A new Carnosaur (Dinosauria: Theropoda) from the Upper Morrison Formation (Late Jurassic, Tithonian) of Colorado

Sebastian Dalman

Fort Hays State University, sebastiandalman@yahoo.com

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A NEW CARNOSAUR (DINOSAURIA: THEROPODA)
FROM THE UPPER MORRISON FORMATION
(LATE JURASSIC, TITHONIAN)
OF COLORADO

being

A Thesis Presented to the Graduate Faculty
of the Fort Hays State University in
Partial Fulfillment of the Requirements for
the Degree of Master of Science

by

Sebastian G. Dalman
B.S., University of Massachusetts

Date ____________________  Approved ________________________________
                                  Major Professor

Approved ______________________________
                                  Chair, Graduate Council
ABSTRACT

A disarticulated skeleton of a theropod from the Late Jurassic (Tithonian) strata of McElmo Canyon in Montezuma County, Colorado was discovered in 1953 by the late J. T. Gregory and D. Techter. For nearly 55 years the specimen remained unnoticed in the collection of the Yale Peabody Museum of Natural History in New Haven, Connecticut. Several cranial and postcranial elements are relatively well preserved and include the premaxilla, maxilla, dentary, teeth, quadratojugal, braincase, metacarpals, partial pubis and ischium, astragalus, partial tibia and fibula, metatarsals, pedal phalanges, and several partially preserved ribs. The specimen represents a new genus and species of basal carcharodontosaurid, which shares some morphological similarities with Late Jurassic allosaurids. As such, the new genus and species is the first unequivocal carcharodontosaurid from the Late Jurassic of North America. The presence of a North American carcharodontosaurid during the Late Jurassic provides evidence that the clade may have originated on that continent and that the Carcharodontosaurus split from the allosaurids in the Middle or Early Jurassic.
ACKNOWLEDGMENTS

This thesis was made possible through the help, advice and support of many individuals. A very special thanks to Dr. Richard J. Zakrzewski, my advisor, who had the expertise to guide me through many difficult situations. Thanks also to the members of my graduate committee, Dr. Reese E. Barrick, Dr. Greg H. Farley, Dr. Robert B. Channell, and Dr. Philip J. Currie, for reviewing my thesis and making recommendations along the way. Many thanks to Stephen L. Brusatte of the Columbia University, New York and Dr. Roger B. J. Benson of the University of Cambridge, London, United Kingdom for providing many manuscripts of the most recent research on theropod dinosaurs.

Also, thanks to my parents, Peter and Irena Dalman, and my sister Anna Dahlmann for always being there for me. You will never know how much I appreciate your love and great support!
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INTRODUCTION

Fossils of allosaurid theropods are the most common dinosaurs in the Late Jurassic of North America. A massive accumulation of bones belonging to individuals of various sizes of a single species, *Allosaurus fragilis* (Marsh, 1877), occur in the Cleveland-Lloyd Dinosaur Quarry in Utah that lies within the Brushy Basin Member of the Late Jurassic Morrison Formation. Originally, the genus *Allosaurus* also included several other species from North America: *A. atrox*, *A. amplexus*, *A. ferox*, *A. jimmdseni*, *A. lucaris*, *A. valens*, and *A. triherodon* (= *Laelaps triherodon*), *Saurophaganax maximus* and one species from Portugal *A. europaeus*. However, the North American species are no longer recognized as valid (except for *S. maximus*) and along with the genera, *Labrosaurus* and *Antrodeus* are considered synonyms of *A. fragilis*. The Portuguese material of *Allosaurus* was discovered in 1999 in Lourinha Formation (Kimmeridgian) and was formerly referred to *A. fragilis*. However, with the subsequent discovery of a partial skull and cervical vertebrae it was decided the specimen (ML 415) represents a new species, *A. europaeus* (Mateus et al. 2006).

However, Loewen (2004) believes there are two species of *Allosaurus* in the Morrison Formation *A. fragilis* and *A. jimmdseni*, whereas the others are synonyms of either *A. fragilis* or *A. jimmdseni*. These two species are geographically separated where *A. jimmdseni* has only been recovered from the Salt Wash Member in Utah and *A. fragilis* from northern and southern Wyoming (Loewen, 2004). However, the geographic range of *Allosaurus* was much greater, because isolated specimens have been found in Colorado, Montana, New Mexico, Oklahoma, South Dakota, and Utah.
A specimen of a theropod YPM 57589 was discovered in 1953 by the late J. T. Gregory and D. Techter in McElmo Canyon in Montezuma County, Colorado near the top of the Upper Morrison Formation (Tithonian). The specimen was found in a hard conglomeratic matrix, which still encases some of the bones. It consists of many cranial and postcranial elements, some of which are fragmentary and others, such as the left pes, are complete. The tooth morphology of the new specimen indicates close affinity to allosaurid and carcharodontosaurid theropods but more similar to the latter group.

The occurrence of carcharodontosaurid theropods in North America is thus far very rare. The most complete North American carcharodontosaurid yet described is *Acrocanthosaurus atokensis* from the Early Cretaceous of Oklahoma. *Acrocanthosaurus* was a very large predator with close affinities to *Allosaurus* and to the Late Cretaceous *Carcharodontosaurus, Eocarcharia, and Giganotosaurus* (Sereno and Brusatte, 2008; Brusatte et al. 2009). *Acrocanthosaurus* lived in North America during the Aptian and Albian stages of the Early Cretaceous. The presence of YPM 57589 in the Tithonian, places the rise of the clade in latest stage of the Late Jurassic, which makes YPM 57589 older than *Acrocanthosaurus* by approximately 35 million years. This find is the earliest record of a carcharodontosaurid, which suggests that their group may have originated in North America. Carcharodontosaurids represent some of the largest predators that lived during the Early and Middle Cretaceous throughout Gondwana, with some species present in Asia. In South America the occurrence of carcharodontosaurids ranges from the Barremian (127-120 my) to the Turonian (93-89 my). Novas et al. (2005) suggested that the replacement of carcharodontosaurids, including spinosaurids and other fauna in Gondwana and Laurasia, occurred on a global scale. Carcharodontosaurids were replaced
by the smaller predators, abelisaurids in Gondwana and by tyrannosaurids across North America and Asia.

Institutional abbreviations—AMNH, American Museum of Natural History, New York, NY; BYUVP, Brigham Young University Vertebrate Paleontology, Provo, Utah; CLDQ, Cleveland-Lloyd Dinosaur Quarry, Cleveland, Utah; FPDM, Fukui Prefectural Museum Fukui, Japan; ML, Museu da Lourinhã, Lourinhã, Portugal; YPM, Yale Peabody Museum of Natural History, New Haven, Connecticut.

METHODS

All available cranial and postcranial skeletal elements were measured with a metric ruler and protractor. All morphological features of the bones were compared with other large theropod taxa from the Late Jurassic and from the Early and Late Cretaceous. Taxa included *Acrocanthosaurus atokensis* Stoval and Langston, 1950; *Aerosteon ricicoloradiensis* Sereno et al., 2008; *Allosaurus europaeus* Mateus et al. 2006; *Allosaurus fragilis* Marsh, 1877; *Aucasaurus garridoi* Coria et al., 2002; *Australovenator wintonensis* Hocknull et al., 2009; *Bahariasaurus ingens*, Stromer, 1934; *Carcharodontosaurus saharicus* Stromer, 1931; *Carnotaurus sasteri* Bonaparte, 1985; *Ceratosaurus nasicornis* Marsh, 1884; *Chilantaisaurus tashuikouensis* Hu, 1964; *Condorraptor currumili* Rauhut, 2005; *Dubreuillosaurus valesdunensis* Allain, 2002; *Duriavenator hesperis* Waldman, 1974; *Edmarka rex* Bakker et al. 1992; *Eocarcharia dinops* Sereno and Brusatte, 2008; *Eustreptospondylus oxoniensis* Walker, 1964; *Fukuiraptor kitadanensis* Azuma and Currie, 2000; *Giganotosaurus carolinii* Coria and Salgado, 1995; *Lourinhanosaurus antunesi* Mateus, 1998; *Magnosaurus nethercombensis* von Huene, 1932; *Majungasaurus crenatissimus* Depéret, 1896; *Mapusaurus roseae*

The phylogenetic position of YPM 57589 was determined by subjecting 264 morphological characters to a cladistic analysis using Hennig86 (Farris, 1988). Two hundred and thirteen of the characters were taken from Benson et al. (2009) and I added 51 additional characters to the analysis. A total of 31 taxa were used in the cladistic analysis. The most basal Early Jurassic theropods *Syntarsus kayentakatae* and *Dilophosaurus wetherilli* were chosen for the outgroups. The analysis produced a strict consensus cladograms (Fig. 80) and a reduced consensus cladogram (Fig. 81) that show the relationship of YPM 57589 and YPM 57726 to other theropods used in this study.

All of the skeletal elements listed for the new species bear two numbers. The first number, YPM 57589 or YPM 57726 is the catalog number, whereas the number in parentheses that follows the catalog number is the field number.

**GEOLOGICAL SETTING**

Field notes (July 20 to July 23, 1953) of J. T. Gregory and D. Techter indicate that YPM 57589 and YPM 57726 were collected in southwestern Colorado at McElmo
Canyon from the top of the Morisson Formation. 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 YPM 57589 and YPM 57726 were collected is 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 my to 147.82 ± 0.63 my, which indicate an age of Kimmeridgian to Tithonian. Bralower et al. (1990), Harland et al. (1990), and Obradovich (1993) also indicated that the Brushy Basin Member in southwestern Colorado is Kimmeridgian to early Tithonian in age. The age of the Morrison Formation 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).

There are at least four theropod genera from the Late Jurassic of Portugal, which also occur in the Morrison Formation, including *Allosaurus*, *Aviatyrannis*, *Ceratosaurus*, and *Torvosaurus*. YPM 57589 and the *Lourinhanosaurus antunesi* are unique theropods for both the Morrison and the Lourinhã formations.

**SYSTEMATIC PALEONTOLOGY**

**SAURISCHIA** Seeley, 1888

**THEROPODA** Marsh, 1881

**TETANURAE** Gauthier, 1986

**ALLOSAUROIDEA** Currie and Zhao, 1994

**CARCHARODONTOSAURIDAE** Stromer, 1931

*MONTEZUMASARUS* gen. nov.
Diagnosis—same as for type species.

Type Species—Montezumasaurus froesei sp. nov.

Etymology—Montezumasaurus named after Montezuma County, Colorado where the specimen was discovered, and saurus, New Latin, “lizard”, from the Greek sauros.

MONTEZUMASAURUS FROESEI sp. nov.

Diagnosis—Allosauroid theropod with the following autapomorphies: antorbital fossa absent; subnarial foramen absent; the premaxilla with equal length and height; the angle between the interpremaxillary articular surface and the lateral surface of the main body of the premaxilla ~ 20°; the premaxillary angle between ventral and anterior margin 55°; paradental groove on the medial surface of the maxilla absent; deep interdental plates with dorsoventrally oriented grooves; interdental plates fused in premaxilla, maxilla, and dentary; quadrate contact of the quadratojugal in line with rostral quadratojugal ramus; slender neck of the pubic peduncle of the ischium; metatarsal II and IV subequal in length.

Holotype—YPM 57589, premaxilla, maxilla, frontal, postorbital, jugal, quadratojugal, quadrate, braincase, dentary, 26 isolated fragmentary teeth, partially preserved ribs scapula, metacarpals, pubic peduncle of ilium, pubis, ischium, tibia, fibula, astragalus, four metatarsals, eight pedal phalanges, including one pedal ungual phalanx, collected by the late J. T. Gregory and D. Techter on July 21, 1953.

Etymology—The species name froesei honors Edgar Froese, the founder and leader of the New Age band Tangerine Dream.

Type Locality—The holotype was recovered from the north side of McElmo Canyon, in Montezuma County, Colorado.
Formation and Age—Montezumasaurus froesei was found in situ, many of the bones are still encased in a hard conglomeratic matrix, a typical lithology of the upper Morrison Formation. These sediments are of the Late Jurassic age (Tithonian). The specimen is housed at the Yale Peabody Museum of Natural History in New Haven, Connecticut.

DESCRIPTION AND COMPARISONS

The type specimen of Montezumasaurus froesei (YPM 57589) consists of well-preserved fragmentary cranial and postcranial skeletal elements.

CRANIAL SKELETON

Premaxilla—The left premaxilla of Montezumasaurus froesei YPM 57589 (18-H 6293) is well preserved (Fig. 1). It is approximately 11 cm long and 11 cm high. There are four teeth in the premaxilla, which is the same number as in Acrocanthosaurus, Carcharodontosaurus, Giganotosaurus, and most other theropods. In Allosaurus, there are five premaxillary teeth and three in Torvosaurus. The medial side of the bone is cemented to the conglomeratic matrix; covering most of the important features. The body of the premaxillary is slightly trapezoidal. The labial and the lower margins of the premaxillary are subparallel. The anterior margin 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°, which is the same as in Torvosaurus tanneri (BYUVP 4882). In Ceratosaurus the premaxillary angle is 80°, whereas in Allosaurus the angle is 72° (Britt, 1991). According to Britt (1991) Allosaurus, Ceratosaurus, and Torvosaurus are distinguished from each other based on various premaxillary angle measurements. The alveoli for the premaxillary teeth are slightly
elliptical in shape (Fig. 2). The length of each of the alveoli is 2 cm. The angle, as measured between the articular surface and the center of the most mesial and most distal alveoli, is 20°, whereas in *Allosaurus* the angle is between 25° and 30°. The consequence of this small angle is that the snout is relatively narrow. Similar conditions are also present in other large theropods such as *Acrocanthosaurus*, *Carcharodontosaurus*, *Giganotosaurus*, and *Shaochilong*. All these genera have relatively short premaxillae. According to Brusatte et al. (2010), the reconstructed premaxilla of *Shaochilong* also bears four premaxillary teeth, which may also be true for the African carcharodontosaurid *Eocarcharia*. However, four premaxillary teeth are also present in abelisaurid theropods *Abelisaurus comahuensis*, *Aucasaurus garridoi*, *Carnotaurus sastrei*, *Majungasaurus crenatissimus*, and *Scorpiovenator bustingorryi*. Some workers (e.g., Coria and Salgado, 1995; Lamanna et al. 2002; Sereno et al. 2004) have suggested that abelisaurids and carcharodontosaurids might be related.

The lateral surface of the premaxillary body of *Montezumaurus* is smooth and lacks any kind 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 *Montezumaurus froesei* YPM 57589 (18-E 6293) is partially preserved, but is missing part of the posterior region (Fig. 3). The body of the preserved part of the maxilla is triangular and its length is approximately 17.7 cm. However, the original length would have been approximately 35.4 cm, whereas the entire length of the skull would have been approximately 80 cm. These estimates are based on the length proportions of other large-bodied theropods such as *Acrocanthosaurus*
*atokensis* and *Allosaurus fragilis*. The estimated length of the skull of *Montezumasaurus* is similar to that of an adult *Allosaurus fragilis* whose skull length is 76 cm.

The dorsal and ventral margins of the maxilla are approximately twice as long as the anterior margin. The bone 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 the specimen of *Torvosaurus tanneri* (BYVP 9122). The premaxilla-maxilla contact is not visible due to the presence of surrounding matrix. The body of the maxilla is relatively deep anteriorly. In *Allosaurus*, the maxilla is not as deep as it is in *Montezumasaurus*.

The maxilla of *Montezumasaurus* shows some similarities to the maxilla of *Acrocanthosaurus*. As in *Acrocanthosaurus* the subnarial foramen in *Montezumasaurus* is absent, but it is present in *Allosaurus*. The subnarial foramen is also absent in other derived allosauroid and carcharodontosaurid theropods such as *Carcharodontosaurus Sinraptor*, *Giganotosaurus*, *Neovenator*, *Shaочilong*, and *Sinraptor* and the abelisaurids, including *Aucasaurus*, *Carnotaurus*, *Ekrixinatosaurus*, *Indosuchus*, and *Majungasaurus*. Therefore, absence of the subnarial foramen represents a diagnostic character in *Abelisauridae*, *Carcharodontosauridae*, *Neovenatoridae*, and *Sinraptoridae*.

According to Brusatte et al. (2010), many basal tetanurans possess a distinct anterior ramus of the maxilla that projects from the main body of the maxilla anterior to the ascending ramus. The ascending ramus in most basal tetanurans is triangular and the anterodorsal process contacts the nasal, which is not preserved in *Montezumasaurus*. However, the anterior ramus of the maxilla preserves the base of the ascending ramus,
which gives an idea of its overall shape that when reconstructed would be similar to that of Acrocanthosaurus, Eocarcharia, or Shaochilong.

The specimen of Montezumasaurus froesei YPM 57589 (18-K 6293) represents a mix of bones from the skull and from the postcranial skeleton, which include two partially preserved tooth sockets 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. The ventral side of the sandstone matrix bears an impression of the left ischium, which has the same field number as the ischium (Fig. 4).

Jugal—YPM 57589 (19-A 6293) represents a partially preserved postorbital process of the left jugal (Fig. 5). The lateral surface of the bone is heavily damaged. Therefore, whether the surface was ornamented or not, remains unknown. The length of the preserved bone is 10 cm, the width at the base is 6.5 cm, and the width at the top is 2 cm. The shape of the bone is slightly convex at the base and less convex at the top. The bone is encased in hard conglomeratic matrix. In general, the bone differs from the jugal of Allosaurus by being more robust with a small slot for the postorbital contact.

In Montezumasaurus, the angle of the postorbital contact is at 70°, whereas in Allosaurus it is at 80°. The angle of the postorbital contact in Montezumasaurus is similar to that of Giganotosaurus. The overall morphology of the postorbital process of the jugal of Montezumasaurus resembles closely that of carcharodontosaurid theropods. The angle of the postorbital contact is much steeper in other genera such as Acrocanthosaurus Monolophosaurus, and Sinraptor.

Quadratojugal—The quadratojugal of Montezumasaurus froesei YPM 57589 (18-Z 6293) is well preserved. The bone is split in half vertically and the two parts are
mirror images of each other (Fig. 6). However, both pieces of the bone are encased in hard matrix.

The length of the preserved quadratojugal is 16 cm and its height is 14.5 cm. YPM 57589 (19-C 6293) preserves the remaining part of the quadratojugal. When associated, the entire bone would reach the length of 23.5 cm (Fig. 7). The base of the dorsal quadratojugal ramus is 8 cm wide, and its distal portion is 4 cm. The angle between dorsal quadratojugal ramus and the rostral quadratojugal ramus in Montezumassaurus is approximately 90°, whereas in Allosaurus the angle is 75°. The dorsal quadratojugal ramus in Montezumassaurus is relatively straight, whereas in Allosaurus it is bent forward. Similar conditions to that of Montezumassaurus are observable in the reconstructed skull of Torvosaurus tanneri (BYUVP). 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. The length of the quadrate contact in Montezumassaurus is 4.5 cm and the height is 6 cm. This contact is broader ventrally, which then forms a slot for the contact with the quadrate. The rostral quadratojugal ramus is approximately 13 cm long. It is highest caudally and reaches a height of 6 cm, but it tapers rostrally with height of 1 cm in its rostral portion. Additionally, the ventral side of the rostral quadratojugal ramus is in line with the quadrate contact. A similar condition is also present in Allosaurus jimmadseni. However, in A. jimmadseni the quadrate contact bends dorsally, whereas in Montezumassaurus it forms a relatively round structure that is not bent.

**Quadrate**—YPM 57589 (18-A 6293) represents a partially preserved left quadrate (Fig. 8). The bone is split in half and both lateral and medial sides are filled with
hard sandstone matrix. The length of the bone is 13 cm; minimum width is 3.5 cm; maximum width is 6 cm. 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. The bone is robust and closely resembles that of *Torvosaurus tanneri* (BYUVP 5110). The bone preserves a small portion of the shaft. The shaft is relatively straight and longer than that of *Allosaurus*, but shorter than in *Torvosaurus*. A small portion of the lateral quadrate condyle is preserved in the specimen YPM 57589 (18-A 6293). However, the overall shape of this particular structure is unknown for this specimen.

The quadrate of *Montezumasaurus* is primitive. It is relatively tall as in other medium and large theropods, including *Acrocanthosaurus*, *Ceratosaurus*, *Sinraptor*, and most abelisaurids. Although, the quadrate condyle for the articulation with the quadrate contact of the quadratojugal and for the articulation with the lower jaw is missing, the posterior end of the bone appears to be much thinner, whereas in *Allosaurus* the structure is very robust. The medial view of the quadrate of *Montezumasaurus* is morphologically similar to that of *Sinraptor dongi*. Another interesting feature observed in all allosauroid and carcharodontosaurid theropods, including *Acrocanthosaurus*, *Allosaurus*, *Eocarcharia*, *Giganotosaurus*, *Mapusaurus*, *Shaochilong*, and *Sinraptor* is the presence of a quadratic foramen (Currie and Zhao, 1993; Coria and Salgado, 1995; Coria and Currie, 2006; Eddy, 2008; Brusatte et al. 2009; Brusatte et al. 2010). However, it is unclear whether the quadrate of *Montezumasaurus* possessed the quadratic foramen due
to poor preservation of the bone. According to Currie (2006), theropods such as *Ceratosaurus, Coelophysis*, abelisaurids, including *Torvosaurus* all lack quadratic foramen. Therefore, absence of the quadratic foramen represents a diagnostic character for Abelisauridae, Ceratosauridae, and Megalosauridae.

**Postorbital**—YPM 57589 (19-A 6293) represents what appears to be a partially preserved postorbital (Fig. 9). The postorbital lies on top of the same conglomeratic matrix next to the partially preserved jugal. The length of the specimen is 9.5 cm and the width is 2.5 cm. Most of the bone is heavily damaged and an adequate description cannot be provided for it. The postorbital in allosauroid and carcharodontosaurid theropods is similar in shape. However, the postorbital in carcharodontosaurid theropods appears to be more massive than it is in *Allosaurus* and *Sinraptor*. The overall morphology of the postorbital of *Montezumosaurus* cannot be compared to any known genera due to its poor preservation. However, what is preserved is much taller than in *Allosaurus*, which suggests that the skull of *Montezumosaurus* might have been relatively tall.

**Frontal**—YPM 57589 (18-? 6293) represents a small fragment of a frontal (Fig. 10). Estimates of the size of the restored bone are as follow: length 5 cm, width 8 cm, minimum thickness 3 mm, mid thickness 1.5 cm, and maximum thickness 3 cm. The bone is slightly convex dorsally and flat ventrally. The frontal anteriorly contacts the prefrontal and posteriorly the postorbital. However, most of the anterior and posterior parts of the bone are missing including the median surface with midline suture. It is possible that the bone was at least twice as long as it is wide, which is similar to other large theropods including *Acrocanthosaurus* and *Allosaurus*. 
The dorsal surface of the frontal is smooth. Morphologically the frontal resembles that of *Allosaurus*; however, the contact surfaces for postorbital and prefrontal are not as steep as they are in *Allosaurus*. The ventral surface of the frontal of *Montezumasaurus* is relatively flat, whereas in *Allosaurus* it is slightly convex. In *Acrocanthosaurus*, the frontal is distinct. The bone has the same proportions as that of *Allosaurus* with the length being two times its width. However, the overall morphology of the frontal of *Acrocanthosaurus* differs from that of *Allosaurus*. The posterior side of the frontal in *Acrocanthosaurus* is rounded, whereas in *Allosaurus* it is triangular. The lateral side of the frontal of *Montezumasaurus* is similar in shape to that of *Acrocanthosaurus*. The posterior side of the frontal of *Montezumasaurus* is raised and is thicker than its anterior side, which represents a condition similar to that of *Acrocanthosaurus*.

**Braincase**—YPM 57589 (18-Z 6293) is a well-preserved braincase (Fig. 11). The height of the braincase is 23 cm and the width is 9 cm. In the dorsal view, the length of the braincase as measured from the anterior to the posterior end is 12.5 cm. The width of the anterior end of the braincase in dorsal view is 9 cm, the mid section is 4 cm, and posterior end is 7 cm. The length of the braincase in the ventral view when measured from the anterior to the posterior end is 10.5 cm, the mid section is 6 cm, the posterior end is 7.5 cm. Parts of the braincase are only partially preserved, including the basipterygoid and parietal.

The parietal of *Montezumasaurus* differs from that of *Allosaurus*, in that it is more robust and longer (Fig. 12), whereas in *Allosaurus* the parietal is relatively short. The basipterygoid process projects slightly forward and downward and is similar to that of *Acrocanthosaurus, Allosaurus, Giganotosaurus*, and *Piatnitzkysaurus* (Fig. 13). However,
the basipterygoid process in *Montezumasaurus* appears to be much longer than it is in *Piatnitzkysaurus*. In *Piatnitzkysaurus*, the basipterygoid processes are relatively short and broad structures and are oriented more anteriorly than ventrally (Rauhut, 2004). In most other theropods, including *Montezumasaurus*, the basipterygoid processes diverge greatly. The lateral surface of the basipterygoid process in *Montezumasaurus* is sculptured, whereas in *Allosaurus* the basipterygoid has a smooth surface. Therefore, a sculpted basipterygoid process in *Montezumasaurus* represents a diagnostic character.

**Dentaries**—There are two partially preserved anterior right dentaries. One dentary belongs to the holotype of *Montezumasaurus*, whereas the other represents the second individual of *Montezumasaurus* YPM 57726 (Figs. 14 and 15). According to the field notes of Gregory and Techter and their map of the specimen in situ, these two dentaries were found in close proximity to each other and represent two individuals of approximately the same size.

**Dentary 1**—A partial right dentary belongs to the holotype of *Montezumasaurus froesei* YPM57589 (18-C 6293). The length of the preserved dentary fragment is 15 cm long and its height is 9 cm. The bone, in cross section, preserves a single unerupted tooth (Fig. 16). 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 completely destroyed and filled in with hard matrix. The interdental plates are fused. The height of the interdental plate measured from the top of the splenial contact is 2.5 cm. The splenial contact is a convex structure with overall height of 3 cm and contacts the splenial medially (Fig. 17).

**Dentary 2**—A partially preserved right dentary YPM 57726 (19-A 6293) belongs to the second individual of *Montezumasaurus*. The bone was found near the holotype of
M. froesei. The specimen preserves five alveoli, containing five partially preserved teeth (Fig. 18). The alveoli are elliptical in shape. The lateral surface of the bone is smooth and featureless and similar to that of the holotype of M. froesei. The interdental plates are fused the same as in the holotype of M. froesei. The dentary contacts the splenial medially, which is similar to the holotype of M. froesei and to Allosaurus. However, the splenial contact is much deeper than it is in Allosaurus; it narrows anteriorly, widens posteriorly, and forms a V structure (Fig. 19). The ventro-posterior part of the dentary is much thinner than the anterior part of the bone. Both dentaries are robust and thicker than that of Allosaurus.

An additional fragment of a dentary (19-B 6293) is also attributable to the YPM 57726 (19-A 6293) based on the same bone coloration (Fig. 20). 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 is uniform in thickness and thicker than the dorsal side of the bone. The dorsal side of the bone is thick in what I refer to as the possible anterior end, and half way towards the posterior end the bone narrows uniformly. It is unclear where in the dentary this bone was located; however, it is possible that it might be the most distal part of the dentary or splenial.

The dentaries in more advanced carcharodontosaurid genera including Giganotosaurus, Mapusaurus, and Tyrannotitan are more massive than in less advanced forms.

**Teeth**—YPM 57589 (19-A 6293) is a single well-preserved premaxillary tooth (Fig. 21). In lingual view, the tooth is convex with small flattened areas on the rostral and caudal sides (Fig. 22). Several other teeth are preserved in the following specimens
representing anterior parts: 18-E 6293 and 18-A 6293. Specimen 18-E 6293 consists of several teeth with roots encased in hard sandstone matrix (Figs. 23 and 24), whereas specimen 18-A 6293 consists of eight partially preserved teeth encased in hard conglomeratic matrix (Fig. 25). In specimen 18-A 6293 the teeth are broken exposing their cross section. Some of the teeth preserved in this matrix are very large, even much larger than those of *Allosaurus*. It is possible that these teeth represent maxillary teeth from the mid-section of the maxilla. One tooth, in particular, exposed in the matrix is the largest in the series of teeth found in other cranial fragments of *Montezumasaurus* (Fig. 26). The tooth is flattened on both sides. Its width from the anterior carina to the posterior carina is approximately 3.2 cm, whereas in *Allosaurus* the range of the tooth width is from 2 cm to 2.5 cm. This tooth of *Montezumasaurus* strongly resembles the right maxillary tooth of *Fukuiraptor kitadaniensis* (FPDM-V971223). Both species have narrow, blade-like cheek teeth. All described carcharodontosaurid theropods including *Carcharodontosaurus iguidensis*, *C. saharicus*, *Eocarcharia dinops*, *Giganotosaurus carolinii*, and *Tyrannotitan chubutensis* had narrow, blade-like teeth located in the premaxillae, maxillae, and dentaries. The degree of curvature of *Montezumasaurus* can be determined in some teeth. Sereno et al. (1998) suggested that tooth crowns with significant curvature are plesiomorphic in Theropoda, whereas teeth that lack curvature or with much reduced curvature are considered the derived state and, therefore, a synapomorphy of Spinosaurinae. According to Smith (2007), this character represents a useful phylogenetic feature. The premaxillary and maxillary teeth of *Montezumasaurus* possess moderate curvatures. However, in mesial view the curvature of the tooth is greater than it is in labial view. The angle of the curvature of the premaxillary tooth of
Montezumasaurus in labial and lingual views is 20º, whereas the angle in mesial view is 14º. In Allosaurus, the angle of the premaxillary tooth in labial view is 20º and in mesial view, it is 10º. Additionally the rostral carina of the premaxillary tooth in Montezumasaurus is oriented medially, whereas in Allosaurus the rostral carina runs through the middle of the tooth. In labial view, the rostral side of the tooth has great convexity, whereas in the caudal side is flattened.

The denticles are minute and similar to those of other allosauroid theropods including Acrocanthosaurus, Allosaurus, Fukuiraptor, and Sinraptor. Not all the teeth preserve denticles due to their poor preservation. Therefore, there is no consistent denticle number on any tooth of Montezumasaurus. However, some of the preserved denticles are similar to those of the Late Cretaceous carcharodontosaurids including Carcharodontosaurus, Giganotosaurus, and Tyrannotitan.

The length of the root of Montezumasaurus is difficult to estimate because most of the teeth are heavily damaged. However, there is a single root, which is encased in hard sandstone matrix. The preserved root is 6.5 cm long. Therefore, it is possible that it is a maxillary tooth, because the maxilla of Montezumasaurus is relatively deep, which indicates that the roots of the teeth are relatively long. The maxilla of Allosaurus is not as deep and the roots of the teeth are not as long as in Montezumasaurus.

The number of premaxillary, maxillary, and dentary teeth vary in allosaurid and carcharodontosaurid theropods. The number of premaxillary teeth in allosaurid theropods is Allosaurus (5), Fukuiraptor (4), Saurophaganax (4), and Sinraptor (4); whereas in carcharodontosaurid theropods, including Montezumasaurus, Acrocanthosaurus, Carcharodontosaurus, Giganotosaurus, Mapusaurus, Shaochilong, and Tyrannotitan is
four. The maxillary tooth count in allosaurid theropods is *Allosaurus fragilis* (15), *A. jimmadseni* (16), *Fukuiraptor* (14), *Sinraptor* (15), *Saurophaganax* (17). The dentary tooth count in allosaurid theropods also varies *Allosaurus fragilis* (17), *A. jimmadseni* (18), *Fukuiraptor* (16), *Saurophaganax* (19), and *Sinraptor* (16).

The variation in tooth count in carcharodontosaurid theropods is greater than that of allosaurid theropods. *Montezumasaurus froesei* is the oldest member of the clade that possesses four premaxillary teeth, a common characteristic of all the carcharodontosauroids. The species is from the Late Jurassic (Tithonian 144 my). The maxillary and dentary tooth count remains unknown for *Montezumasaurus* due to the incompleteness of the maxillae and dentaries. *Tyrannotitan chubutensis* is a large carcharodontosaurid theropod from the Early Cretaceous (Aptian 118 my). The reconstructed skull is based upon incomplete cranial material. Therefore, it is unclear what the maxillary and dentary tooth counts were. However, as in all other carcharodontosauroids the suggested premaxillary tooth count remains four. *Acrocanthosaurus atokensis* is the second well-documented carcharodontosaurid theropod from North America and the first from which a complete tooth count can be obtained. It has four premaxillary teeth, 16 maxillary and 16 dentary teeth. The species lived during the Early Cretaceous (Late Aptian to Early Albian 116 my to 110 my).

A difference in maxillary tooth count is seen in *Eocarcharia dinops* with 15 teeth. This species is from the late Early Cretaceous (Late Albian to Early Cenomanian 110 my). The premaxillary tooth count in *Eocarcharia* is the same as in the previously mentioned two taxa of carcharodontosauroids. The dentary of *Eocarcharia* is unknown and the tooth count cannot be determined.
The skull of *Carcharodontosaurus saharicus* was reconstructed from incomplete cranial material. However, its preserved maxilla bears 14 teeth and the suggested tooth count for the dentary is also 14. However, whether *Carcharodontosaurus* had 14 dentary teeth is unclear. This species lived during the late Early Cretaceous (Late Albian to Early Cenomanian 100 my to 93 my). During the early Late Cretaceous (Late Cenomanian 99 my) *C. iguidensis* lived in Africa. The species is known from a well-preserved left maxilla, which bears 14 teeth. The premaxilla and dentaries are missing. Therefore, there is no conclusive evidence of the exact tooth count of *C. iguidensis*. *Giganotosaurus carolinii* is from the early Late Cretaceous (Cenomanian 97 my). The premaxillary tooth count is four as in other carcharodontosaurids, the maxillary tooth count is 16, and the dentary tooth count is also 16. *Mapusaurus roseae* is a close relative of *Giganotosaurus*. Both species are from the Cenomanian, however, *Mapusaurus* is younger than *Giganotosaurus* by 2 my. The reconstructed skull of *Mapusaurus* is based upon relatively well-preserved cranial material. The premaxilla bears four teeth, the maxilla 15 teeth, and dentaries have 19 teeth. *Shaochilong maortuensis* represents, thus far, the youngest member of the clade and its reconstructed skull is based upon incomplete cranial material. The species is from the mid Late Cretaceous (Turonian 92 my). Only a single maxilla of *Shaochilong* is preserved, in which tooth count is 12. The reconstructed premaxilla suggests there were four teeth as in other described carcharodontosaurid theropods. Therefore, variation in tooth count in carcharodontosaurids is seen only in the maxilla and dentary.

According to Currie et al. (2003), the variation in tooth number in large closely related theropods is due to taking on different prey items and possibly hunting in different
environments. A good example of tooth variation is observed in the Late Cretaceous Albertosaurinae theropods such as *Albertosaurus sarcophagus* and *Gorgosaurus libratus*. The maxillary tooth count is greater in *Gorgosaurus* than it is in *Albertosaurus*. The geographical occurrence between these two species is different, *Albertosaurus* is found in only Alberta; whereas *Gorgosaurus* is found in Alberta, northern Alaska, and Montana. Russell (1970) hypothesized that the more common *Gorgosaurus* actively hunted hadrosaurs, whereas *Daspletosaurus* and *Albertosaurus* hunted ceratopsian and ankylosaurian dinosaurs. However, the geographical separation between *Montezumassaurus* and *Allosaurus* was not large, because these two genera are present in the Morrison of Colorado. A favorable prey item of large bodied carcharodontosaurids that lived during the Late Cretaceous of South America were most likely sauropods. Thus far, *Allosaurus* is the best-documented theropod from the Morrison and even its specific prey, the long neck sauropods (Bakker et al., 1992; Madsen, 1993), is thought to be known. However, *Allosaurus* and *Torvosaurus* might have hunted other smaller theropods such as *Ceratosaurus, Ornitholestes* or *Stokesosaurus* (Smith, 1998). However, it is unclear if *Montezumassaurus* hunted similar prey items.

**AXIAL SKELETON**

**Ribs**—The remains of *Montezumassaurus froesei* include several rib fragments (Fig. 27). There are at least four ribs preserved, which include the following specimens: 18-A 6293, 18-U 6293, 18- 6293, and unnumbered. The length of 18-A 6293 is 8.5 cm and it most likely represents the distal part of one of the thoracic ribs. Specimen 18-U 6293 is crushed and encased in hard sandstone matrix (Fig. 28). Its length is 6.5 cm. On the reverse side of the matrix is another partially preserved rib. This rib fragment bears
the same number as the latter. This particular rib fragment is the largest among preserved ribs from *Montezumasaurus* (Fig. 29). Its dimensions are length 6 cm, and width 2.5 cm. The last rib 18-6293 represents the best-preserved distal portion of a thoracic rib (Fig. 30). The length of the rib is 9.5 cm. The bone in cross-section is relatively rounded laterally, and the medial side is flat. The lateral side has a shallow groove. In *Allosaurus*, the groove on the thoracic ribs is located on the anterior and posterior side. Therefore, the position of the groove on the rib is a diagnostic character for *Montezumasaurus*.

**POSTCRANIAL SKELETON**

**Scapula**—YPM 57589 (18-G 6293) represents the distal end of the right scapula (Fig. 31). The length of the preserved bone is 12 cm and its width is 9.5 cm. The bone is encased in hard matrix. However, seen in cross section the bone is convex, and if articulated the proximal end would have been relatively short and robust similar in shape to *Torvosaurus*.

**Manus**—Three partial metacarpals of the right manus 18-6293 are preserved (Figs. 32, 33, 34). All three metacarpals are missing their distal ends. The width of the proximal end of the metacarpal I is 4 cm. The ventral side of the bone bears two distinct fossae (Fig. 35). The surface is smooth and lacks any kind of ornamentation. Metacarpal I of *Montezumasaurus* is more robust than that of *Allosaurus*, with similar morphology to that of *Torvosaurus*. The width of the proximal end of metacarpal II is 5 cm, and its height is 3.5 cm. The outer surface of the proximal articulation is a round and lacks any kind of ornamentation. The proximal articular surface is a round depression and a small portion of the bone is missing. The ventral region of the bone is flat and preserves a small fossa, which probably represents a pathological structure because the bone surface is
heavily damaged and reveals its inner structure. Metacarpal III preserves a small portion of the shaft. The bone is approximately 3.5 cm wide and 4 cm high at its proximal end. The proximal articulation is round and lacks any kind of ornamentation. The shaft of metacarpal III is damaged. However, it is unusually robust. It is much more heavily built than in any other large-bodied theropods. In *Allosaurus*, metacarpal III is more delicately built and almost two times thinner than in *Montezumasaurus*. Therefore, the manus of *Montezumasaurus* is more massive and probably more powerful than that of *Allosaurus* and even that of *Torvosaurus* and other carcharodontosaurid theropods. It is also possible that the front limbs of *Montezumasaurus* were proportionally longer than those of *Allosaurus*.

**Ilium**—YPM 57589 (18-F 6293) represents the left pubic peduncle of the ilium of *Montezumasaurus froesei* (Fig. 36). Its length is 15 cm, height is 11 cm, and width is 7 cm. The neck of the pubic peduncle of the ischium is slender. The lateral surface of the bone is partially preserved, and the medial surface is heavily damaged. The articular surface for the contact with the pubis is slightly convex and ends with a small protruding notch. The notch might be just a remnant of a broken bone. The overall morphology of the bone differs from that of *Allosaurus* and *Torvosaurus*. In *Allosaurus*, the pubic peduncle is longer and less robust, whereas in *Torvosaurus* it is broad. The posterior region of the bone in *Montezumasaurus* is slightly concave, whereas in *Allosaurus* and *Torvosaurus* there are deeper concavities.

**Pubis**—YPM 57589 (18-L 6293) consists of two fragments, which represent the distal portion of the pubic shaft (Fig. 37). The most distal fragment of the pubis is 9.5 cm wide and 7 cm long, whereas the other fragment is 7.5 cm wide and 10 cm long. In cross
section, both elements are elliptical. Unfortunately, the rest of the pubis is missing. However, it is unclear if this particular element closely resembled that of *Allosaurus*. The pubis of *Allosaurus* is a robust structure. The shaft itself is much thicker than that of *Montezumasaurus*.

**Ischium**—YPM 57589 (18-K 6293) represents a partially preserved left ischium of *Montezumasaurus froesei* (Fig. 38). The bone consists of the proximal articulation and a small portion of the shaft. The following features are distinguishable: iliac articulation, pubic articulation, and obturator notch. The ischium of *Montezumasaurus* does not show the separation of the obturator notch from the pubic articulation of the ischium. This characteristic is also present in *Ceratosaurus*, whereas in *Allosaurus*, *Bahariasaurus*, and *Carcharodontosaurus* the ischium clearly shows an obturator notch separate from the pubic articulation of the ischium (Stromer, 1931, 1934; Rauhut, 1995). The lateral surface of the bone, especially part of the proximal articular surface, is encased in hard matrix. The ischium is broad proximally and thin distally with a relatively narrow medial part. The length of the preserved bone is 24 cm and the width is 19 cm. The width of the shaft close to the proximal articulation is 10.5 cm, whereas its distal end is 5.5 cm. The lateral surface of the bone is slightly convex, whereas its medial side is flat. The iliac articulation is oval and has a shallow fossa for the articulation with the ischial peduncle of the ilium.

**Tibia**—YPM 57589 (18-H 6293) represents the proximal articulation of the left tibia (Fig. 39). The bone is large and robust. It is approximately 18 cm wide on its lateral side when measured from the anterior to the posterior margins. The bone preserves the base of the cnemial crest and parts of lateral and medial condyles. However, as in other
carnosaurs including *Acrocanthosaurus*, *Allosaurus*, and *Megalosaurus* the cnemial crest is not as pronounced as it is in abelisauroid theropods. Most of the dorsal region of the bone is destroyed.

**Fibula**—YPM 57589 (18-L 6293) includes 22 fragmentary elements, which belong to a single fibula (Fig. 40). The outer surface of these fragments is heavily damaged and no adequate data can be provided.

**Astragalus**—YPM 57589 (19-C 6293) is a partially preserved left astragalus (Fig. 41). The length and the height of the bone is 10 cm. The bone preserves the following structures: anterior horizontal groove, ascending process, and shallow fossa. The bone is a concave structure and it lies cemented on top of hard conglomeratic matrix. The exposed surface of the astragalus is smooth. The overall morphology of the astragalus of *Montezumasaurus* differs from that of *Allosaurus*. In the astragalus of *Montezumasaurus* there is a relatively deep groove below the base of the ascending process, whereas in *Allosaurus*, there is no evidence of a deep groove below the base of the ascending process.

**Pes**—*Montezumasaurus froesei* includes a relatively well-preserved left pes (Fig. 42). The pes consists of the following bones: four metatarsals and eight pedal phalanges, including one ungual phalanx. When articulated the pes measures 70 cm long. Therefore, based on the pes length the height of the animal at the hips can be estimated at 280 cm. The height at the hips is estimated by the multiplication of the pes length by four (Thulborn, 1990).

**Metatarsals**—YPM 57589 (18-P 6293) represents metatarsal I (Fig. 43). The bone is missing a small portion of the most proximal end. It is approximately 5.5 cm long. Metatarsal I of *Montezumasaurus* is more massive than that of *Allosaurus*. Both collateral
ligament pits are preserved. However, the medial pit is much deeper than the lateral. A relatively deep fossa for insertion of M. digitorum longus is visible above the lateral condyle. The depth of the fossa that separates the condyles is 1 cm. The distal articulation of the bone bears two condyles that are missing a small portion of the posterior side. The maximum width of the distal end is approximately 3.5 cm. The medial condyle appears more pronounced than the lateral condyle.

YPM 57589 (18-M 6293) represents a complete metatarsal II (Fig. 44). The anterior end of the distal articulation bears a well-preserved but relatively shallow fossa for insertion of M. extensor digitorum. The length of the bone is 33.5 cm. The bone is robust, straight, and has a uniformly wide shaft. The proximal articulation is flat and featureless. The medial side of the proximal articulation is missing a small portion of the bone. The same is true for the lateral side in which a small piece of a bone is missing in its posterior region. When reconstructed the shape of the proximal articulation of the bone (Fig. 45) resembles that of Torvosaurus tanneri (BYUVP 5147). The distal end of the shaft is bent slightly forward, which is a characteristic for Acrocanthosaurus, Allosaurus, Megalosaurus, and Torvosaurus. The distal articulation has well-preserved collateral ligament pits that are relatively deep (Fig. 46). The medial pit is much deeper than the lateral pit. The medial condyle is also much larger than the lateral condyle. The height of the lateral condyle when measured from the top of the collateral ligament pit 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. The depth of the fossa that separates the condyles is 2.5 cm. Posterior to the fossa that separates the condyles is another much deeper fossa (Fig. 47). The much larger medial condyle articulates with phalanx I. The
anterior end of the distal articulation bears a well-preserved but relatively shallow fossa for insertion of M. extensor digitorum (Fig. 48). The posterior surface of the bone exhibits a longitudinally striated facet that is present approximately at the mid section of the bone (Fig. 49). The facet represents the insertion for the M. gastrocnemius pars medialis (Carrano and Hutchinson, 2002). Adjacent to the proximal end of the insertion for the M. gastrocnemius is a small depression that represents the articulation for metatarsal I.

YPM 57589 (18-N 6293) represents metatarsal III with the proximal articulation missing (Fig. 50). It is the largest bone in the foot. The proximal portion of the shaft is relatively round for the most part, but it is flattened in mid section all the way to the distal articulation of the bone. The lateral sides of the shaft are flattened towards the posterior surface of the bone forming a V-like cross section (Fig. 51). Both collateral ligament pits are preserved, and each is relatively deep and round. The distal articulation is broad and it has a shallow sulcus that separates the condyles, which articulate with phalanx 1-III (Fig. 52). The anterior side of the distal articulation preserves a relatively deep fossa for insertion of the M. extensor digitorum longus (Fig. 53). The posterior side of the distal articulation has a relatively deep fossa that shows a distinct separation of the two condyles, a feature that is common in tetanuran theropods (Fig. 54).

YPM 57589 (18-O 6293) is part of a metatarsal IV. The anterior of the distal articulation preserves a shallow fossa for insertion of the M. extensor digitorum longus (Fig. 55). The fossa is more laterally oriented than anteriorly. Metatarsal IV is missing half of the shaft, including the proximal articulation. The length of the preserved bone is 23 cm. However, if articulated it would be approximately the same length as metatarsal II.
The bone is D-shaped in cross section (Fig. 56). The anterior of the shaft is round, whereas the posterior of the shaft is flat and broad. The medial and lateral sides of the shaft are featureless. The lateral side of the shaft at its posterior region has a pronounced notch that is located approximately 9 cm from the distal articulation. Two flat depressions are present on the bone. These depressions (Fig. 57) extend along the posteromedial and posterior faces and are the place for the insertion of the M. gastrocnemius pars lateralis (Carrano and Hutchinson, 2002). The shaft narrows where it reaches the distal articulation. The distal articulation is relatively small D-shaped structure (Fig. 58). 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 (Fig. 59). At the posterior of the distal articulation, a shallow fossa separates the condyles. The distance from the condyles as measured from the middle is 5 cm, whereas the depth of the fossa that separates the condyles is 1 cm.

Phalanges—Almost all of the phalanges of the left pes of Montezumasaurus froesei (YPM 57589) are preserved. The only phalanges that are missing are 1-I and 2-I, and phalanx 4-IV. Additionally, a single partial ungual phalanx of the pedal digit IV is preserved, whereas unguals for digits I, II, and III are missing.

Phalanx 1-II (18-Q 6293) is well-preserved. The length of the bone is 13 cm. The hyperextensor pit is relatively deep and well preserved (Fig. 60). The proximal articulation is larger than the distal articulation and is a round and featureless structure. The posterior surface bears a single fossa that articulates with metatarsal II. The ventral side of the bone is damaged. However, the remaining borderline of the bone surface is present, which indicates that it was a round structure. The shaft is relatively short. The
distal articulation consists of two condyles, medial and lateral. The condyles are separated by a relatively deep fossa (Fig. 61). The depth of the fossa in the anterior region is 2 cm. Both collateral ligament pits are preserved. The medial ligament pit is deeper than the lateral (Fig. 62).

Phalanx 2-II (18-S 6293) is well-preserved. The length of the phalanx is 8 cm. The hyperextensor pit is very shallow and not well defined (Fig. 63). The proximal articulation is round and featureless. The shape of the bone resembles phalanx 1-II. The posterior surface of the bone is flat and round. The shaft is short. The overall shape of the shaft is round. The distal articulation is relatively narrow. Both collateral ligament pits are preserved. The medial pit is pushed inward, which makes the pit deeper than it might have been originally (Fig. 64). The preserved inner borderline of the pit indicates it was much deeper than the lateral pit. The distal articulation preserves two very pronounced condyles, lateral and medial, which are separated by a relatively deep fossa (Fig. 65). The distance between the condyles in the anterior region of the bone is 3 cm. The depth of the fossa that separates the condyles in the anterior region is 1 cm.

Phalanx 1-III (18-J 6293) has the entire distal articulation, including the shaft missing (Fig. 66). The proximal articulation is round. The posterior surface is slightly depressed and forms a fossa for the contact with metatarsal III (Fig. 67). The outer surface of the bone is wrinkled. The reason for these wrinkles remains unknown. However, it is possible that the wrinkles are pathological structures and represent a possible bacterial infection.

Phalanx 2-III (18-R 6293) has a length of 8 cm. The hyperextensor pit in the dorsal region of the bone is round and relatively deep and it extends to the lateral edges
of the condyles and occupies the anterior part of the shaft (Fig. 68). 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 posterior region of the proximal articulation consists of two shallow fossae for the articulation with phalanx 1-III (Fig. 69). The ventral region of the bone is flat and fan-like. The shaft is round, short, and wider than high. The width of the distal articulation is the same as the proximal articulation. The condyles of the distal articulation are of uniform size. The distance between the condyles in the anterior region is 4.5 cm. The condyles are separated by relatively shallow fossa with depth in the anterior region of 0.5 cm. Both collateral ligament pits are preserved. The collateral ligament pits are filled with hard matrix and no further information can be provided about their morphology (Fig. 70).

Phalanx 3-III (18-P 6293) (Fig. 71) is relatively short when compared to other phalanges in the pes. It is ventrally flat in the proximal articular region. The posterior region of the proximal articulation is D-shaped and has shallow fossae that articulate with phalanx 2-III (Fig. 72). Like the rest of the phalanges, the outer surface of the proximal articulation lacks any kind of ornamentation. The shaft is short. The condyles of the distal articulation are almost making contact with the distal part of the proximal articulation and they are separated from each other by a deep fossa (Fig. 73). The distance between condyles in the anterior region is 3 cm. The depth of the fossa that separates the condyles in the anterior region is 0.5 cm. Both collateral ligament pits are preserved. The medial pit is filled with hard matrix. The dorsal surface of the bone is damaged and no further characteristics can be determined.
Phalanx 1-IV (18-S 6293) is 8 cm long. The dorsal side of the distal articulation preserves a shallow hyperextensor pit (Fig. 74). The proximal articulation is round. However, its lateral side is skewed more towards the medial region where it forms a notch-like structure. The dorsal region of the proximal articulation is wrinkled mostly in one area on the lateral side of the bone. The wrinkles as seen on the other phalanges of *Montezumasaurus froesei* might represent pathological structures. The posterior surface of the bone is covered with hard matrix. Therefore, no data are available for this particular structure. The ventral region of the proximal articulation is concave (Fig. 75). The medial condyle is two times larger than the lateral condyle. The distance between condyles in the anterior region is 4 cm. The depth of the fossa that separates the condyles in the anterior region is 1.5 cm. Both collateral ligament pits are preserved in the bone. The lateral pit is partially preserved and important characters are missing. The medial ligament pit is filled with hard matrix. The shaft of the bone is short.

Phalanx 2-IV (18-W 6293) (Fig. 76) is short and appears to have no shaft. The proximal and distal articulations almost contact each other and their widths are approximately the same. Both the length and the width of the bone are 6 cm. The proximal articulation lacks any kind of ornamentation. The borderline of the mediolateral surface is wrinkled as it is seen in some other phalanges. The proximal articulation is D-shaped. There is no visible fossa on the posterior surface due to the presence of hard matrix. The ventral region of the proximal articulation preserves two condyles, medial and lateral. The medial condyle is larger than the lateral. The distance between condyles is 1 cm in the anterior region. Both collateral ligament pits are preserved in the bone. The medial pit is filled with hard matrix. Therefore, its depth is difficult to determine. The
lateral pit is partially preserved because most of the dorsal part of the lateral condyle is missing. However, the remaining part of the pit suggests that the structure was not deep. The dorsal region of the distal articulation is heavily damaged. Therefore, important data are unobtainable.

Phalanx 3-IV (18-Y 6293) (Fig. 77) is 6 cm long. The proximal and distal articulations are of the same width. The proximal articulation is heavily damaged especially in the dorsal region. The overall shape of the posterior surface is a D, as are most of the phalanges of Montezumasaurus. Both condyles are preserved on the bone. However, the medial condyle is only partially preserved and most of its dorsal region is missing. The distance between condyles in the anterior region is 3 cm. The depth of the fossa that separates condyles is 1 cm in the anterior region. Only one collateral ligament pit of the lateral side is preserved.

The ungual IV (18-X 6293) (Fig. 78). The estimated length of the bone is 3 cm. Most of the bone surface is damaged and no measurements can be obtained except for its general dimensions. In the dorsal-posterior region, the bone preserves a relatively long dorsal process. The length of the process is approximately 1.5 cm.

DISCUSSION

Almost all of the bones of the holotype of Montezumasaurus froesii YPM 57589 belong to a single individual, with the exception of one partially preserved right dentary YPM 57726 (19-B 6293), which belongs to a second individual. However, it is unclear whether Montezumasaurus is an adult or subadult. According to Brusatte et al. (2010), the maturity in theropods can be recognized by the fusion of the sutures of the interfrontal, frontal-parietal, and most of the braincase. Sereno and Brusatte (2008) argued that
although cranial fusion in theropods can be used as a sign of maturity, the ontogeny of fusion requires further study.

*Montezumasaurus* is considered to be the oldest member of the Carcharodontosauridae, a clade of large bodied theropods, which were thought to be restricted to Gondwana (Allain, 2002; Novas et al. 2005). Several diagnostic characters support a carcharodontosaurid affinity for *Montezumasaurus*. These include laterally flattened maxillary and dentary teeth, deep interdental plates, reduced antorbital fossa on the lateral surface of the maxilla, deep maxillary body, and robust and relatively straight metatarsals.

Recent studies show that carcharodontosaurid theropods were present in North America and China during the Early and late Early Cretaceous (Sereno et al. 1996; Harris, 1998; Brusatte and Sereno, 2007; Brusatte et al. 2009; Brusatte et al. 2010). The Laurasian carcharodontosaurids include *Acrocanthosaurus atokensis* in North America and *Shaochilong maortuensis* in China (Brusatte et al. 2010). The discovery of *Montezumasaurus* and its interpretation as the oldest carcharodontosaurid provides evidence that the clade might have originated in North America during the terminal stage of the Late Jurassic. Therefore, the presence of *Montezumasaurus* in the Tithonian (147 my) suggests that carcharodontosaurid theropods split from the Allosauridae much earlier. Rauhut (1995) suggested that the separation of these two clades took place in the Middle Jurassic or in earlier stages of the Late Jurassic. It is possible that during the Early Cretaceous the Laurasian carcharodontosaurids might have radiated to Gondwana in search of new habitable places. The radiation of carcharodontosaurids might have taken place as early as the beginning of the Early Cretaceous. Brusatte et al. (2010) considered
the carcharodontosaurid radiation of the Early–Mid Cretaceous as a global event. Some of the largest members of the clade that lived in South America include *Giganotosaurus carolinii, Mapusaurus roseae*, and *Tyrannotitan chubutensis*. Carcharodontosaurids are also known from the Late Cretaceous of Africa *Carcharodontosaurus iguidensis, C. saharicus*, and *Eocarcharia dinops* (Stromer, 1931; Brusatte and Sereno, 2007; Sereno and Brusatte, 2008). During the Late Cretaceous in Gondwana carcharodontosaurids were replaced by one of the most diverse clades of theropods, the Abelisauridae. Carcharodontosaurids are unknown from three incompletely sampled landmasses: Europe, Australia, and Antarctica (Weishampel et al. 2004; Brusatte and Sereno, 2008; Brusatte et al. 2010).

**Phylogeny**

Analysis of the data matrix resulted in 100 most parsimonius trees. The cladogram has a consistency index (C.I) of 49% and a retention index (R.I.) of 85% and 245 steps length. The strict consensus cladogram (Fig. 79) shows a close relationship among carcharodontosaurid taxa nested within Allosauroida. The reduced consensus cladogram (Fig. 80) shows similar results. According to Coria and Currie (2006) Carcharodontosauridae represents a monophyletic group, which is diagnosed by having heavily sculpted facial bones, a suborbital shelf formed by the papebral, a small suborbital process on the postorbital, a lacrimal recess, tooth crowns with moderate curvature, flat, blade-like premaxillary, maxillary and dentary teeth, deep interdental plates in premaxilla, maxilla, and dentaries, absence of subnarial foramen, and slender neck of the pubic peduncle of the ischium.
Montezumasaurus is nested within Carcharodontosauridae by sharing similar characteristics with Acrocanthosaurus and Eocarcharia such as tooth crowns with moderate curvature, blade-like maxillary and dentary teeth, deep interdental plates in premaxilla, maxilla, and dentary, absence of subnarial foramen, and slender neck of the pubic peduncle of the ischium.

CONCLUSIONS

Montezumasaurus froesei from the Late Jurassic of North America is interpreted as the most basal carcharodontosaurid theropod. It also represents the earliest recorded occurrence of Carcharodontosauridae in North America. Therefore, it is possible that the Carcharodontosauridae originated in North America. Recent discoveries of various theropod taxa establish the presence of Carcharodontosauridae in Africa, South America, and most recently in Asia (Brusatte et al. 2009).

Four large theropod genera are found in the Morrison Formation of the U.S. and the Lourinhã and Alcobaça formations of Portugal: Allosaurus, Ceratosaurus, Torvosaurus, and Aviatyrannis = Stokesosaurus (Mateus et al. 2006). Mateus et al. (2006) suggested that during the Late Jurassic, the presence of these typical North American theropod genera shows that there were land connections with the Iberian landmass. However, some Iberian isolation, before the Kimmeridgian, might have allowed theropod speciation that formed new endemic species. The transgression events led to some isolation of continental areas (Chure, 2000; Holtz et al., 2004). These events might have triggered the speciation in regions of the Iberian landmass and in North America, South America, and Africa. As a result some endemic species might have appeared on each
continent. Perhaps *Montezumasaurus* represents such taxon, which thus far only appears in the fossil record of North America.

**LITERATURE CITED**


Britt, B. 1991. Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. Brigham Young University Geological Studies 37:1–72.


Loewen, M. A. 2004. Variation and stratigraphic distribution of Allosaurus within the Late Jurassic Morrison Formation. Denver Annual Meeting of Geological Society of America 36:524A.


APPENDIX 1: MORPHOLOGICAL CHARACTERS

List of 264 characters and their state used in the phylogenetic analysis of *Montezumasaurus froseei*. The majority of characters are from Benson et al. (2009). The number in brackets after the formal character state is the character number from Benson et al. (2009). No number in brackets indicates a new character introduced in this study.

**Cranial Characters**

1. Premaxilla, height against length: longer than tall (0) length and height subequal (1) length and height equal (2)
2. Premaxillary body in front of external naris: shorter than body below naris and angle between anterior and alveolar margin higher than 75º (0) longer than body below naris and angle less than 70º with external naris overlapping the premaxillary tooth row (1) much longer than body below naris, naris located posterior to premaxillary tooth row (2) [ch. 1]
3. Premaxilla, interpremaxillary suture during ontogeny: open (0) fused (1) [ch. 2]
4. Premaxilla-nasal suture, form: V-shaped (0) W-shaped (1) [ch. 3]
5. Premaxilla, subnarial posterior process: strongly reduced in width, but still contacting the nasal (0) strongly reduced process does not contact the nasals and the maxilla forms part of the posteroventral border of the external nares (1) [ch. 4]
6. Subnarial foramen on the premaxilla-maxilla suture: absent (0) present (1) [ch. 5]
7. Premaxilla, palatal process: moderate (0) enlarged (1) [ch. 6]
8. Constriction between articulated premaxillae and maxillae: absent and anterior end of upper and lower jaws convergent (0) present and anterior end of upper and lower jaws expended into a premaxillary/dentary rosette [ch. 7]
9. Premaxillary-maxillary articulation: scarf or butt joint (0) interlocking (1) [ch. 8]  
10. Maxilla: featureless and triangular shape (0) sculpted and triangular shape (1)  
11. Maxilla: low anteriorly (0) tall anteriorly (1)  
12. Maxilla, subnarial foramen: present (0) absent (1)  
13. Maxilla, proportions of anterior ramus: absent or anteroposteriorly short (0)  
   prominent (1) extremely elongated (2) [ch. 9]  
14. Maxilla, anterior end of alveolar border: straight or slightly up curved (0) sharply up  
   curved such that the first maxillary tooth project anteroventrally (1) [ch. 10]  
15. Maxilla, anterior margin of antorbital fossa: rounded or pointed (0) squared (1) (ch. 11)  
16. Maxilla, ventral extent of antorbital fossa: does not extend far ventrally (0) extends  
   around half the height of the jugal process or further (1) [ch. 12]  
17. Maxilla, lateral lamina obscuring anteroventral corner of antorbital fossa in lateral  
   view: absent (0) present as stout lip (1) large shelf (2) [ch. 13]  
18. Maxilla, premaxillary foramen: small foramen (0) large fenestra (1) [ch. 14]  
19. Maxillary fenestra: absent (0) present as subcircular fossa (1) present penetrating the  
   maxilla from lateral to medial (2) [ch. 15]  
20. Maxilla, pneumatic region on medial side of maxilla posteroverentral to maxillary  
   fenestra: absent (0) present (1) [ch. 16]  
21. Maxilla, pneumatic fossa (excavatio pneumatica) in ascending process: absent (0)  
   present as a fossa (1) fenestra (2) [ch. 17]
22. Maxilla: position of anteromedial process: ventral, immediately dorsal to interdental plates (0) dorsal, immediately ventral to dorsal surface of maxillary anterior ramus [ch. 18]

23. Maxilla, anteromedial process: ridged flange/fluted prong (0) long, and plate shaped (1) [ch. 19]

24. Maxilla, secondary plate formed form enlarged maxillary component: absent (0) present (1) [ch. 20]

25. Maxillary interdental plates: separated (0) fused (1) [ch. 21]

26. Maxillary interdental plates: fully visible (0) bases concealed in medial view by medial wall of bone (1) [ch. 22]

27. Medial surface of maxillary interdental plates: smooth or finely pitted (0) dorsoventrally striated (1) [ch. 23]

28. Maxillary interdental plates: extend ventrally as far as lateral wall of maxilla (0) fall short of ventral level of lateral wall of maxilla (1) [ch. 24]

29. Nasals, shape in dorsal view: expending posteriorly (0) of subequal width throughout their length (1) [ch. 25]

30. Nasals, in adults: unfused (0) fused (1) [modified ch. 26]

31. Nasals, median horn: absent (0) present (1) [ch. 27]

32. Nasals, pronounced lateral rims: absent (0) present (1) tall, parasagittal crests (2) [ch. 28]

33. Nasals, dorsal surface: smooth (0) rugose and premaxillae and maxillae rugose (1) very coarsely rugose with numerous large excrescences and premaxillae and maxillae rugose (2) [ch. 29]
34. Dorsal extent of antorbital fossa: dorsal rim of antorbital fossa below nasal suture, or formed by this suture (0) antorbital fossa extending onto the lateral surface of the nasals (1) [ch. 30]

35. Nasal antorbital fossa: visible in lateral view (0) occluded in lateral view by a ventrolaterally overhanging lamina (1) [ch. 31]

36. Pneumatic foramen in the nasals: absent (0) present (1) [ch. 32]

37. Jugal, postorbital process: long and lightly built with relatively big slot for the postorbital contact (0) short, robust with small slot for the postorbital contact (1)

38. Jugal, postorbital contact: with 70º-angle (0) with 80º-angle (1)

39. Jugal, anterior end: posterior to internal antorbital fenestra, but reaching its posterior rim (0) excluded from the internal antorbital fenestra (1) expressed at the rim of the internal antorbital fenestra and with a distinct process that extends anteriorly underneath it (2) [ch. 33]

40. Jugal pneumatization: absent, jugal plate-like (0) present, jugal pneumatized by a foramen in the posterior rim of the jugal antorbital fossa (hollow internally and transversely expended) (1) [ch. 34]

41. Lacrimal, orientation of ventral process: strongly sloping anteroventrally (0) erect or nearly vertical (1) sloping posteroventrally (2) [ch. 35]

42. Lacrimal, dorsoventral thickness of the anterior process: very slender, greatly reduced in height (0) moderate, less than (1) thick, greater than (2) anteroposterior thickness of ventral ramus (3) [ch. 37]

43. Lacrimal ‘horn’: absent (0) small rugosity (1) robust rugose ridge (2) distal conical ‘horn’ (3) [ch. 38]
44. Lacrimal fenestra: absent (0) present as a large suboval recess (1) present as small foramen (2) [ch. 39]

45. Lacrimal recess: single opening (0) multiple openings (1) [ch. 40]

46. Lacrimal, morphology of lateral lamina of ventral process: anteriormost point situated around mid-height of ventral process (0) anteriormost point situated dorsal to mid-height of ventral process and a distinct rugose patch is present on the lateral surface (1) [ch. 41]

47. Lateral blade of lacrimal overhangs antorbital fenestra: yes (0) no (1) [ch. 42]

48. Suborbital process of lacrimal: absent (0) present (1) [ch. 43]

49. Postorbital-lacrimal contact: absent (0) present (1) [ch. 44]

50. Postorbital, lateral surface of anterior process: thin and unornamented or weakly rugose (0) dorsoventrally thickened into a laterally projecting and highly rugose platform (1) [ch. 45]

51. Postorbital, supraorbital shelf formed mostly by an additional ossification: absent (0) present (1) [ch. 46]

52. Supratemporal fossa, postorbital participation: present (0) present but restricted to anterior process (1) present but restricted to posterior process (2) [ch. 47]

53. Postorbital, cross-section of the jugal process: triangular (0) U-shaped (1) thin sheet (2) [ch. 48]

54. Postorbital, ventral extent of jugal process: substantially above ventral margin of orbit: yes (0) no (1) [ch. 49]
55. Postorbital, jugal process: ventrally directed and tapering (0) with a small anterior spur indicating the lower delimitation of the eyeball (1) large curving flange (2) [ch. 50]
56. Squamosal constriction of the lateral temporal fenestra: absent (0) present (1) (ch. 51)
57. Squamosal, anterodorsal lamina: emarginated by supratemporal fenestra (0) unemarginated (1) [ch. 52]
58. Quadrate: tall (0) short (1)
59. Quadrate, quadratic foramen: absent (0) present (1)
60. Quadrate, pterygoid blade: medial surface not sculpted (0) medial surface sculpted (1)
61. Quadrate, height of dorsal ramus: less than (0) or subequal to (1) height of the orbit (2) [ch. 53]
62. Pneumatization of the quadrate: absent (0) present (1) [ch. 54]
63. Quadrate foramen: developed as a distinct opening between the quadrate and quadratojugal (0) absent (1) [ch. 55]
64. Mandibular joint: approximately straight below the quadrate head (0) significantly posterior to quadrate head (1) significantly anterior to quadrate head (2) [ch. 56]
65. Quadrate, depression and foramen on medial surface in the vicinity of the mandibular condyle: absent (0) fossa adjacent to mandibular condyle, foramen more dorsally at base of pterygoid process (1) [ch. 57]
66. Quadratojugal: ventral side of the dorsal quadratojugal ramus slightly bent upward and robust (0) ventral side of dorsal quadratojugal ramus straight and in line with quadrate contact (1)
67. Quadratojugal-squamosal contact: narrow (0) slightly broad (1) broad (2)
68. Quadratojugal fused to quadrate in adults: no (0) yes (1) [ch. 58]

69. Quadratojugal, anteriormost point of the jugal process relative to lateral temporal fenestra: ventral (0) anterior (1) [ch. 59]

70. Orbit, shape: dorsoventrally tall, ‘keyhole’-shaped (0) expanded and subcircular (1) [ch. 60]

71. Supratemporal fossa anteromedial corner: open dorsally (0) roofed over by shelf of frontal-parietal (1) [ch. 61]

72. Nuchal plate of parietal with respect to postorbital attachments: not parallel (0) parallel (1) [ch. 62]

73. Nuchal wedge and parietal alae: small (0) hypertrophied and elevated (1) [ch. 63]

74. Supraoccipital, contribution to dorsal margin of the foramen magnum large (0) reduced (1) absent (2) [ch. 64]

75. Occipital region of the skull faces: posteriorly (0) posteroventrally (1) [ch. 65]

76. Basal tubera width: > or = (0) < occipital condyle width (1) [ch. 66]

77. Basioccipital apron, fossa ventral to occipital condyle: narrow and groove-like (0) broad depression approximately two-thirds the width of the occipital condyle (1) [ch. 67]

78. Neck of occipital condyle invaded by ventrolateral pair of pneumatic cavities that join medially: absent (0) present (1) [ch. 68]

79. Exit of cranial nerves X and XI: laterally through the jugular foramen (0) posteriorly through a foramen lateral to the exit of the cranial nerve XII and the occipital condyle (1) [ch. 69]
80. Exoccipital-opisthotic, posteroventral limit of contact with basisphenoid separated from basal tubera by a notch: no (0) yes (1) [ch. 70]

81. Paraoccipital processes: directed laterally or dorsally (0) directed ventrally (1) [ch. 71]

82. Ventral rim of the basis of the paraoccipital processes: above or level with the dorsal border of the occipital condyle (0) situated at mid-height of occipital condyle or lower (1) [ch. 72]

83. Basipterygoid: process: smooth surface (0) sculpted surface (1)

84. Basipterygoid processes: located anterior or anteroventral to basal tubera (0) located ventral to basal tubera (1) [ch. 73]

85. Interorbital region in adults: unossified (0) ossified (1) [modified ch. 74]

86. Median ridge separates exits of sixth cranial nerves: present (0) absent (1) [ch. 75]

87. Palatine, jugal process: tapered (0) expended (1) [ch. 76]

88. Dentary: dorsal splenial contact and ventral splenial contact of equal thickness (0) dorsal splenial contact thicker than ventral splenial contact (1)

89. Dentary: adductor fossa relatively wide and deep posteriorly (0) adductor fossa narrower and shallower posteriorly (1)

90. Dentary, anterior end in lateral view: blunt and unexpanded (0) dorsoventrally expanded, rounded and slightly upturned (1) with anteroventral process appearing ‘squared off’ in lateral view (2) [modified ch. 77]

91. Dentary: straight in dorsal view (0) curved anteromedially (1) [ch. 78]

92. Dentary, size of anterior most alveoli: approximately subequal in size (0) third alveolus circular and enlarged (1) [ch. 79]
93. Dentary, longitudinal groove housing dorsally situated row of neurovascular foramina on lateral surface: absent or weak (0) present and well-defined (1) [ch. 80]

94. Dentary, paradental groove wide anteriorly: no, narrow anteriorly (0) yes (1) [ch. 81]

95. Dentary, number of Meckelian foramina: one (0) two (1) [ch. 82]

96. Premaxillary teeth: great curvature (0) moderate curvature (1) lack curvature (2)

97. Premaxillary teeth: curvature in labial and lingual views > curvature in mesial view (0) curvature in labial and lingual views < curvature in mesial view (1)

98. Premaxillary teeth, number: three (0) four (1) five (2) six or seven (3) [ch. 83]

99. Premaxillary teeth, rostral carina of the crown: oriented in the middle of the tooth (0) oriented more lingually in the tooth (1)

100. Premaxillary teeth, mesial carina situated: on labial surface of tooth (0) on lingual surface of tooth, teeth D-shaped in cross section (1) [ch. 84]

101. Premaxillary teeth: all approximately equal size (0) some significantly larger than others (1) [ch. 85]

102. Maxillary teeth, crown: semi rounded and bullet shaped (0) flattened and large (1)

103. Maxillary teeth, number: 12-14 (0) 15-17 (1) 20 or more (2) [ch. 86]

104. Ratio of dentary to maxillary teeth: 0.80-1 (0) 0.70-0.78 (1) [ch. 87]

105. Maxillary and dentary teeth, serrations: present (0) absent (1) [ch. 88]

106. Teeth, mesial carina of lateral teeth: extends to base of crown (0) terminates around mid-height of crown or more dorsally (1) [ch. 89]

107. Teeth, interdenticular sulci on lateral teeth: absent (0) present (1) [ch. 90]

108. Tooth crowns: labioligually compressed (0) basal cross-section subcircular (1) [ch. 91]
109. Tooth row: ends beneath orbit (0) ends at the anterior rim of the orbit (1) completely antorbital, tooth row ends anterior to the vertical strut of the lacrimal (2) [ch. 92]

110. Crown striations: absent (0) present (1) [ch. 93]

111. Teeth, distal root shape: broad (0) strongly tapered (1) [ch. 94]

112. Teeth, enamel wrinkles: absent (0) present, extending as bands across labial and lingual tooth surface (1) present adjacent to carinae but do not extend across labial and lingual tooth surface (2) [ch. 95]

113. Crown curvature: present (0) absent (1) [ch. 96]

114. Splenial, anteroventral foramen: completely enclosed in the splenial (0) opened anteroventrally (1) [ch. 97]

115. Horizontal shelf on the lateral surface of the surangular anteroventral to the mandibular condyle: absent or only a small ridge (0) prominent (1) [ch. 98]

116. Anterior portion of the surangular: less than half the height of the mandible above the mandibular fenestra (0) more than half the height of the mandible at the level of the mandibular fenestra (1) [ch. 99]

117. Surangular, number of posterior surangular foramina: one (0) two (1) [ch. 100]

**Axial Characters**

118. Axial intercentrum, orientation of ventral surface relative to axis: subparallel or anteroventrally inclined (0) anterodorsally oriented (1) [ch. 101]

119. Axis, pleurocoel in centrum: absent (0) present (1) [ch. 102]

120. Axis, neural spine shape: dorsal end transversely flared (0) transversely compressed (1) [ch. 103]
121. Axial diapophyses: moderate (0) reduced/absent (1) [ch. 104]

122. Axial parapophyses: moderate/prominent (0) reduced/absent (1) [ch. 105]

123. Axial neural spine: broad (prominent spinopostzygapophyseal laminae) (0) invaginated laterally (1) [ch. 106]

124. Ventral keel in anterior cervicals/axis: present (0) absent/developed as a weak ridge (1) [ch. 107]

125. Presacral vertebrae: not elongated (0) elongated, cervical vertebrae at least three times as long as high and dorsal vertebrae at least twice as long as high (1) [ch. 108]

126. Presacral vertebral pneumaticity: pleurocoels developed as deep and uninvaginated depressions (0) large chambers within centrum (camerate) (1) subdivided into sub-chambers (camellate) (2) [ch. 109]

127. Anterior cervical vertebrae: transverse distance between prezygapophyses less than width of neural canal (0) prezygapophyses situated lateral to the neural canal (1) [ch. 110]

128. Number of pleurocoels in cervicals: two, arranged horizontally with posterior most pleurocoel situated in posterior half of centrum (0) one (1) two on some centra, posteriormost pleurocoel situated in anterior half of centrum (2) [ch. 111]

129. Middle cervical vertebrae, pleurocoel presents centrum through parapophysis: no (0) yes (1) [ch. 112]

130. Anterior surface presacral vertebrae: amphiplatyan or amphicoelous (0) convex (1) [ch. 113]

131. Posterior cervical ribs and centra in adults: separate (0) fused (1) [modified ch. 114]
132. Dorsal vertebrae, pleurocoels: absent (0) present in anterior dorsals (‘pectorals’) (1) present in all dorsals (2) [ch. 115]

133. Anterior dorsal vertebrae, ventral keel: absent or developed as a weak ridge (0) pronounced, around one-third the height of and inset from the lateral surfaces of the centrum (1) [ch. 116]

134. Dorsal vertebrae, hyposphene: laminae diverge ventrolaterally to form a triangular shape in posterior view (0) laminae vertical forming a sheet-like hyposphene (1) [ch. 117]

135. Dorsal vertebrae, distinct step-like ridge lateral to hyposphene, running posterodorsally from the dorsal border of the neural canal to the posterior edge of the postzygapophyses: absent (0) present (1) [ch. 118]

136. Dorsal vertebrae, neural spines: transversely compressed sheets (0) transversely broadened anteriorly and posteriorly and central regions of lateral surface embayed by deep vertically oriented troughs (1) [ch. 119]

137. Dorsal vertebrae, neural spine height: low, 1.3 or less times centrum height (0) moderate, 1.4-1.7 times centrum height (1) tall, 1.9 or more times centrum height (2) [ch. 120]

138. Posterior dorsal vertebrae, parapophyses: on short pedicles of flush with neural arch (0) on long ‘stalks’ almost as long as transverse processes (1) (ch. 121)

139. Posterior dorsal vertebrae, transverse processes, accessory centrodiapophyseal lamina: absent (0) present (1) [ch. 122]

140. Posterior dorsal vertebrae, neural spines, basal webbing: absent (0) present (1) [ch. 123]
141. Posterior dorsal vertebrae, neural spines: oriented vertically or posteriorly (0) 
    oriented anteriorly (1) [ch. 124]
142. Sacral vertebrae, number: five (0) six (1) [ch. 125]
143. Sacral centra, pleurocoels: absent (0) present (1) [ch. 126]
144. Sacrum, fenestrae between sacral neural spines: absent (0) present (1) [ch. 127]
145. Proximal caudal vertebrae, ventral surface: groove (0) distinct sunken groove (1) 
    robust ventral ridge (2) [ch. 128]
146. Proximal caudal vertebrae, pleurocoels: absent (0) present (1) [ch. 129]
147. Medial caudal vertebrae, anterior margin of neural spines: straight (0) with 
    anterior spur or with distinct kink, dorsal part of anterior margin more strongly 
    inclined posteriorly than ventral part (1) [ch. 130]
148. Neural spines of mid-caudals: rod-like and posteriorly inclined (0) subrectangular 
    and sheet-like (1) rod-like and vertical (2) [ch. 131]
149. Prezygapophyses of distal caudal vertebrae: not elongated (0) strongly elongated, 
    overhanging at least one-quarter of the length of the preceding centrum (1) [ch. 132]
150. Chevrons, anterior process: absent/weak (0) large (1) [ch. 133]
151. Chevrons, proximal articular surface: distal transverse ridge dividing surface into 
    anterior and posterior facets (0) no ridge, low mounds may be present, one on each 
    side, laterally (1) [ch. 134]
152. Mid-caudal chevrons: rod-like or slightly expanded ventrally (0) L-shaped (1) [ch. 
    135]
153. Anterior middle caudal chevrons, distal end: expanded anteroposteriorly (0) 
    unexpanded (1) [ch. 136]
154. Ribs, cranial intercostal ridge: oriented anteriorly and posteriorly (0) oriented laterally (1)

**Appendicular Characters**

155. Scapula, mid and posterior region: long and narrow (0) short and broad (1)

156. Scapula, shape of posterior region: long and narrow (0) short and broad (1)

157. Scapula, length to minimum height ratio: less than seven (0) 7.5-9 (1) more than 10.5 (2) [ch. 137]

158. Scapula, transition between acromial process and scapular blade: gradual, at an oblique angle (0) abrupt, approximately perpendicular (1) [ch. 138]

159. Anterior margin of the scapulocoracoid: indented or notched between the acromial process of the scapula and coracoid suture (0) smoothly curved and uninterrupted across the contact between the scapula and coracoid (1) [ch. 139]

160. Coracoid, ventral part anterior to the glenoid facet: approximately level with the rim of the facet (0) with tapering posteroventral process (1) [ch. 140]

161. Coracoid tubercle (= acrocoracoid process or biceps tubercle): absent or poorly developed (0) conspicuous and well developed as a tuber (1) developed as an obliquely oriented ridge (2) [ch. 141]

162. Humerus to femur length ratio: at least 0.4 (0) 0.35 or less (1) [ch. 142]

163. Humerus, shape in lateral view: sigmoidal (0) straight (1) [ch. 143]

164. Humerus, deltopectoral crest length to humeral length ratio: less than 0.4 (0) 0.43-0.49 (1) more than 0.52 (2) [ch. 144]
165. Humerus, deltopectoral crest orientation: longitudinal (0) oblique distolaterally and apex of crest oriented laterally rather than anteriorly from the humeral shaft (1) [ch. 145]

166. Humerus, anterior surface of bone adjacent to ulnar condyle: smooth or gently depressed (0) bears well-defined fossa (1) [ch. 146]

167. Humerus, prominent ulnar epicondyle: absent (0) present (1) [ch. 147]

168. Ulna, length to minimum circumference ratio: less than 2.3 (0) more than 2.6 (1) [ch. 148]

169. Ulna, proximal end with hypertrophied medial and lateral processes: no (0) yes (1) [ch. 149]

170. Radial external tuberosity and ulnar internal tuberosity, size: low and rounded (0) hypertrophied (1) [ch. 150]

171. Radius: straight (0) curves laterally (1) [ch. 151]

172. Radius, tuber around mid-length on posteromedial surface: absent (0) present (1) [ch. 152]

173. Metacarpal I: small and lightly built (0) robust (1)

174. Metacarpal II: small and lightly built (0) robust (1)

175. Metacarpal III: small and lightly built (0) robust (1)

176. Large distal carpal, capping I and parts of II: absent (0) present (1) [modified ch. 153]

177. Metacarpals, ratio of transverse width of proximal articular ends to minimum transverse width: < 2 (0) > 2 (1) [ch. 154]

178. Metacarpal I, length to minimum width ratio: 1.4-1.9 (0) 2.4 or higher (1) [ch. 155]
179. Contact between metacarpal I and metacarpal II: metacarpals contact each other at their bases only (0) metacarpal I closely appressed to proximal half of metacarpal II (1) [modified ch. 156]

180. Metacarpal III to metacarpal II width ratio: < 0.55 (0) > 0.35 (1) [modified ch. 157]

181. Metacarpal IV: present (0) absent or extremely reduced (1) [modified ch. 158]

182. Manual ungual I, enlarged and elongated: no (0) yes (1) [ch. 159]

183. Fusion between pelvic elements in adults: absent (0) present (1) [ch. 160]

184. Ilium, anterior margin of preacetabular process, profile: gently convex (0) straight (1) [ch. 161]

185. Vertical ridge on iliac blade above acetabulum: absent (0) developed as a low swollen ridge with associated foramina (1) present as a well-developed ridge (2) [ch. 162]

186. Ilium, hook-like ventral process on anteroventral margin forming preacetabular notch: absent (0) present (1) [ch. 163]

187. Ilium, preacetabular fossa: absent (0) present (1) [ch. 164]

188. Ilium, pubic peduncle: taller than wide (0) wider than tall (1)

189. Ilium, pubic peduncle: ventral articular surface flat and narrower posteriorly (0) ventral articular surface convex and wide posteriorly (1)

190. Ilium, pubic peduncle size relative to ischial peduncle: subequal (0) larger (1) [ch. 165]

191. Ilium, length to width ratio of pubic peduncle: 1 or lower (0) 1.3-1.4 (1) 1.55-1.75 (2) greater than 2.0 (3) [ch. 166]
192. Ilium, acetabular margin of pubic peduncle: mediolaterally convex or flat (0)
    mediolaterally concave (1) [ch. 167]

193. Ilium, brevis fossa: narrow with subparallel margins (0) strongly expanded
    posteriorly (1) [ch. 168]

194. Ilium, articular facet of pubic peduncle: facing more ventrally than anteriorly and
    without pronounced kink (0) with pronounced kink and anterior part facing almost
    entirely anteriorly (1) [ch. 169]

195. Ilium, supracetabular crest: hood-like and hypertrophied, strongly concave region
    present between shelf and anterior blade of ilium in dorsal view (0) ventrolaterally
    oriented shelf occluding anterodorsal corner of acetabulum in lateral view (1) [ch.
    170]

196. Pubic shaft in lateral view: straight (0) anteriorly convex (1) [ch. 171]

197. Pubis, obturator foramen/notch: completely enclosed (0) open ventrally (1) [ch.
    172]

198. Pubic shaft: meet along entire length (0) meet along entire length in anterior view
    but fenestra present between distal expansions in distal view (1) pubic foramen
    perforating the pubic apron in the distal half of the pubic shaft (2) [ch. 173]

199. Pubic ratio of distal expansion length to shaft length: less than 0.3 (0) more than
    0.5 (1) [ch. 174]

200. Pubis, distal expansion: more posteriorly than anteriorly expanded (0) subequally
    expanded anteriorly and posteriorly (1) [ch. 175]

201. Pubic distal expansions in ventral view: broadly triangular (0) narrow, with
    subparallel margins (1) [ch. 176]
202. Pubic apices in adults: unfused (0) fused (1) [modified ch. 177]
203. Ischium, shaft in lateral view: straight (0) curving anteroventrally (1) [ch. 178]
204. Ischium, surface for articulation with the ilium: flat (0) deeply concave (1) [ch. 179]
205. Ischial antitrochanter: present (0) absent (1) [ch. 180]
206. Ischium, obturator process: confluent with pubic peduncle and foramen present in ischial portion of puboischiadic plate (0) offset from pubic peduncle by a distinct notch (1) [ch. 181]
207. Ischium, ventral notch between obturator-process or flange on ischium: absent (0) present (1) [ch. 182]
208. Ischium, prominent, rugose distal tubercle: absent (0) present (1) [ch. 183]
209. Ischiadic symphysis: unexpanded (0) expanded as apron (1) [ch. 184]
210. Ischium, shape of distal termination: rounded with spatulate outline in lateral view (0) expanded anteroposteriorly/triangular (1) [ch. 185]
211. Ischial terminal process in adults: unfused (0) fused (1) [modified ch. 186]
212. Femoral head orientation: ventromedial (0) horizontal (1) dorsomedial (2) [ch. 187]
213. Femur, groove on proximal surface of head oriented oblique to the long axis of the head: absent (0) present (1) [ch. 188]
214. Femur, oblique ligament groove on posterior surface of head: absent or very shallow (0) deep, bound medially by a well-developed posterior lip (1) [ch. 189]
215. Femur, placement of lesser trochanter: distal (0) proximal (1) [ch. 190]
216. Femur, distinctly projecting accessory trochanter (derived from the anterior trochanter): absent (0) present as a triangular flange projecting from the anterior surface of the lesser trochanter (1) [ch. 191]

217. Femur, forth trochanter: present as a prominent semi-oval flange (0) very weak or absent (1) [ch. 192]

218. Femur, extensor groove: absent, anterior surface of distal femur flat (0) present (1) [ch. 193]

219. Femur, muscle scar situated medially on anterior surface of distal femur: suboval rugose patch not extending to distal end of femur (0) large oval depression (1) [ch. 194]

220. Femoral medial epicondyle (= medial distal crest): stout rigid (0) hypertrophied and flange-like (1) [ch. 195]

221. Femur, lateral condyle: does not project further distally than medial condyle (0) projects distinctly further than medial condyle and distal surface of medial condyle is gently flattened in comparison (1) [ch. 196]

222. Femur, infrapopliteal ridge present posteriorly between medial condyle and crista tibiofibularis: no (0) yes (1) [ch. 197]

223. Femur, long axis of medial condyle in distal view: oriented anteroposteriorly (0) inclined posterolaterally (1) [ch. 198]

224. Tibia, cnemial crest: prominent but not expanded (0) proximodistally expanded (1) [ch. 199]

225. Tibia, lateral condyle: confluent with cnemial crest anteriorly in proximal view (0) strongly offset from cnemial crest by incisura tibialis (1) [ch. 200]
226. Tibia, medial condyle: bulbous eminence, not continuous with posterior surface of head (0) extends distally as a ridge that merges with posterior surface of head (1) [ch. 201]

227. Tibia, lateral ridge for connection with fibula (crista fibularis or fibular flange): present, extending from the proximal articular surface distally (0) present, clearly separated from proximal articular surface (1) [ch. 202]

228. Tibia, fibular flange shape: transversely narrow flange (0) oval mound (1) [ch. 203]

229. Tibia, distal end transversely expanded and articulates with calcaneum: no (0) yes (1) [ch. 204]

230. Tibia, form of medial malleolus: oriented distally and medial surface smooth (0) oriented distally and distinct ‘shoulder’ present in outline of medial surface in posterior view (1) oriented almost medially, ‘shoulder’ absent (2) [ch. 205]

231. Astragalus, horizontal groove: absent (0) present (1)

232. Astragalus, horizontal groove: shallow (0) deep (1)

233. Astragalus, horizontal fossa: absent (0) shallow (1) moderate (2) present and deep (3)

234. Bracing for ascending process of astragalus on anterior side of distal tibia: distinct ‘step’ running obliquely from mediodistal to lateroproximal (0) bluntly rounded vertical ridge on medial side (1) anterior side of tibia more or less flat (2) [ch. 206]

235. Fibula, lateral surface of proximal end: shallow longitudinal trough situated posteriorly (0) trough absent or weak groove present, surface convex (1) [ch. 207]
236. Fibula, deep groove on medial side of proximal end: absent (0) present, but covering less than two-thirds of the width of the fibula (1) present and wide, covering more than two-thirds the width of the fibula (2) present and opening posteromedially (3) [ch. 208]

237. Fibula, anterolateral process: absent (0) developed as a mound-like swelling (1) prominent, anteroventrally curving flange (2) prominent rugose mound (3) [ch. 209]

238. Fibula, ratio of anteroposterior width of distal end to minimum shaft width: 2.3 or greater (0) 1.9-2.1 (1) less than 1.7 (2) [ch. 210]

239. Astragalus, ascending process: arising out of the lateral part of the astragalar body (0) arising out of the complete breadth of the astragalar body (1) [ch. 211]

240. Metatarsal I width and height are equal (0) width greater than height (1)

241. Metatarsal I, proximal articulation: taller than wide (0) wider than tall (1)

242. Metatarsal I: lateral and medial condyles are of equal size (0) medial condyle slightly bigger than lateral condyle (1)

243. Metatarsal I, collateral ligament pit: lateral and medial of equal depth (0) lateral deeper than medial (1) medial deeper than lateral (2)

244. Metatarsal II, proximal articulation: broad, flat and rounded laterally (0) small and rounded laterally (1)

245. Metatarsal II, distal articulation: wider than tall and flat (0) taller than wide and rounded (1)

246. Metatarsal II: lateral condyle wider than tall (0) lateral condyle shorter than tall (1)

247. Metatarsals II, III, IV, collateral ligament pits: lateral and medial of equal depth (0) lateral deeper than medial (1) medial deeper then lateral (2)
248. Metatarsal III, proximal articulation: similar in area to metatarsals II and IV (0) smaller than metatarsals II and IV (1)

249. Metatarsal III, proximal articulation: rectangular, medial and lateral surface flat (0) hourglass-shaped, medial and or lateral surface(s) dorsoventrally concave (1) [modified ch. 212]

250. Metatarsal III, distal articulation: width and height are subequal (0) width greater than height (1)

251. Metatarsal III, distal shaft: round (0) flat and broad (1)

252. Metatarsal III, mid shaft: round and narrow (0) round and broad (1)

253. Metatarsal III posterior shaft: round (0) flat (1) round but laterally flattened (2)

254. Metatarsal III, shaft shape: rectangular (0) wedge-shaped, plantar surface pinched (1) [modified ch. 213]

255. Metatarsal IV, distal articulation: large and flat (0) small and triangular (1)

256. Metatarsal IV: lateral width of condyle equal to its height (0) lateral width of condyle twice the size of its length (1)

257. Metatarsal IV, shaft: relatively straight (0) slightly curved laterally (1) strongly curved laterally (2)

258. Metatarsal IV, distal shaft: round and small (0) round and broad (1) triangular and posteriorly flattened (2)

259. Metatarsal IV, mid shaft: round (0) round anteriorly but flattened posteriorly and D-shaped (1)
260. Metatarsal IV: shallow depression for the insertion of M. gastrocnemius pars lateralis (0) relatively deep depression for the insertion of M. gastrocnemius pars lateralis (1)

261. Metatarsus proportions: elongated (0) elongated and broad (1) short and broad (2)

262. Pedal phalanges, 1-II, 2-II, 1-III, 2-III, 3-III, 1-IV, 2-IV, 3-IV, 4-IV collateral ligament pit: lateral and medial pits are of same depth (0) lateral pit deeper than medial pit (1) medial pit deeper than lateral pit (2)

263. Pedal phalanx, 1-II, 2-II, 1-III, 2-III, 3-III, 1-IV, 2-IV, 3-IV, 4-IV, articular surface: proximal wider than distal (0) both articular surfaces are of same width (1)

264. Pedal phalanx, 1-IV, 2-IV, 3-IV, 4-IV: lateral and medial condyles are of subequal size (0) medial condyle bigger than lateral condyle (2)
APPENDIX 2: DATA MATRIX FOR PHYLOGENETIC ANALYSIS

In this appendix are data matrixes included in the phylogenetic studies. The character scores are used from Benson et al. (2009) in the phylogenetic analysis of basal tetanuran theropods. For this analysis the non-tetanuran theropods, *Syntarsus kayentakae* and *Dilophosaurus wetherilli* represent outgroup. Thirty one genera including one clade are used in this study.

*Syntarsus kayentakae*

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Megalosaurus bucklandii

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Lourinhanosaurus

Poekilopleuron
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Chilantaisaurus

Fukuiraptor

Megaraptor
FIGURE 1. Left PM, premaxilla of *Montezumasaurus froesei* YPM 57589 (18-H 6293) in lateral view. Note that the premaxilla is relatively short and tall. Also note the contact of the premaxilla and M, maxilla (arrow). Scale bar equals 10 cm.
FIGURE 2. Left premaxilla of *Montezumasaurus froesei* YPM 57589 (18-H 6293) in occlusal view. Note the angle of the curvature of the premaxilla and four premaxillary teeth. Scale bar equals 10 cm.
FIGURE 3. Left maxilla of *Montezumasaurus froesei* YPM 57589 (18-E 6293) in lateral view showing *apm*, ascending process of maxilla. Scale bar equals 10 cm.
FIGURE 4. Mix of cranial bones and teeth of *Montezumasaurus floesei* YPM 57589 (18-K 6293). Note an arrow pointing to a single tooth at the middle-top of the matrix. The other two arrows below the tooth point to some of the cranial bones encased in the matrix. Scale bar equals 10 cm.
FIGURE 5. Left jpp, jugal postorbital process of *Montezumasaurus froesei* YPM 57589 (19-A 6293). Note how robust the bone is at its base. Scale bar equals 10 cm.
Figure 6. Left quadratojugal of *Montezumasaurus froesei* YPM 57589 (18-Z 6293) showing the following: **dqjr**, dorsal quadratojugal ramus; **qp**, quadrate process of quadratojugal; **rqjr**, rostral quadratojugal ramus. Note that the base of the **rqjr** is in line with the **qp**. Scale equals 10 cm.
FIGURE 7. Left rqjr, rostral quadratojugal ramus of Montezumasaurus froesei YPM 57589 (19-C 6293). Scale equals 10 cm.
FIGURE 8. Left quadrate of *Montezumasaurus froesei* YPM 57589 (18-A 6293) in medial view. Note parallel lines on the flat surface of the quadrate. These parallel lines represent muscle scars of the pdm, posterior M. adductor mandibular. The following features are preserved, lc, lateral quadrate condyle; h, head of quadrate; ptr, pterygoid ramus of quadrate; qs, quadrate shaft. Scale bar equals 10 cm.
FIGURE 10. Right frontal of *Montezumasaurus froesei* YPM 57589 (18-? 6293) in dorsal view. Scale equals 10 cm.
FIGURE 11. Braincase of *Montezumasaurus froesei* YPM 57589 (18-Z 6293) in left lateral aspect. Scale bar equals 10 cm.
FIGURE 12. Braincase of *Montezumasaurus froesei* YPM 57589 (18-Z 6293) in dorsal view showing the *pa*, parietal and also *ant*, anterior side and *post*, posterior side.

Scale equals 10 cm.
FIGURE 13. Braincase of *Montezumasaurus froesei* YPM 57589 (18-Z 6293) in ventral view showing the bsp, basipterygoid process. Scale bar equals 10 cm.
FIGURE 14. Right dentary of *Montezumasaurus froesei* YPM 57589 (18-C 6293) in lateral view. Scale bar equals 10 cm.
FIGURE 15. Right dentary of second individual of *Montezumasaurus froesei* YPM 57726 (19-A 6293) in lateral view. Scale bar equals 10 cm.
FIGURE 16. Right dentary of *Montezumasaurus froseei* YPM 57589 (18-C 6293) in cross section of the anterior view showing unerupted tooth (arrow).

Scale bar equals 10 cm.
FIGURE 17. Right dentary of *Montezumasaurus froesei* YPM 57589 (18-C 6293) in lingual view showing the *idp*, interdental plates; *spl*, splenial contact; *sr*, splenial ridge of dentary. Scale bar equals 10 cm.
FIGURE 18. Right dentary of second individual of *Montezumasaurus froesei* YPM 57726 (19-A 6293) in occlusal view showing five alveoli with five partially preserved teeth. Scale bar equals 10 cm.
FIGURE 19. Right dentary of second individual of *Montezumasaurus froesei* YPM 57726 (19-A 6293) in lingual view showing the sd, supradentary contact spl, splenial contact; sr; splenial ridge of dentary. Scale bar equals 10 cm.
FIGURE 20. A possible splenial of second individual of *Montezumasaurus froeseti* YPM 57726 (19-A 6293). The bone fragment is seen in medial view. Scale bar equals 10 cm.
FIGURE 22. Premaxillary tooth of *Montezumasaurus froesei* YPM 57589 (19-A 6293) in lingual view. Scale bar equals 5 cm.
FIGURE 23. Teeth (arrows) of *Montezumasaurus froesei* YPM 57589 (18-E 6293) encased in sandstone matrix. Scale bar equals 10 cm.
FIGURE 24. Teeth (arrows) of Montezumasaurus froesei YPM 57589 (18-E 6293) encased in sandstone matrix. Scale bar 5 cm.
FIGURE 25. Teeth (arrows) of *Montezumasaurus froesei* YPM 57589 (18-A 6293) encased in conglomeratic matrix. Scale bar equals 10 cm.
FIGURE 26. Maxillary teeth (arrows) of *Montezumasaurus froesei* YPM 57589 (18-A 6293).
FIGURE 27. Rib fragments of *Montezumasaurus froesei* YPM 57589 (18-A 6293) and (18-U 6293). Scale bar equals 10 cm.
FIGURE 28. Rib fragment (arrow) of *Montezumasaurus froesei* YPM 57589 (18-U 6293) attached to sandstone matrix. Scale bar equals 5 cm.
FIGURE 29. Rib fragment (arrow) of *Montezumasaurus froesei* YPM 57589 (18-U 6293) encased in sandstone matrix. Scale bar equals 5 cm.
FIGURE 30. Fragment of the thoracic rib of *Montezumasaurus froesei* YPM 57589 (18-6293). Thus far the best preserved distal portion preserving a shallow groove (arrow) the *cir*, cranial intercostals ridge. Scale bar equals 5 cm.
FIGURE 31. Distal end of Sc, scapula of *Montezumasaurus froesei* YPM 57589 (18-G 6293) encased in sandstone matrix. Scale bar equals 10 cm.
FIGURE 32. Left metacarpal I of *Montezumasaurus froeseti* YPM 57589 (18-6293) in dorsal view. Scale bar equals 5 cm.
FIGURE 33. Left metacarpal II of *Montezumasaurus froesei* YPM 57589 (18-6293) in dorsal view. Scale bar equals 5 cm.
FIGURE 34. Left metacarpal III of *Montezumasaurus froesei* YPM 57589 (18-6293) in dorsal view. Scale bar equals 5 cm.
FIGURE 35. Left metacarpal I of *Montezumasaurus froesi* YPM 57589 (18-6293) in ventral view showing two distinct fossae (arrows). Scale bar equals 5 cm.
FIGURE 36. Left pubic peduncle of *Montezumasaurus froesei* YPM 57589 (18-F 6293) in lateral view. Scale bar equals 10 cm.
FIGURE 37. Distal portion of the pubic shaft of *Montezumasaurus froesei* YPM 57589 (18-L 6293) in lateral view. Scale bar equals 10 cm.
FIGURE 38. Proximal end of left ischium of *Montezumasaurus froesei* YPM 57589 (18-K 6293) in lateral view. The following features are distinguishable: *il*, iliac articulation; *pu*, pubic articulation; *on*, obturator notch. Scale bar equals 10 cm.
FIGURE 39. Proximal articulation of the left tibia of *Montezumaurus froesei* YPM 57589 (18-H 6293) in lateral view. The following features are distinguishable: **cn**, cnemial crest; **fc**, fibular crest; **lc**; lateral condyles. Scale bar equals 10 cm.
FIGURE 40. Fibula of *Montezumasaurus froesei* YPM 57589 (18-L 6293). Scale bar equals 10 cm.
FIGURE 41. Left astragalus of *Montezumasaurus froesei* YPM 57589 (19-C 6293). The following features are distinguishable: **ap**, ascending process; **ahg**, anterior horizontal groove; **asf**, astragalar shallow fossa. Scale bar equals 10 cm.
FIGURE 42. Associated left pes of *Montezumasaurus froesei* YPM 57589.
FIGURE 43. Left metatarsal I of *Montezumasaurus froesei* YPM 57589 (18-P 6293).

Scale bar equals 5 cm.
FIGURE 44. Left metatarsal II of *Montezumasaurus froesei* YPM 57589 (18-M 6293) in anterior view. Scale bar equals 10 cm.
FIGURE 45. Proximal articulation of the left metatarsal II of *Montezumasaurus froesei* YPM 57589 (18-M 6293). Scale bar equals 10 cm.
FIGURE 46. Distal end of left metatarsal II of *Montezumasaurus froesei* YPM 57589 (18-M 6293) showing clp; collateral ligament pit; lc, lateral condyle. Scale bar equals 10 cm.
FIGURE 47. Distal articulation of metatarsal II of *Montezumassaurus froesei* YPM 57589 (18-M 6293) showing lc, lateral condyles. Scale bar equals 10 cm.
FIGURE 48. Left metatarsal II of *Montezumasaurus froesei* YPM 57589 (18-M 6293) showing a well-preserved *edls*, fossa for the insertion of M. extensor digitorum. Scale bar equals 10 cm.
FIGURE 49. Left metatarsal II of *Montezumasaurus froesei* YPM 57589 (18-M 6293) in posterior view showing small depression below the *gs*, fossa for the insertion for the M. gastrocnemius pars medialis. This depression represents the articular surface for metatarsal I (arrow). Scale bar equals 10 cm.
FIGURE 50. Left metatarsal III of *Montezumasaurus froesei* YPM 57589 (18-N 6293) in anterior view. Scale bar equals 10 cm.
FIGURE 51. Left metatarsal III of *Montezumaisaurus froesei* YPM 57589 (18-N 6293) in cross section. Note that the lateral sides of the shaft are flattened towards the posterior surface of the bone forming a V-like structure (arrows). Scale bar equals 5 cm.
FIGURE 52. Distal articulation of metatarsal III of *Montezumasaurus froesei* YPM 57589 (18-N 6293). Note a very shallow sulcus (arrow) that separates the lateral condyles, which articulate with phalanx I. Scale bar equals 5 cm.
FIGURE 53. Distal end of metatarsal III of *Montezumasaurus froesei* YPM 57589 (18-N 6293) in anterior view. Note the relatively deep edls, fossa for the insertion of the M. extensor digitorum longus (arrow). Scale bar equals 5 cm.
FIGURE 54. Left metatarsal III of *Montezumasaurus froesei* YPM 57589 (18-N 6293) in posterior view. Note a V-like fossa at the distal end (arrows) that separates the lateral condyles, a feature common in tetanuran theropods. Scale bar equals 10 cm.
FIGURE 55. Metatarsal IV of *Montezumasaurus froesei* YPM 57589 (18-O 6293) in anterior view. Note that the anterior of the distal articulation preserves a shallow *edls*, fossa for the insertion of the M. extensor digitorum longus. Scale bar equals 10 cm.
FIGURE 56. Shaft of left metatarsal IV of *Montezumasaurus froesei* YPM 57589 (18-O 6293) exhibiting D-shape. Scale bar equals 5 cm.
FIGURE 57. Metatarsal IV of Montezumasaurus froesei YPM 57589 (18-O 6293) in posterior view. Note two flat depressions are present on the bone. These depressions run down along the posteromedial and posterior faces and are the insertion for the gs, M. gastrocnemius pars lateralis. Scale bar equals 10 cm.
FIGURE 58. Metatarsal IV of *Montezumasaurus froesei* YPM 57589 (18-O 6293) distal articulation. Scale bar equals 5 cm.
FIGURE 59. Left metatarsal IV of *Montezumasaurus froesei* YPM 57589 (18-O 6293) in medial view showing a relatively deep clp, collateral ligament pit, which is deeper than lateral ligament pit. Scale bar equals 10 cm.
FIGURE 60. Phalanx 1 of digit II of *Montezumasaurus froesei* YPM 57589 (18-Q 6293) in dorsal view. A relatively deep **hp**, hyperextensor pit is well preserved at distal end. Scale bar equals 10 cm.
FIGURE 61. Phalanx 1 of digit II of *Montezumaurus froesei* YPM 57589 (18-Q 6293) showing distal articulation. Note a relatively deep fossa (arrow) that separates the lateral condyles. Scale bar equals 10 cm.
FIGURE 62. Phalanx 1 of digit II of Montezumasaurus froesei YPM 57589 (18-Q 6293) with relatively deep clp, collateral ligament pit in medial view. Scale bar equals 10 cm.
FIGURE 63. Phalanx 2 of digit II of *Montezumasaurus froesei* YPM 57589 (18-S 6293) in dorsal view showing a relatively shallow ***hp***, hyperextensor pit (arrow).

Scale bar equals 10 cm.
FIGURE 64. Phalanx 2 of digit II of *Montezumassaurus froesei* YPM 57589 (18-S 6293) with a relatively deep clp, collateral ligament pit in medial view. Scale bar equals 10 cm.
FIGURE 65. Phalanx 2 of digit II of *Montezumasaurus froesei* YPM 57589 (18-S 6293) in anterior view. Scale bar equals 5 cm.
FIGURE 66. Proximal of phalanx 1 of digit III of *Montezumasaurus froesei* YPM 57589 (18-J 6293) in dorsal view. Scale bar equals 10 cm.
FIGURE 67. Phalanx 1 of digit III of *Montezumasaurus froesei* YPM 57589 (18-J 6293) showing a D-shaped proximal articulation and a fossa for the contact with metatarsal III (arrow). Scale bar equals 10 cm.
FIGURE 68. Phalanx 2 of digit III of *Montezumasaurus froseei* YPM 57589 (18-R 6293) in dorsal view with a relatively deep and well-preserved *hp*, hyperextensor pit. Scale bar equals 10 cm.
FIGURE 69. Phalanx 2 of digit III of *Montezumasaurus froesei* YPM 57589 (18-R 6293) in posterior view. Note two shallow fossae for the articulation with phalanx 1 of digit III (arrows). Scale bar equals 10 cm.
FIGURE 70. Phalanx 2 of digit III of *Montezumasaurus froesei* YPM 57589 (18-R 6293) showing clp, collateral pit filled with sandstone matrix. Scale bar equals 10 cm.
FIGURE 71. Phalanx 3 of digit III of Montezumasaurus froesei YPM 57589 (18-P 6293) in dorsal view. Most of the dorsal surface of the phalanx is fragmented.

Scale bar equals 5 cm.
FIGURE 72. Phalanx 3 of digit III of *Montezumasaurus froesei* YPM 57589 (18-P 6293) in posterior view with a D-shaped proximal end, which has shallow fossae (arrows) for the articulation with phalanx 2 of digit III. Scale bar equals 5 cm.
FIGURE 73. Phalanx 3 of digit III of *Montezumasaurus froesei* YPM 57589 (18-P 6293) in ventral view. Scale bar equals 5 cm.
FIGURE 74. Phalanx 1 of digit IV of *Montezumasaurus froesei* YPM 57589 (18-S 6293) in dorsal view with relatively shallow hp, hyperextensor pit (arrow).

Scale bar equals 5 cm.
FIGURE 75. Phalanx 1 of digit IV of *Montezumasaurus froesei* YPM 57589 (18-S 6293) in ventral view. The ventral region (arrow) of the proximal articulation is concave. Scale bar equals 5 cm.
FIGURE 76. Phalanx 2 of digit IV of *Montezumasaurus froesei* YPM 57589 (18-W 6293) in dorsal view. Scale bar equals 5 cm.
FIGURE 77. Phalanx 3 of digit IV of *Montezumasaurus froesei* YPM 57589 (18-Y 6293) in dorsal view. Scale bar equals 5 cm.
FIGURE 78. Ungual phalanx of digit IV of *Montezumasaurus froesei* YPM 57589 (18-X 6293) in lateral view. Scale bar equals 5 cm.
FIGURE 80. Reduced consensus cladogram based on 264 characters.