*, *A. jimmadseni*, and *T. tanneri* the concavity is much deeper.

Pubis. Two isolated fragments represent the distal portion of the pubic shaft (Fig. 15). The most distal fragment of the pubis shaft is 9.5 cm wide and 7 cm long, whereas the other bone fragment is 7.5 cm wide and 10 cm long. In cross-section, both bone fragments have an elliptical shape. Unfortunately, the rest of the pubis is missing, and it is unclear if the pubis of *A. lucasi* closely resembled that of *A. fragilis* and *A. jimmadseni*. The pubis of *A. fragilis* is robust and the shaft itself is much thicker than that of *A. lucasi*.

Ischium. The YPM material includes a partially preserved distal end of the left ischium (Fig. 16). The bone consists of a small portion of the distal shaft. A portion of the lateral surface of the ischium is encased in hard sandstone

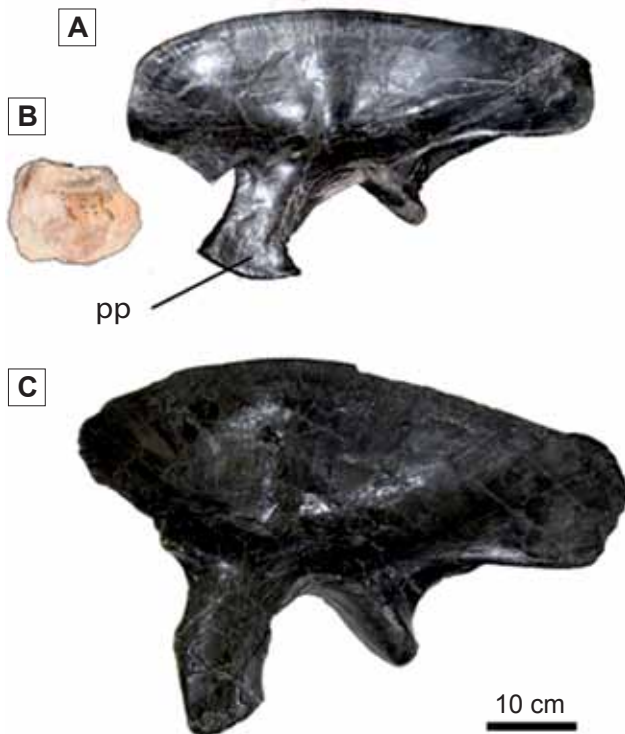


Fig. 14. Pubic peduncle of the left ilium of A, *Allosaurus lucasi* sp. nov. (YPM VP 57589) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA compared with ilium of B, *Allosaurus fragilis* (YPM VP 14554); C – *Allosaurus atrox* (YPM VP 1890)

Note: ilia of *A. fragilis* and *A. atrox* in left lateral view. **Abbreviations:** pp – pubic peduncle



Fig. 15. Two isolated fragments of pubic shaft in lateral view of *Allosaurus lucasi* sp. nov. (YPM VP 57589) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA

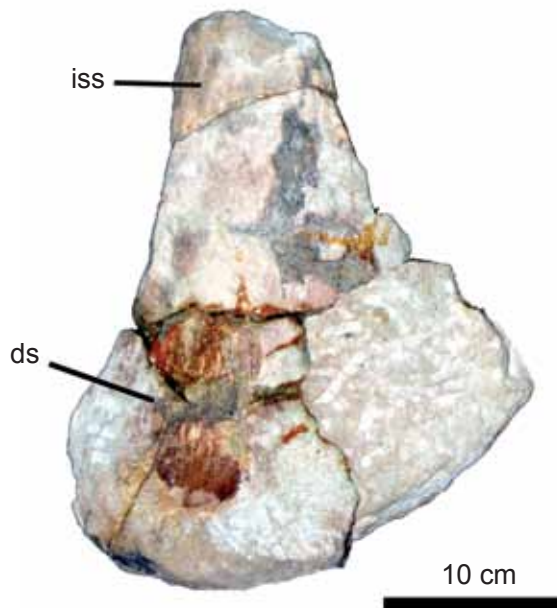


Fig. 16. Left distal ischium in lateral view of *Allosaurus lucasi* sp. nov. (YPM VP 57589) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA

ds – distal symphysis, iss – ischial shaft

matrix. The length of the preserved bone is 24 cm, and the anteroposterior width is 19 cm. The width of the shaft is 5.5 cm, whereas its distal end is 10.5 cm. The lateral surface of the bone is slightly convex, whereas its medial side is flat.

Tibia. The YPM material includes the proximal end of the left tibia (Fig. 17). The bone is large and robust, but is missing most of the shaft and is slightly compressed medio-laterally. The proximal articular end has an overall length of 18 cm. The bone is missing a significant portion of the cnemial crest, and only a small portion is preserved. Both the lateral and medial condyles are also partially preserved. The tibia of *A. lucasi* is morphologically distinct from *A. fragilis*. The medial condyle is ovoid shaped. As in other large-bodied non-avian theropods the condyles in *A. lucasi* are separated from each other by a deep and narrow intercondylar notch. The medial condyle is confluent with the cnemial crest; however, it is not clear whether the dorsal articular surface of the tibia was inclined distolaterally as in *Acrocanthosaurus atokensis* or the medial condyle was at the same level as the anterior end of the tibia as in *A. fragilis*. The lateral condyle is also ovoid shaped and of similar size as the medial condyle. In proximal view the lateral condyle is extended more distally and appears slightly longer than the medial condyle. The lateral condyle is separated from the proximal end of the tibia by a well-developed, but shallow crescentic concavity, the incisura tibialis (Madsen, 1993;

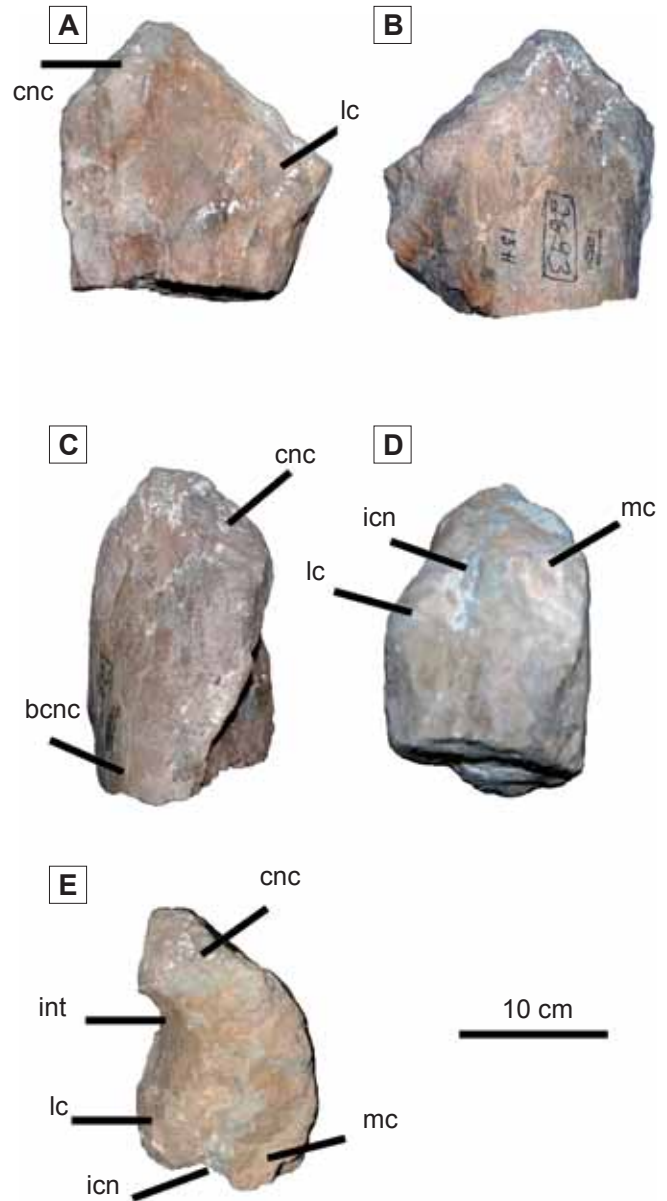


Fig. 17. Left proximal tibia of *Allosaurus lucasi* sp. nov. (YPM VP 57589) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA

A. Lateral. **B.** Medial. **C.** Anterior. **D.** Posterior. **E.** Dorsal views. **Abbreviations:** cnc – cnemial crest; bcnc – base of the cnemial crest; icn – intercondylar notch; mc – medial condyle; lc – lateral condyle; int – incisura tibialis

Azuma, Currie, 2000; Madsen, Welles, 2000; Rauhut, 2003; Benson, 2009). Although the lateral condyle is incomplete, it is tenable that on anterior edge of the condyle there was a well-developed distinct cranio-lateral projection, a feature that is characteristic of basal tetanuran theropods (e.g., *Allo*



Fig. 18. Associated left pedal of *Allosaurus lucasi* sp. nov. (YPM VP 57589) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA

saurus, *Saurophaganax*, and *Torvosaurus*). The craniolateral projection is also present in neoceratosaurs (e.g., *Ceratops* and *Elaphrosaurus*), small coelurid theropods (e.g., *Coelurus*, *Ornitholestes*, and *Tanycolagreus*), and tyrannosaurids (e.g., *Albertosaurus*, *Gorgosaurus*, *Lythronax*, *Tarbosaurus*, and *Tyrannosaurus*).

The cnemial crest in *Allosaurus lucasi* is incomplete; however, as in other large-bodied, non-avian theropods (Benson, 2009) its base arises from the anterior surface of the tibia's shaft and is curved anteroproximolaterally. The cnemial crest is elongated and narrowed transversely.

Pes. *Allosaurus lucasi* has a nearly complete and exceptionally well-preserved left pes (Fig. 18). The pes consists of the following bones: four metatarsals and eight digital phalanges, including one ungual phalanx.

Metatarsal I. The bone is missing a small portion of the most proximal end (Fig. 18). It is approximately 5.5 cm long. It is more massive than that of *Allosaurus fragilis*. Both collateral ligament pits are well-preserved. As in other non-avian theropods the medial pit is much deeper and

slightly larger than the lateral pit. The medial condyle appears more pronounced than the lateral condyle. Both condyles are separated from each other by a characteristic ginglymus, which is approximately 1 cm deep. The maximum transverse width of the distal articular surface is approximately 3.5 cm.

Metatarsal II. The bone is the best preserved and the most complete of all the metatarsals in *Allosaurus lucasi* (Fig. 19). The length of the entire bone is 33.5 cm. The bone is robust, straight, and has a uniformly wide shaft. The flat medial surface of the metatarsal shaft indicates that the bone was closely appressed to the metatarsal III for most of its length. The proximal articulation is typical for a theropod (Carrano, 2007), which is flat and featureless. The medial and lateral sides of the proximal articulation are missing a small portion of the bone. When reconstructed, the shape of the proximal articulation resembles to some extent that of *Torvosaurus tanneri* (Britt, 1991). The distal end of the shaft is bent slightly forward as in *Acrocanthosaurus atokensis*,

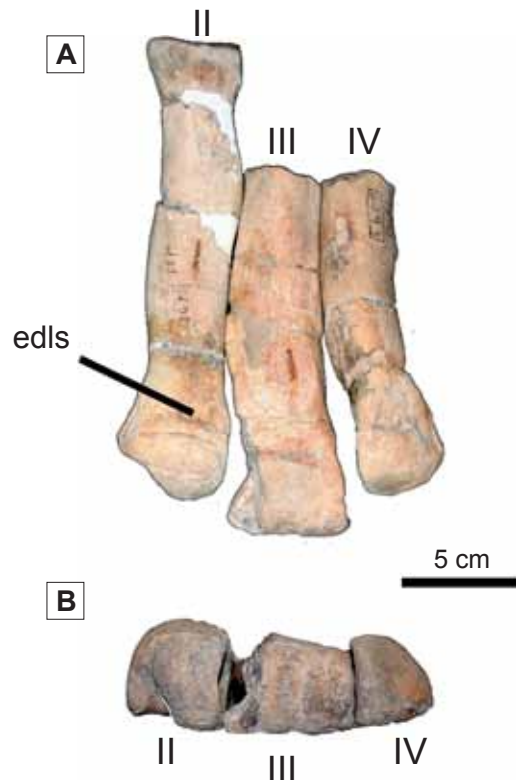


Fig. 19. Articulated left metatarsals of *Allosaurus lucasi* sp. nov. (YPM VP 57589) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA

A. Anterior. **B.** Distal views. **Abbreviations:** edls – fossa for insertion of *M. extensor digitorum longus*

Allosaurus fragilis, *Megalosaurus bucklandii*, and *Torvosaurus tanneri*. The distal articulation has well-preserved collateral ligament pits that are relatively deep. The medial pit is much deeper and larger than the lateral pit. As in other basal and derived tetanuran theropods the medial condyle in *Allosaurus lucasi* is flattened and much larger than the lateral condyle, which is acuminate. The height of the lateral condyle is 4.5 cm, whereas the height of the medial condyle is 6.5 cm. The distance between the condyles when measured from their apices is 5 cm. In distal view the condyles are separated from each other by a deep fossa. In posterior view the condyles are separated by a deep ligament fossa, which has a depth of 2.5 cm. The much larger medial condyle articulates with the corresponding phalanx II-1. The anterior face of the distal articulation has a well-preserved shallow fossa, which is interpreted as the insertion site of *M. extensor digitorum longus* (Carrano, 2007). The posterior face of the metatarsal has a longitudinally striated facet that is located approximately at the mid-section of the bone. The facet represents the insertion for the *M. gastrocnemius pars medialis* (Carrano, Hutchinson, 2002; Carrano, 2007). Adjacent to the proximal end of the insertion site for the *M. gastrocnemius pars medialis* is a small depression that represents the articulation for metatarsal I (Tarsitano, 1983).

Metatarsal III. The metatarsal III is largest bone in the foot (Fig. 19). The bone is missing the proximal end. In the most proximal region the shaft is round. The lateral sides of the shaft are flattened towards the posterior surface of the bone forming a V-like cross section. As in most other theropods (Snively *et al.*, 2004) the shaft is medially deflected. The medial face of the shaft has a large flat facet for the articulation with metatarsal II. The facet occupies approximately two-thirds of the length of the bone. A prominent ridge extends distally down along the anteromedial edge of the metatarsal shaft. The lateral facet for the articulation with metatarsal IV is also pronounced and of similar length as that for metatarsal II. The distal articulation is broad transversely and roller-like and has a shallow fossa that separates the condyles. Both condyles articulate with the corresponding phalanx III-1. Both collateral ligament pits are preserved, equally deep, and circular shaped. The anterior face of the distal articulation preserves a deep pronounced fossa for insertion of the *M. extensor digitorum longus* (Carrano, 2007), which is mediolaterally wide. The posterior face of the distal articulation has a deep fossa that separates the two condyles, a feature that is common in tetanuran theropods (Carrano *et al.*, 2012).

Metatarsal IV. This bone is missing the proximal end and a portion of the proximal shaft (Fig. 19). When reconstructed it is approximately the same length as the metatarsal II. The shaft is D-shaped in cross section as in most other large-bodied basal and derived tetanuran theropods and also

in abelisaurids (Carrano, 2007). The medial surface of the shaft is flat for most of its length, which indicates that the bone was closely appressed to metatarsal III for most of its length. The distal end of the metatarsal IV is not strongly diverged as in *Allosaurus fragilis* and *A. jimmadseni*. The lateral face of the shaft at its posterior region has a pronounced tuberosity that is located approximately 9 cm above the lateral condyle.

The anterior face of the distal end of metatarsal preserves a shallow fossa for the insertion of the *M. extensor digitorum longus*. The fossa is more laterally oriented than anteriorly. Two other shallow depressions extend along the posteromedial face of the shaft. These characteristic depressions are interpreted as the insertion sites for the *M. gastrocnemius pars lateralis* (Carrano, Hutchinson, 2002).

Near the distal articulation the shaft is slightly narrow. The distal articulation is a small, D-shaped structure. The length/width ratio of the distal articular surface is 1.2. Both collateral ligament pits are preserved. The medial collateral ligament pit is a shallow depression; however, it is much deeper than the lateral ligament pit. In posterior view of the distal articulation, a shallow fossa separates the condyles.

Phalanges. Almost all of the phalanges of the left pes of *Allosaurus lucasi* are preserved (Fig. 20). The only phalanges that are missing are I-1 and I-2, and phalanx IV-4. Additionally, a single partial ungual phalanx of the pedal digit IV is preserved, whereas the unguals for digits I, II, and III are missing.

Phalanx II-1 is well-preserved. The length of the phalanx is 13 cm. The proximal articulation is larger in surface area than the distal articulation. The ventral side of the bone is damaged. The shaft is relatively short. The distal articulation preserves both condyles: medial and lateral. Anteriorly, the condyles are separated by a deep fossa that forms a characteristic ginglymus, as in other basal tetanuran theropods. The depth of the sulcus is approximately 2 cm. Both collateral ligament pits are well-preserved. The medial ligament pit is deeper than the lateral, as in most theropods. The hyperextensor pit is large, round, and well defined.

Phalanx II-2 is complete and well-preserved and has the length of approximately 8 cm. The proximal articulation is round and featureless and resembles phalanx II-1. The shaft is short and round. The transverse width of the distal end of the phalanx is nearly the same as the proximal end. Both collateral ligament pits are preserved. The medial pit is pushed inward, which makes it deeper than it might have been originally. Both condyles, lateral and medial, are pronounced, and are separated by a deep sulcus.

Phalanx III-1 presents only the proximal end. The proximal articulation is round and has a shallow depression for the articulation with the distal end of metatarsal III.

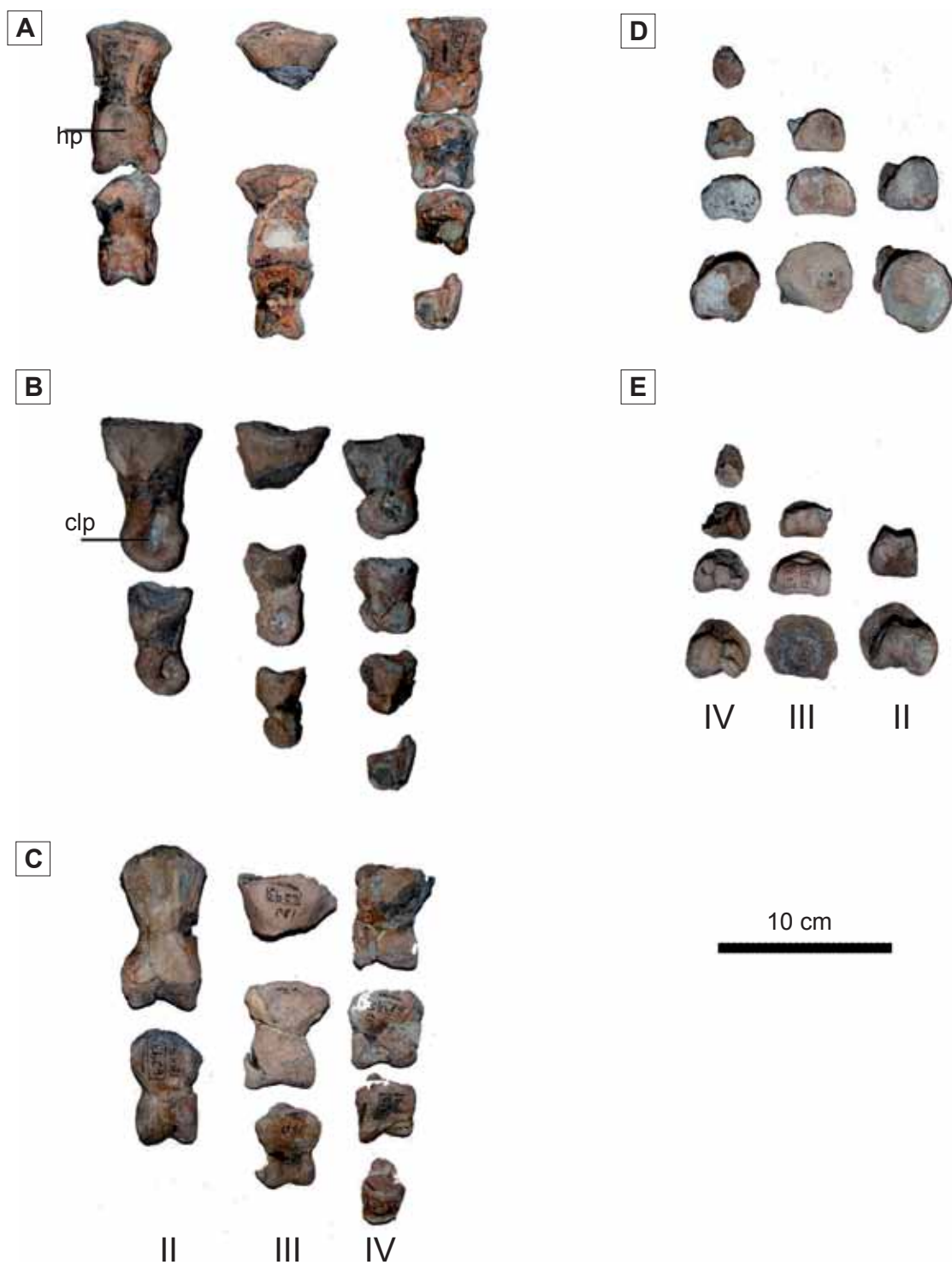


Fig. 20. Left pedal phalanges of *Allosaurus lucasi* sp. nov. (YPM VP 57589) from the Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA

A. Dorsal. B. Lateral. C. Ventral. D. Proximal. E. Distal views. **Abbreviations:** clp – collateral ligament pit; hp – ‘hyperextensor’ pit

Phalanx III-2 is complete and exceptionally well-preserved and has a length of 8 cm. The proximal articulation is wider than high and is D-shaped. No visible ornamentation of any kind can be seen on the outer surface of the bone. The proximal articular surface has two shallow fossae for the articulation with phalanx III-1. The shaft is round and short, and wider than high. The transverse width of the distal articulation is the same as the proximal articulation. The condyles of the distal articulation are of equal sizes and are separated from one another by a shallow sulcus with a depth of 0.5 cm. Both collateral ligament pits are preserved, but are filled with hard sandstone matrix. The hyperextensor pit in the dorsoanterior region of the phalanx is extensive, deep and transversely wide.

Phalanx III-3 is proportionally short compared to phalanx III-2 and flat ventrally. The proximal articular surface is D-shaped and has two shallow fossae for the articulation with phalanx III-2. As the other phalanges, the outer surface of the proximal articulation of phalanx III-3 lacks any kind of ornamentation. The shaft is extremely short and the condyles of the distal articulation are almost making contact with the proximal end of the phalanx. The condyles are separated by a deep sulcus with a depth of 0.5 cm. Both collateral ligament pits are preserved. The medial pit is filled with hard matrix. The dorsal surface of the bone is crushed.

Phalanx IV-1 is exceptionally well-preserved and has a length of 8 cm. The proximal articulation is round, but its lateral side is skewed medially, as in other large-bodied non-avian theropods. The ventral surface of the proximal articulation is concave. The medial condyle is two times larger than the lateral condyle. The condyles are separated by a 1.5 cm deep sulcus. Both collateral ligament pits are preserved in the phalanx. The lateral pit is only partially preserved, and the medial ligament pit is filled with hard sandstone matrix. The shaft of the phalanx is short. The hyperextensor pit is small and shallow.

Phalanx IV-2 is proportionally shorter than phalanx IV-1. The shaft is extremely short, and the proximal and distal ends of the phalanx almost contact each other. The proximal articulation is D-shaped. The medial condyle is larger than the lateral. Both collateral ligament pits are preserved in the phalanx. The medial pit is filled with hard sandstone matrix. The lateral pit is partially preserved because most of the dorsal surface of the lateral condyle is missing. However, the remaining part of the pit suggests that it was not deep. The dorsal region of the distal articulation is crushed.

Phalanx IV-3 is also proportionally smaller than the previous phalanx and is approximately 6 cm long. The proximal and distal articulations have the same transverse widths. The proximal articulation is heavily damaged, especially its dorsal surface. The overall shape of the proximal articular surface is a D-shape. Both condyles are preserved in the pha-

lanx. However, the medial condyle is only partially preserved and most of its dorsal surface is missing. The condyles are separated by a deep sulcus with a depth of 1 cm. Only the lateral collateral ligament pit is preserved.

The ungual phalanx of digit IV is only partially preserved, missing the entire anterior region. The estimated length of the preserved bone fragment is 3 cm. Most of the bone surface is damaged, and no measurements can be obtained except for its general dimensions. In the dorsoposterior region, the bone preserves a relatively long dorsal process. The length of the process is approximately 1.5 cm.

DISCUSSION

Allosaurus lucasi represents the fourth unambiguous species of the North American Late Jurassic *Allosaurus*. The genus is the most abundant and the best known large-bodied basal tetanuran theropod in the world and is found throughout the entire Morrison Formation in Arizona, Colorado, Montana, New Mexico, South Dakota, Utah, and Wyoming (Gilmore, 1920; Smith *et al.*, 1999; Brusatte, Sereno, 2008; Carrano *et al.*, 2012). *Allosaurus* is largely represented by subadult and adult examples; however, young juveniles are also known, but are scarce (Madsen, 1993; Foster, 2003, 2007; Foster, Chure, 2006). Until now three species of *Allosaurus* were known in the Morrison Formation, *Allosaurus atrox*, *A. fragilis* and *A. jimmadseni* (Marsh, 1878; Madsen, 1993; Chure, 2000; Heckert *et al.*, 2003; Loewen, 2004, 2009). These taxa had the same temporal occurrence and most likely shared the same ecosystems (Loewen, 2004). The genus is also present in Andrés, Praia de Vale Frades and Guimarães, Leiria, Alcobaça and Porto Novo Members, Lourinhã Formation (Kimmeridgian–Tithonian) of Portugal and is referred to a new species *A. europaeus* by Mateus *et al.* (2006), which suggests that *Allosaurus* was both taxonomically and morphologically more diverse than previously believed. However, other workers (Malafaia *et al.*, 2007, 2010) suggested that *A. europaeus* is morphologically more similar to *A. fragilis*, and thus, may belong to this taxon. Therefore, more detail studies of the *Allosaurus* materials from Portugal are still needed.

The identification of *Allosaurus lucasi* as a new species of *Allosaurus* not only supports the evidence for the diversity of this genus in North America, but also suggests that the genus was present at the very end of the Jurassic. The Morrison Formation is mostly Kimmeridgian and Early Tithonian in age (Foster, 2003).

A contemporary of *Allosaurus lucasi* is a large allosauroid *Saurophaganax maximus* (Ray, 1941; Chure, 1995) from the Stovall Quarry 1, east of Kenton, Cimarron County, Oklahoma. Both taxa have been found at the top of the Mor-

risson Formation (Tithonian). However, since its discovery the validity of *Saurophaganax* has been debated (Carrano *et al.*, 2012). Some workers (*e.g.*, Paul, 1988; Smith, 1998; Holtz *et al.*, 2004) referred it to a large *Allosaurus maximus*. Chure (1995) identified two apomorphies on the skeleton of *Saurophaganax*, which validate its taxonomic status. Recently the validity of *Saurophaganax* was supported by the phylogenetic analysis of Carrano *et al.* (2012). In 1995, a partial skeleton of *Saurophaganax* consisting of several proximal caudal vertebrae, a partial right ilium, ischium and a nearly complete left hind limb was discovered at the Peterson Quarry in New Mexico (Lucas, 1993, 2009, 2014), thus suggesting a much larger paleogeographic occurrence of this rare theropod.

Although *Allosaurus lucasi* and *Saurophaganax maximus* are largely fragmentary, they most likely do not represent a single species. There is minimal overlapping material between both taxa, and some of the overlapping bones are incomplete or poorly preserved. *A. lucasi* has a more complete skull, whereas the skull of *S. maximus* is unknown, and only a single isolated right postorbital, two partial quadrates, and three poorly preserved tooth crowns are preserved. Both taxa are also of different body lengths: *A. lucasi* approximately 10 m or slightly longer and *S. maximus* 14 m. However, overall body size may be of little value, especially when dealing with similar morphology (Chure, 1995). But, both taxa can be distinguished from one another on the basis of several morphological characters, including the following: *A. lucasi*, a tall quadrate, strongly removed posteriorly lateral condyle of tibia, shallow but extensive incisura tibialis, whereas *S. maximus*, large lateral condyle of tibia that is more centered and occupies almost half the length of the tibial head. Both taxa exhibit a slightly divergent fourth metatarsal. Further, *A. lucasi* can be also distinguished from *A. fragilis* and *A. jimmadseni* by a relatively short premaxilla and deep maxilla, which may have resulted in a much shorter and deeper skull in *A. lucasi* (Pl. 1: 1, 2). Another characteristic that distinguishes *A. lucasi* from both these taxa is the position of the antorbital fossa relative to the lateral alveolar margin. In *A. lucasi* the fossa was situated much higher and was not as extensive as in *A. fragilis* and *A. jimmadseni*, which extended nearly to the lateral alveolar margin. The overall length of the more complete maxilla of *A. lucasi* was most likely similar to adults of *A. fragilis* (Carpenter, 2010) from the Cleveland Lloyd Quarry, Utah. However, the anterior portion of the maxilla of *A. lucasi* is much deeper than of *A. fragilis*. Premaxillary length reduction has also been observed in neoceratosaur theropods such as the North American *Ceratosaurus*, and in the majority of abelisaurid theropods such as *Abelisaurus comahuensis*, *Aucasaurus garridoi*, *Carnotaurus sastrei*, *Rugops primus*, and *Skorpiovenator bustingorryi* (Bonaparte, Novas, 1985; Bonaparte *et*

al., 1990; Coria *et al.*, 2002; Sereno *et al.*, 2004; Canale *et al.*, 2008). The aliorami tyrannosaurids such as the most recently described *Qianzhousaurus sinensis* (Lü *et al.*, 2014) pushed the length reduction of the premaxillae to the extreme.

The quadratojugal of *Allosaurus lucasi* is very characteristic and differs from *A. fragilis* and *A. jimmadseni*. It is more robust and has a short jugal process and short quadrate process of the quadratojugal.

Allosaurus lucasi may be the stratigraphically youngest representative of the genus *Allosaurus*, which provides evidence for the diversity of allosauroid theropods during the Late Jurassic/Early Cretaceous in North America. This suggests that *Allosaurus*-like theropods were still present at the very end of the Jurassic and may have continued into the Cretaceous. However, more specimens are still waiting to be discovered to see how far the genus continued on its evolutionary path. *A. lucasi* provides further evidence of a distinctive upper Morrison dinosaur fauna, which was first suggested by Bakker (1986) and later supported by the discovery and description of a diplodocoid sauropod *Suuwasea emilieae* (Harris, Dodson, 2004) from the uppermost Morrison Formation of Montana.

Acknowledgments. I wish to thank Daniel L. Brinkman and Christopher Norris for access to the specimens. I thank Dr. Spencer G. Lucas for inviting me to contribute to this special volume of *Volumina Jurassica*. Special thanks go to Joseph Lyons for taking the photograph of all the specimens. I thank Dr. John Foster, Dr. Adrian Hunt, and an anonymous reviewer for the reviews and comments on the final version of this paper, which greatly improved its content. I wish to thank Dr. Roger B.J. Benson, Daniel L. Brinkman, Dr. Steve L. Brusatte, Dr. Ken Carpenter, Denver Fowler, Dr. Peter Galton, and Dr. Spencer G. Lucas for providing important literature on theropod dinosaurs, which greatly aided in this research. Lastly, I wish to thank the late Dr. Joseph T. Gregory and his field crew Robert Clem, A. Richard Diebold Jr., Jean Dudley, David Parsons, David Techter, and John T. Walker, for the discovery of this important specimen. This work honors them both and their work continues to inspire.

REFERENCES

- AZUMA Y., CURRIE P.J., 2000 — A new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan. *Canadian Journal of Earth Sciences*, **37**: 1735–1753.
- BAKKER R.T., 1986 — The Dinosaur Heresies New Theories Unlocking the Mystery of the Dinosaurs and Their Extinction. Citadel Press, Kensington Publishing.
- BENSON R.B.J., 2009 — A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the

- relationships of Middle Jurassic theropods. *Zoological Journal of the Linnean Society*, doi: 10.1111/j.1096-3642.2009.00569.x.
- BONAPARTE J.F., NOVAS F.E., 1985 — *Abelisaurus comahuensis*, n. gen., n. sp., Carnosauria del Cretacico tardio de Patagonia. *Ameghiniana*, **21**: 259–265.
- BONAPARTE J.F., NOVAS F.E., CORIA R.A., 1990 — *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Natural History Museum of Los Angeles County, Contributions in Science*, **416**: 1–41.
- BRALOWER T.J., LUDWIG K.R., OBRADOVICH J.D., JONES D.L., 1990 — Berriasian (Early Cretaceous) radiometric ages from the Grindstone Creek section, Sacramento Valley, California. *Earth and Planetary Science Letters*, **98**: 62–73.
- BRITT B.B., 1991 — Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. *Brigham Young University Geology Studies*, **37**: 1–72.
- BRUSATTE S.L., SERENO P.C., 2008 — Phylogeny of Allosauroida (Dinosauria: Theropoda): comparative analysis and resolution. *Journal of Systematic Palaeontology*, **6**: 155–182.
- BRUSATTE S.L., BENSON R.B.J., CHURE D.J., XU X., SULLIVAN C., HONE D.W.E., 2009 — The first definitive carcharodontosaurid (Dinosauria, Theropoda) from Asia and delayed ascent of tyrannosaurids. *Naturwissenschaften*, **96**: 1051–1058.
- BRUSATTE S.L., BENSON R.B.J., HUTT S., 2008a — The osteology of *Neovenator salerii* (Dinosauria: Theropoda) from the Wealden Group (Barremian) of the Isle of Wight. *Palaeontographical Society Monographs*, **162**: 1–75.
- BRUSATTE S.L., BENSON R.B.J., ZHAO X.-J., CURRIE P.J., 2008b — The skull of *Monolophosaurus jiangi* (Dinosauria: Theropoda) and its implications for early theropod phylogeny and evolution. *Zoological Journal of the Linnean Society*, **158**: 573–607.
- BRUSATTE S.L., CHURE D.J., BENSON R.B.J., XU X., 2010 — The osteology of *Shaochilong maortuensis*, a carcharodontosaurid (Dinosauria, Theropoda) from the Late Cretaceous of Asia. *Zootaxa*, **2334**: 1–46.
- CANALE J.I., SCANFERLA C.A., AGNOLIN F.L., NOVAS F.E., 2008 — New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. *Naturwissenschaften*, **96**: 409–414.
- CARPENTER K., 2010 — Variation in a population of Theropoda (Dinosauria): *Allosaurus* from the Cleveland-Lloyd Quarry (Upper Jurassic), Utah, USA. *Paleontological Research*, **14**: 250–259.
- CARR T.D., 1999 — Craniofacial ontogeny in the Tyrannosauridae (Dinosauria, Coelurosauria). *Journal of Vertebrate Paleontology*, **19**: 497–520.
- CARR T.D., WILLIAMSON T.E., 2004 — Diversity of late Maastrichtian Tyrannosauridae (Dinosauria: Theropoda) from western North America. *Zoological Journal of the Linnean Society*, **142**: 479–523.
- CARRANO M.T., 2007 — The appendicular skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology Memoire*, **8**, 2: 163–179.
- CARRANO M.T., HUTCHINSON J.R., 2002 — The pelvic and hindlimb musculature of *Tyrannosaurus rex* (Dinosauria, Theropoda). *Journal of Morphology*, **253**: 207–228.
- CARRANO M.T., BENSON, R.B.J., SAMPSON S.D., 2012 — The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology*, **10**: 211–300.
- CHURE D.J., 1995 — A reassessment of the gigantic theropod *Saurophagus maximus* from the Morrison Formation (Upper Jurassic) of Oklahoma, USA. In: Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers (eds A. Sun, Y. Wang): 103–106. China Ocean Press, Beijing, China.
- CHURE D.J., 2000 — A new species of *Allosaurus* from the Morrison Formation of Dinosaur National Monument (Utah and Colorado) and a revision of the theropod family Allosauridae. PhD dissertation. Columbia University, New York.
- CORIA R.A., CURRIE P.J., 2006 — A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas*, **28**: 71–118.
- CORIA R.A., SALGADO L., 1995 — A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature*, **377**: 224–226.
- CORIA R.A., CHIAPPE L.M., DINGUS L., 2002 — A new close relative of *Carnotaurus sastrei* Bonaparte 1985 (Theropoda: Abelisauridae) from the Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology*, **22**: 460–465.
- CURRIE P.J., 2006 — On the quadrate of *Sinraptor dongi* (Theropoda: Allosauroida) from the Late Jurassic of China. In: Mesozoic Vertebrates and Paleoenvironments. Tributes to the career of Prof. Dan Grigorescu: 111–115. Ars Docendi, Bucharest.
- CURRIE P.J., CARPENTER K., 2000 — A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas*, **22**: 207–246.
- CURRIE P.J., ZHAO X.-J., 1993 — A new carnosaur (Dinosauria: Theropoda) from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences*, **30**: 2037–2081.
- EDDY D.R., 2008 — A re-analysis of the skull of *Acrocanthosaurus atokensis* (NCSM 14345): implications for allosauroid morphology, phylogeny, and biogeography. MSc thesis, North Carolina State University, Raleigh, North Carolina.
- EDDY D.R., CLARKE J.A., 2011 — New information on the cranial anatomy of *Acrocanthosaurus atokensis* and its implications for the phylogeny of Allosauroida (Dinosauria: Theropoda). *PLoS ONE*, **6**: 1–55.
- FOSTER J., 2003 — Paleontological analysis of the vertebrate fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain Region, USA. *New Mexico Museum of Natural History and Science Bulletin*, **23**: 1–95.
- FOSTER J., 2007 — The gargantuan to minuscule: the Morrison menagerie, part II. In: Jurassic West, the dinosaurs of the Morrison Formation and their world (Ed J.O. Farlow): 162–252. Indiana University Press.
- FOSTER J.R., CHURE D.J., 2006 — Hindlimb allometry in the Late Jurassic theropod dinosaur *Allosaurus*, with comments on its abundance and distribution. *New Mexico Museum of Natural History and Science Bulletin*, **36**: 119–122.

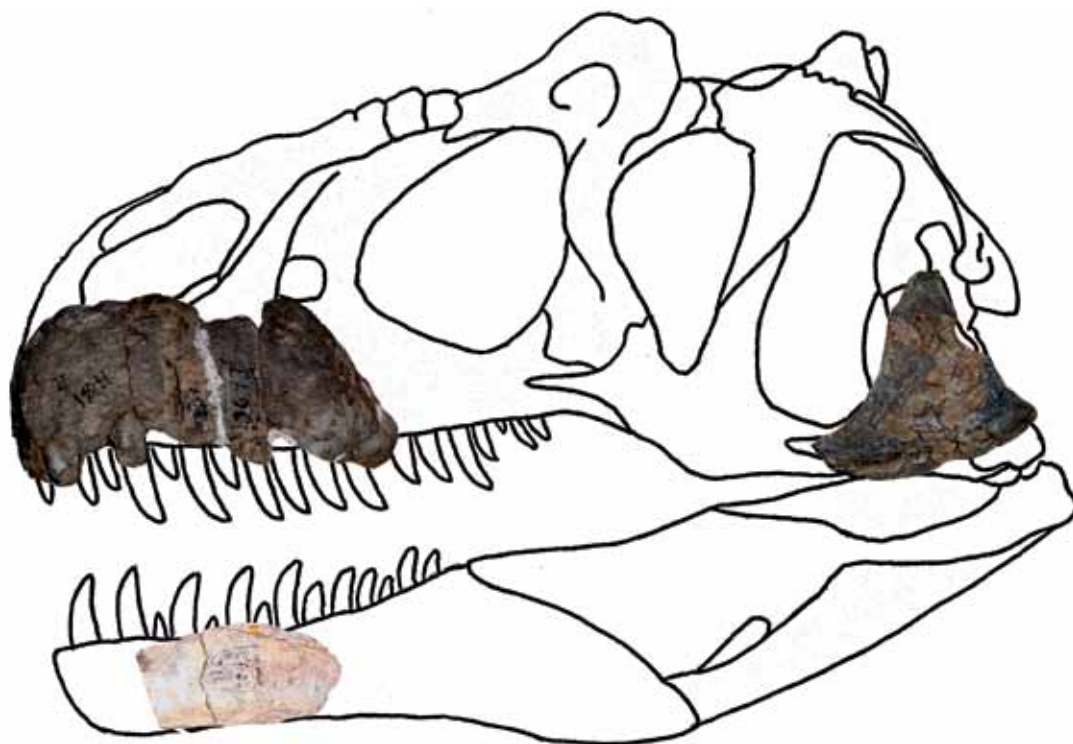
- GALTON P.M., JENSEN J.A., 1979 — A new large theropod dinosaur from the Upper Jurassic of Colorado. *Brigham Young University Geology Studies*, **26**: 1–12.
- GAUTHIER J., 1986 — Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences*, **8**: 1–55.
- GILMORE C.W., 1920 — Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *Bulletin of the United States National Museum*, **110**: 1–154.
- HARLAND W.B., ARMSTRONG R.L., COX A.V., CRAIG L.E., SMITH A.G., SMITH D.G., 1990 — A geologic time scale. Cambridge University Press.
- HARRIS J.D., DODSON P., 2004 — A new diplodocoid sauropod dinosaur from the Upper Jurassic Morrison Formation of Montana, USA. *Acta Palaeontologica Polonica*, **49**: 197–210.
- HECKERT A.B., SPIELMAN J.A., LUCAS S.G., ALTENBERGER R., RUSSELL D.M., 2003 — An Upper Jurassic theropod dinosaur from the Section 19 Mine, Morrison Formation, Grants Uranium District. New Mexico Geological Society Guidebook, 54th Field Conference, Geology of the Zuni Plateau: 309–314.
- HOLTZ T.R. JR., MOLNAR R.E., CURRIE P.J., 2004 — Basal Tetanurae. In: *The Dinosauria 2nd Edition* (eds D.B. Weishampel, P. Dodson, H. Osmólska): 71–110. University of California Press.
- HUENE F.V., 1920 — Bemerkungen zur Systematik und Stammesgeschichte einiger Reptilien. *Zeitschrift für Induktive Abstammungs- und Vererbungslehre*, **24**: 209–212.
- JENSEN J.A., 1985 — Uncompahgre dinosaur fauna: a preliminary report. *Great Basin Naturalist*, **45**: 710–720.
- KOWALLIS B.J., CHRISTIANSEN E.H., DEINO A.L., PETERSON F., TURNER C.E., KUNK M.J., OBRADOVICH J.D., 1998 — The age of the Morrison Formation. *Modern Geology*, **22**: 235–260.
- LOEWEN M.A., 2004 — Variation and stratigraphic distribution of *Allosaurus* within the Late Jurassic Morrison Formation. *Geological Society of America Abstracts with Programs*, **36**: 524A.
- LOEWEN M.A., 2009 — Variation in the Late Jurassic theropod dinosaur *Allosaurus*: ontogenetic, functional, and taxonomic implications. PhD Thesis, University of Utah.
- LUCAS S.G., 1993 — Dinosauria of New Mexico. New Mexico Academy of Science.
- LUCAS S.G., 2009 — The age of dinosaurs in New Mexico. New Mexico Museum of Natural History and Science.
- LUCAS S.G., 2014 — Dinosaur century 100 years of dinosaur discoveries in New Mexico. New Mexico Museum of Natural History and Science.
- LÜ J., YI L., BRUSATTE S.L., YANG L., LI H., CHEN L., 2014 — A new clade of Asian Late Cretaceous long-snouted tyrannosaurids. *Nature Communications*, **5**: 3788 doi: 10.1038/ncomms4788.
- MADSEN J.H., Jr., 1993 — *Allosaurus fragilis* a revised osteology. *Utah Geological and Mineral Survey Bulletin*, **109**: 1–163.
- MADSEN J.H., Jr., WELLES S.P., 2000 — *Ceratosaurus* (Dinosauria, Theropoda) a revised osteology. *Utah Geological Survey, Miscellaneous Publication*, **00-2**: 1–80.
- MALAFIA E., DANTAS P., ORTEGA F., ESCASO F., 2007 — Nuevos restos de *Allosaurus fragilis* (Theropoda: Carnosauria) del yacimiento de Andrés (Jurásico Superior; centro-oeste de Portugal). In: *Cantera Paleontológica*. Diputación Provincial de Cuenca, Cuenca: 255–271.
- MALAFIA E., ORTEGA F., ESCASO F., DANTAS P., PITMENTEL N., GASULLA J.M., RIBEIRO B., BARRIGA F., SANZ J.L., 2010 — Vertebrate fauna at the *Allosaurus* fossil-site of Andrés (Upper Jurassic), Pombal, Portugal. *Journal of Iberian Geology*, **36**: 193–204.
- MARSH O.C., 1878 — Notice of new dinosauria reptiles. *American Journal of Science (ser. 3)*, **15**: 241–244.
- MARSH O.C., 1881 — Principal characters of American Jurassic dinosaurs — part 5; *American Journal of Science (ser. 3)*, **21**: 417–423.
- MATEUS O., 2006 — Late Jurassic dinosaurs from the Morrison Formation (USA), the Lourinhã and Alcobaça formations (Portugal), and the Tendaguru Beds (Tanzania): A comparison. *New Mexico Museum of Natural History and Science Bulletin*, **36**: 233–231.
- MATEUS O., WALEN A., ANTUNES M.T., 2006 — The large theropod fauna of the Lourinhã Formation (Portugal) and its similarity to that of the Morrison Formation, with a description of a new species of *Allosaurus*. In: (eds J.R. Foster, S.G. Lucas): 123–129. Paleontology and geology of the Upper Jurassic Morrison Formation. *New Mexico Museum of Natural History and Science Bulletin*, **36**.
- MOLNAR R.E., 2008 — Reconstruction of the jaw musculature of *Tyrannosaurus rex*. In: (eds P. Larson, K. Carpenter): 255–281. *Tyrannosaurus rex* the tyrant king. Indiana University Press.
- NAISH D., 2003 — A definitive allosauroid (Dinosauria; Theropoda) from the Lower Cretaceous of East Sussex. *Proceedings of the Geologists' Association*, **114**: 319–326.
- OBRADOVICH J.D., 1993 — A Cretaceous time scale. In: (eds W.G. E. Caldwell, E. G. Kauffman): 379–129. Evolution of the Western Interior Basin. *Geological Association of Canada, Special Paper*, **39**.
- O'SULLIVAN R.B., 1997 — The Jurassic section along McElmo Canyon in southwestern Colorado. New Mexico Geological Society Guidebook, 48th Field Conference, Mesozoic Geology and Paleontology of the Four Corners Region, 109–114.
- PAUL G., 1988 — *Predatory Dinosaurs of the World*. Simon and Schuster, New York.
- PÉREZ-MORENO B.P., CHURE D.J., PIRES C., MARQUES DA SILVA C., PÓVOAS L., CACHÃO M., SANZ J.L., GALOPIM DE CARVALHO A.M., 1999 — On the presence of *Allosaurus fragilis* (Theropoda: Carnosauria) in the Upper Jurassic of Portugal: first evidence of an intercontinental dinosaur species. *Journal of the Geological Society, London*, **156**: 449–452.
- POL D., RAUHUT O.W.M., 2012 — A Middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs. *Proceedings of the Royal Society B*, doi: 10.1098/rspb.2012.0660.
- RAUHUT O.W.M., 2003 — The interrelationships and evolution of basal theropod dinosaurs. *The Palaeontological Association, Special Papers in Palaeontology*, **69**: 1–213.
- RAY G.R., 1941 — Big for his day. *Natural History*, **48**: 36–39.
- SAMPSON S.D., WITMER L.M., 2007 — Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. In: *Majungasaurus*

- crenatissimus* from the Late Cretaceous of Madagascar (eds S.D. Sampson, D.W. Krause): 32–102. *Society of Vertebrate Paleontology Memoir*, **8**, 2.
- SEELEY H.G., 1887 — On the classification of the fossil animals commonly named Dinosauria. *Proceedings of the Royal Society of London*, **43**: 165–171.
- SERENO P.C., NOVAS F.E., 1993 — The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. *Journal of Vertebrate Paleontology*, **13**: 451–476.
- SERENO P.C., BECK A.L., DUTHEIL D.B., GADO B., LARSON H.C.E., LYON G.H., MARCOT J.D., RAUHUT O.W.M., SADLEIR R.W., SIDOR C.A., VARRICCHIO D.J., WILSON G.P., WILSON J.A., 1998 — A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science*, **282**: 1298–1302.
- SERENO P.C., WILSON J.A., CONRAD J.L., 2004 — New dinosaurs link southern landmasses in the Mid-Cretaceous. *The Royal Society London B*, **271**: 1325–1330.
- SMITH J.B., 2007 — Dental morphology and variation in *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. In: *Majungasaurus crenatissimus* from the Late Cretaceous of Madagascar (eds S.D. Sampson, D.W. Krause): 103–126. *Society of Vertebrate Paleontology Memoir*, **8**, 2.
- SMITH D.K., 1998 — A morphometric analysis of *Allosaurus*. *Journal of Vertebrate Paleontology*, **18**: 126–142.
- SMITH D.K., RICHMOND D.R., BYEE P.J., 1999 — Morphological variation in a large specimen of *Allosaurus fragilis*, Upper Jurassic Morrison Formation, Eastern Utah. In: *Vertebrate Paleontology in Utah* (Ed. D.D. Gillette): 135–141. *Utah Geological Survey Miscellaneous Publication*, **99-1**.
- SNIVELY E., RUSSELL A.P., POWELL G.L., 2004 — Evolutionary morphology of the coelurosaurian arctometatarsus: descriptive, morphometric and phylogenetic approaches. *Zoological Journal of the Linnean Society*, **142**: 525–553.
- TARSITANO S.F., 1983 — Stance and gait in theropod dinosaurs. *Acta Palaeontologica Polonica*, **28**: 251–264.
- TURNER C.E., PETERSON F., 2004 — Reconstruction of the Upper Jurassic Morrison Formation extinct ecosystem – a synthesis. *Sedimentary Geology*, **167**: 309–355.
- ZHAO X.-J., CURRIE P.J., 1993 — A large crested theropod from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences*, **30**: 2027–2036.

PLATE 1

Fig. 1, 2 Partial reconstruction of skull elements of *Allosaurus lucasi* (YPM VP 57589) based on available cranial elements from the Upper Jurassic Morrison Formation (Tithonian) McElmo Canyon, Montezuma County, Colorado, USA (1) compared to the skull of *Allosaurus fragilis* (Madsen, 1993) from the Upper Jurassic Morrison Formation (Kimmeridgian) Cleveland-Lloyd Quarry, Utah, USA (2) . Not to scale

1



2



Sebastian G. DALMAN — Osteology of a large allosauroid theropod from the Upper Jurassic (Tithonian) Morrison Formation of Colorado, USA

