

Chimerism of specimens referred to *Saurophaganax maximus* reveals a new species of *Allosaurus* (Dinosauria, Theropoda)

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Abstract: *Saurophaganax maximus* is the designation of material attributed to a massive theropod dinosaur recovered from the Kenton 1 Quarry in the Kenton Member of the Upper Jurassic Morrison Formation of Oklahoma. The theropod was originally given the name *Saurophagus maximus*, but was later revised to *Saurophaganax maximus* because the former did not conform to the International Commission on Zoological Nomenclature standards. Several autapomorphies were described for *S. maximus* including the postorbital lacking a postorbital boss, the atlas lacking facets for a proatlas, cervical vertebrae with nearly vertical postzygapophyses, unique accessory laminae on the holotype neural arch, pneumatized post-pectoral dorsal centra, craniocaudally expanded chevrons, laterally bowed femora, tibiae without an astragalar buttress and more prominent distomedial crest, and less distally divergent fourth metatarsals. However, our re-evaluation shows that some of the elements originally used to distinguish *Saurophaganax* from *Allosaurus* are more parsimoniously referred to diplodocid sauropods found in the same quarry rather than an allosaurid. Additionally, the holotype neural arch cannot be confidently assigned to a theropod, making *Saurophaganax maximus* a *nomen dubium*. The presence of at least one skeletally mature theropod was confirmed through paleohistology of a fourth metatarsal. Despite the similarity of the decisively theropod material to known species of *Allosaurus*, some elements feature subtle autapomorphies that suggest they pertain to a distinct species, which we describe as *Allosaurus anax* sp. nov.

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INTRODUCTION

Saurophaganax maximus is the taxonomic designation of material ascribed to a massive theropod dinosaur from the Late Jurassic epoch discovered in the Kenton Member of the Morrison Formation in western Oklahoma, U.S.A. (Chure 1995; Richmond et al. 2020). Its fossils were originally excavated by John Willis Stovall in 1931 and 1932 near the town of Kenton (Hunt and Lucas 1987). Stovall gave the fossils the name *Saurophagus maximus* in

a popular magazine article titled “Big for his day” (Ray 1941) but never described the species in detail (Hunt and Lucas 1987). However, Camp et al. (1953) indicated that *Saurophagus* was preoccupied by a tyrant flycatcher, now known as the great kiskadee, *Pitangus sulphuratus*, that was described by Swainson and Richardson (1831). Additionally, Ray (1941) did not conform to the standards of the International Commission on Zoological Nomenclature (ICZN) as it did not properly diagnose and describe a holotype, thus making *Saurophagus max-*

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imus a nomen nudum (Camp et al. 1953). Although Hunt and Lucas (1987) maintained that Ray (1941) followed ICZN protocol and that *Saurophagus maximus* should be considered valid, later studies agreed with Camp et al. (1953) and considered *Saurophagus a nomen nudum* (Chure 1995, 2000; Czaplewski et al. 1994). Chure (1995) gave *Saurophagus* a more formal description and provisionally distinguished the taxon from *Allosaurus fragilis*, renaming it *Saurophaganax maximus* following ICZN protocol. However, Smith (1998) considered *Saurophaganax* to be a species of *Allosaurus*, describing it as *Allosaurus maximus* with the same holotype specimen as Chure (1995). Recent publications have largely referred to the material as *Saurophaganax* rather than *Saurophagus* or *Allosaurus maximus* (Brusatte and Sereno 2008; Carrano et al. 2012). *Saurophaganax maximus* remains poorly known largely because referred elements are fragmentary and weathered, and were prepared and recovered by minimally trained Works Progress Administration (WPA) employees (Brusatte and Sereno 2008; Chure 1995, 2000). Additionally, little cranial material is known; only three heavily worn and restored teeth, two broken quadrates, and a postorbital have been referred to *Saurophaganax* (Chure 1995, 2000). As a result, the phylogenetic position of *S. maximus* has been contested since its initial description (Carrano et al. 2012). Some authors have considered *Saurophaganax* to be synonymous with *Allosaurus* (Hunt and Lucas 1987; Smith 1998; Smith et al. 1999). Consequently, *S. maximus* has been omitted from theropod phylogenies (Brusatte and Sereno 2008). In light of this taxonomic uncertainty and further knowledge of allosauroid diversity accumulated in recent years, a reevaluation of *Saurophaganax maximus* is timely and may resolve its taxonomic status and contribute to a better understanding of allosauroid anatomy, paleobiology, and diversity.

In total, 227 associated elements from four separate quarries have been referred to *Saurophaganax maximus* (Lauren Hall pers. comm. 2024; Hall and Weil 2023). These same quarries primarily yielded sauropod postcrania, with material attributed to *Apatosaurus*, *Brachiosaurus*, *Barosaurus*, *Diplodocus*, *Camarasaurus*, *Camptosaurus*, *Stegosaurus*, *Allosaurus*, and *Ceratosaurus* (Lauren Hall pers. comm. 2024; Hall and Weil 2023; Hunt and Lucas 1987). However, the *Saurophaganax* material considered for evaluating its taxonomic status, including its initial description, was limited to the Kenton 1 Quarry, ‘pit’ 1, also known as the Kenton V92 locality (Chure 1995, 2000; Hunt and Lucas 1987; Richmond et al. 2020). Three autapomorphic elements were originally used to distinguish *Saurophaganax maximus* from *Allosaurus fragilis*, including the holotype partial neural arch (OMNH 1123), a referred atlas (OMNH 1135), and referred fragmentary

chevrons (OMNH 1685, OMNH 1438, OMNH 1102) (Chure 1995). This list of diagnostic elements was further expanded to include a referred right postorbital (OMNH 1771), a cervical vertebra (OMNH 2146), dorsal centra (OMNH 1450, OMNH 1906), femora (OMNH 1708, OMNH 2114, OMNH 10381), tibiae (OMNH 1370, OMNH 2149), and fourth metatarsals (OMNH 1193, OMNH 1306, OMNH 1936) (Chure 2000).

The *Saurophaganax* elements from Kenton 1 Quarry were found associated, but not articulated, alongside those of other dinosaurs in a bonebed (Carrano et al. 2012; Chure 1995; Hunt and Lucas 1987). This means that assessing the taxonomic status of each of these elements is essential for determining whether they belonged to a single taxon. Additionally, a map for the Kenton 1 Quarry is notably lacking, so the relative positions of the different elements is unknown (Chure 1995, 2000; Hunt and Lucas 1987). In this paper, we primarily compare these purportedly autapomorphic *Saurophaganax* fossils to the homologous elements of other theropod dinosaurs as well as other large dinosaurs from the Morrison Formation. The results of this analysis indicate that some of the autapomorphic elements used to diagnose *Saurophaganax maximus* can be more parsimoniously attributed to a diplodocid sauropod found in the Kenton 1 Quarry rather than the giant theropod. Additionally, we do not find that the holotype neural arch can be confidently assigned to a theropod, making *Saurophaganax a nomen dubium*. Some previously reported autapomorphies described in decisively theropod material could not be validated. Nevertheless, some of the material from Quarry 1 previously assigned to *S. maximus* seems to represent an allosaurid diagnosably distinct from both *Allosaurus fragilis* and *Allosaurus jimmadseni*.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
 SAURISCHIA Seeley, 1887
 THEROPODA Marsh, 1881
 TETANURAE Gauthier, 1986
 CARNOSAURIA von Huene, 1920
 ALLOSAUROIDEA Marsh, 1878
 ALLOSAURIA Paul, 1988
 ALLOSAURIDAE Marsh, 1878
Allosaurus Marsh, 1877
Allosaurus anax sp. nov.

Etymology: The specific name *anax* is Greek for ‘king, lord, or chieftain’ and honors the updated name given to the Kenton Quarry 1 allosaurid by Chure (1995) when he renamed *Saurophagus* to *Saurophaganax*. Thus, *Allosaurus anax* means ‘different lizard king’.

Holotype: OMNH 1771, a large allosaurid postorbital recovered from the Kenton 1 Quarry that displays no cranial ornamentation, no rugose ridge or boss on the anterolateral margin of the postorbital, a significantly reduced or absent dorsolateral ridge and fossa on the posterior bar, and a knob of bone on the posterior margin of the ventral bar.

Referred Material: OMNH 2146 – cervical vertebra with nearly vertical postzygapophyses; OMNH 1450, OMNH 1906 – pneumatic post-pectoral dorsal centra; OMNH 1426, OMNH 1694, OMNH 1695 – fibulae with medial fossae.

Holotype Locality: OMNH 1771 was recovered from the Kenton 1 (V92) Quarry in western Oklahoma.

Holotype Horizon: OMNH 1771 was collected from the Kenton Member of the Upper Jurassic Morrison Formation (Richmond et al. 2020).

Referred Localities: Material referred to *Allosaurus anax* was recovered from the Kenton 1 Quarry.

Age: The Kenton Member correlates with the Brushy Basin Member of the Morrison Formation, which is 153–145 million years old based on single crystal $^{40}\text{Ar}/^{39}\text{Ar}$ radiometric dating (Kowallis et al. 1991; Richmond et al. 2020).

Diagnosis: A species of *Allosaurus* capable of attaining a much larger size than other species of *Allosaurus*, displaying no rugose cranial ornamentation on the lateral surface of the postorbital, an absent or significantly reduced dorso-lateral ridge of the postorbital, and an absent or extremely shallow lateral fossa on the posterior bar of the postorbital, hourglass-shaped dorsal centra with pneumatic foramina, and three shallow fossae on the medial surface of the proximal fibula. We tentatively consider a thickened bulge on the posterior border of the ventral bar of the postorbital and nearly vertical postzygapophyses on some cervical vertebrae to represent autapomorphies as well.

MATERIALS AND METHODS

Institutional Abbreviations

AMNH FARB, American Museum of Natural History Fossil Amphibians, Reptiles, and Birds Collection, New York, New York, USA; BYUVP, Brigham Young University Vertebrate Paleontology Collection, Provo, Utah, USA

DFN, Douglass field number; DINO, Dinosaur National Monument, Vernal, Utah, USA; FSAC, Faculté des Sciences of Casablanca University, Casablanca, Morocco; MMCh-PV, Museo Municipal “Ernesto Bachmann,” Neuquén, Argentina; MOR, Museum of the Rockies, Bozeman, Montana, USA; OMNH, Sam Noble Museum, Norman, Oklahoma, USA; UUV, University of Utah Paleontology Collection, Salt Lake City, Utah, USA

Comparative Material and Literature

We compared the fossils referred to *Saurophaganax maximus* to that of material referred to *Apatosaurus* sp. in the OMNH collection (Tab. 1). Particular focus was given to material collected from the Kenton 1 Quarry, designated as the V92 locality by OMNH collections (Richmond et al. 2020). Material that was too damaged to be of taxonomic value, such as the three teeth referred to *S. maximus*, were not considered for this analysis. We also consulted descriptions of *Saurophaganax maximus* (Chure 1995, Chure 2000), *Allosaurus fragilis* (Gilmore 1920; Madsen 1976; Smith et al. 1999), *Allosaurus jim-madseni* (Chure 2000; Chure and Loewen 2020; Loewen 2009; Snively et al. 2013), *Sinraptor dongi* (Currie and Zhao 1993), *Acrocantnosaurus atokensis* (Harris 1998), *Tyrannotitan chubutensis* (Canale et al. 2015; Novas et al. 2005), *Lusovenator santosi* (Malafaia et al. 2020), *Torvosaurus tanneri* (Britt 1991; Galton and Jensen 1979; Hanson and Makovicky 2013), *Torvosaurus gurneyi* (Hendrickx and Mateus 2014); *Ceratosaurus nasicornis* (Gilmore 1920); *Ceratosaurus magnicornis* (Madsen and Welles 2000), *Ceratosaurus dentisulcatus* (Madsen and Welles 2000), *Dilophosaurus wetherelli* (Marsh and Rowe 2020), *Apatosaurus louisae* (Gilmore 1936), *Diplodocus carnegii* (Hatcher 1901; Holland 1906), *Barosaurus lentus* (Hanik et al. 2017; McIntosh 2005; Melstrom et al. 2016), and *Camarasaurus* sp. (Madsen et al. 1995; Woodruff and Foster 2017). Each of these taxa is either a sauropod collected from the Morrison Formation or theropod dinosaur used to assess the position of *Saurophaganax*. Other large carnivores from the Morrison Formation, such as *Torvosaurus* and *Ceratosaurus*, were compared to the theropod material referred to *Saurophaganax* as well. No material referable to *Torvosaurus* has been recovered from the Kenton quarries (Lauren Hall pers. comm. 2024; Hall and Weil 2023, Hunt and Lucas 1987). Although a handful of fragmentary elements from these localities have been referred to *Ceratosaurus*, none were recovered from the Kenton 1 Quarry; in any event, this referral is dubious (Lauren Hall pers. comm. 2024; Hall and Weil 2023; Hunt and Lucas 1987).

Taxonomic Analyses

All of the material referred to *Saurophaganax maximus* was examined to assess its taxonomic status, with particular focus given to elements that distinguished it from *Allosaurus*. Photographs of specimens were collected either using a DSLR camera or an iPhone 15, and 3D photogrammetric models were created using Photocatch 1.7.1. When appropriate for comparisons between specimens, measurements were taken using digital calipers. The Kenton quarries primarily yielded sauropod postcrania (Hunt and Lucas 1987). Material assigned to

Table 1. Type and referred specimens of *Saurophaganax* and selected comparative elements of *Apatosaurus* assessed in this paper. All elements listed are from the Kenton 1 Quarry (V92) with the sole exception of OMNH 2010 from the Kenton 6 quarry (V95).

Taxon Referral	Specimen Number	Element
<i>Saurophaganax maximus</i>	OMNH 1771	Postorbital
<i>Saurophaganax maximus</i>	OMNH 2145	Quadrate
<i>Saurophaganax maximus</i>	OMNH 1142	Quadrate
<i>Saurophaganax maximus</i>	OMNH 1135	Atlas Vertebra
<i>Saurophaganax maximus</i>	OMNH 2010	Cervical Vertebra
<i>Saurophaganax maximus</i>	OMNH 2146	Cervical Vertebra
<i>Saurophaganax maximus</i>	OMNH 1123	Holotype Neural Arch
<i>Saurophaganax maximus</i>	OMNH 1188	Dorsal Centrum
<i>Saurophaganax maximus</i>	OMNH 1189	Dorsal Centrum
<i>Saurophaganax maximus</i>	OMNH 1450	Dorsal Centrum
<i>Saurophaganax maximus</i>	OMNH 1905	Dorsal Centrum
<i>Saurophaganax maximus</i>	OMNH 1906	Dorsal Centrum
<i>Saurophaganax maximus</i>	OMNH 1102	Chevron
<i>Saurophaganax maximus</i>	OMNH 1104	Chevron
<i>Saurophaganax maximus</i>	OMNH 1438	Chevron
<i>Saurophaganax maximus</i>	OMNH 1439	Chevron
<i>Saurophaganax maximus</i>	OMNH 1684	Chevron
<i>Saurophaganax maximus</i>	OMNH 1685	Chevron
<i>Saurophaganax maximus</i>	OMNH 1935	Humerus
<i>Saurophaganax maximus</i>	OMNH 1371	Femur
<i>Saurophaganax maximus</i>	OMNH 1708	Femur
<i>Saurophaganax maximus</i>	OMNH 2114	Femur
<i>Saurophaganax maximus</i>	OMNH 10381	Femur
<i>Saurophaganax maximus</i>	OMNH 1369	Proximal Half Tibia
<i>Saurophaganax maximus</i>	OMNH 1370	Tibia
<i>Saurophaganax maximus</i>	OMNH 1949	Prox. Tibia Fragment
<i>Saurophaganax maximus</i>	OMNH 2149	Dist. Tibia Fragment
<i>Saurophaganax maximus</i>	OMNH 1426	Fibula
<i>Saurophaganax maximus</i>	OMNH 1694	Fibula
<i>Saurophaganax maximus</i>	OMNH 1695	Fibula
<i>Saurophaganax maximus</i>	OMNH 1193	Metatarsal IV
<i>Saurophaganax maximus</i>	OMNH 1306	Metatarsal IV
<i>Saurophaganax maximus</i>	OMNH 1464	Metatarsal IV
<i>Saurophaganax maximus</i>	OMNH 1936	Metatarsal IV
<i>Apatosaurus</i> sp.	OMNH 1366	Dorsal Vertebra
<i>Apatosaurus</i> sp.	OMNH 1440	Dorsal Vertebra
<i>Apatosaurus</i> sp.	OMNH 1700	Chevron

Saurophaganax was compared to sauropod elements from Quarry 1 to determine whether any could be assigned to Sauropoda. Specimens that could be confidently referred to the Quarry 1 allosaurid were subsequently compared to both *Allosaurus fragilis* and *Allosaurus jimmadseni*. Any differences not plausibly explained by taphonomy, preparation, ontogeny and allometry, or individual

variation were considered autapomorphies of the Quarry 1 allosaurid. The ontogenetic stages of many specimens are unknown, so similarly sized elements of closely related taxa were assumed to represent similar ontogenetic stages. Size and relative development of external morphological features correlate better in *Allosaurus* than earlier diverging theropods (Griffin and Nesbitt 2016), which supports this assumption. Björk diagrams of superimposition were used to test previously reported autapomorphic differences (i.e., less laterally bowed fourth metatarsals) in the bones of *Saurophaganax* relative to those of *Allosaurus*. These diagrams use common congruent points as landmarks to ground specimen comparison (Carpenter 2010). Landmarks were selected according to the features that were preserved across all specimens. Body mass estimates were calculated using minimum circumference measurements of the three Quarry 1 theropod femora following Campione et al. (2014) using the MASSTIMATE package in R (Campione 2020), which facilitated widespread comparison to other theropod taxa.

Histological Analyses

A fourth metatarsal from the Kenton 1 quarry, referred to *Saurophaganax maximus* (OMNH 1464), was sectioned at mid-diaphysis using standard petrographic thin sectioning techniques (Lamm 2013) to assess its skeletal maturity. The specimen was embedded in polyester resin and mounted on a glass slide with cyanoacrylate. Wafers were ground and polished using a Buehler Ecomet4 variable speed grinding wheel and silicon carbide grit paper. Slides were then imaged using a Nikon Ni Eclipse petrographic microscope. The taxonomic referral of OMNH 1464 to a massive theropod was confirmed before sectioning (see Results section below). Distal limb elements often exhibit characteristics of skeletal maturity before more proximal elements (Lieberman et al. 2003). As such, a metatarsal may reach maturity before the entire skeleton. However, barring additional information, we assume that the apparent relative maturity of the metatarsal is representative of the whole skeleton (i.e., a skeletally mature metatarsal is indicative of a skeletally mature individual).

RESULTS: DESCRIPTION AND DIAGNOSTIC COMPARISONS

Postorbital

As in *Allosaurus* and many other theropods (Britt 1991; Chure and Loewen 2020; Madsen 1976; Madsen and Welles 2000), the right postorbital OMNH 1771 (Fig. 1) exhibits a distinct T-shape formed by an anterior bar, a posterior bar, and a ventral bar. The posterior bar of this speci-

men has a broken squamosal process, but it likely would have tapered to a point as seen in both species of *Allosaurus* (Chure and Loewen 2020; Madsen 1976). The lateral surface of the posterior bar is largely smooth except for a few well-defined toolmarks. No prominent dorsolateral ridge or lateral fossa is present (Chure and Loewen 2020). In medial view, a curved ridge runs from the inferior surface of the contact with the laterosphenoid to the squamosal process as in *Allosaurus fragilis* (Madsen 1976). The anterior bar is thick and features a smooth lateral surface with no rugose ornamentation. The ventral bar is straight but broken. Its anteromedial border bears a ridge that facilitated articulation with the jugal while the posterior margin of the bar is much thinner, with the exception of a thickened protrusion approximately $\frac{3}{4}$ down its length. This knob is roughly spherical and is visible on the posterior border of the ventral bar in lateral view. Both the surface of and area around

the bulge are both formed from finished bone, indicating that this feature is not a remnant of the concretionary layer that frequently covers specimens from the Kenton quarries. (Richmond et al. 2020). On the medial side of the anterior bar, the contact surface with the laterosphenoid is ovoid and bears clearly visible, matrix-infilled pneumatopores, as in *Allosaurus fragilis* (Madsen 1976). The posterior border is damaged, but largely complete; both the anterior and dorsal borders of the element are well-preserved.

OMNH 1771 has previously been distinguished from the postorbitals of *Allosaurus fragilis* and *Allosaurus jim-madseni* by having a smooth lateral surface without cranial ornamentation (Chure 2000; Chure and Loewen 2020). Additionally, the postorbitals of OMNH 1771 and *A. jim-madseni* both lack the postorbital boss present in *A. fragilis* (Chure 2000; Chure and Loewen 2020). OMNH 1771 is conspicuously distinct from the condition seen in

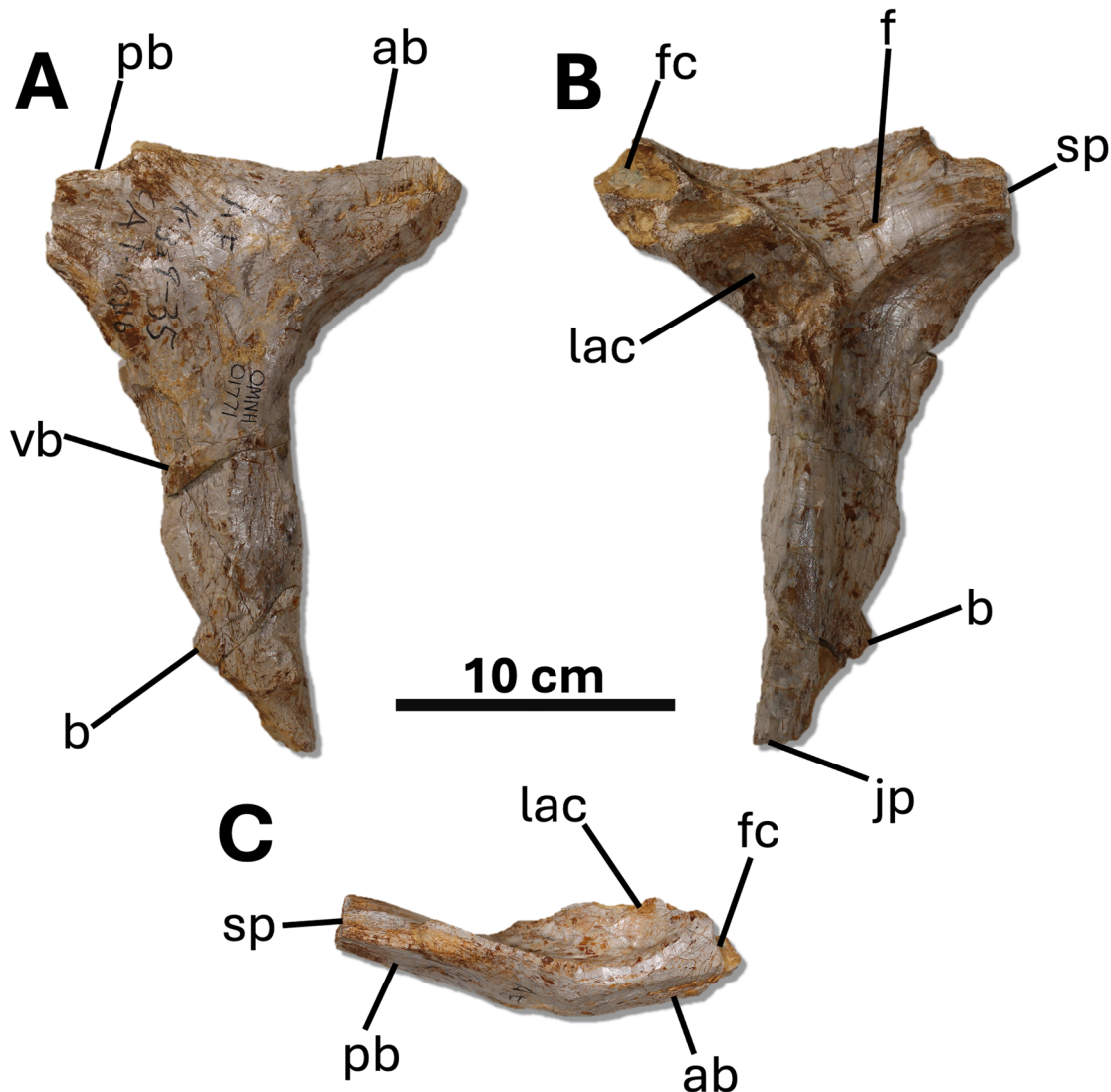


Figure 1. Right postorbital OMNH 1771 referred to *Saurophaganax maximus* in A, lateral; B, medial; and C, dorsal views. Abbreviations: ab, anterior bar; b, posteromedial bulge; f, foramen; fc, contact with frontal bone; jp, jugal process; lac, contact with laterosphenoid; pb, posterior bar; sp, squamosal process; vb, ventral bar.

diplodocids, such as *Diplodocus*, in which the postorbitals possess more strongly anteriorly curved ventral bars that contribute to the inferior border of the orbit and are much less distinctly T-shaped (Holland 1906). Additionally, the anterior bar in OMNH 1771 is significantly more prominent than that of *Diplodocus carnegii* in lateral view (Holland 1906). OMNH 1771 is identical to the postorbital of *Allosaurus fragilis* in medial view, with pneumatopores in the oval-shaped contact with the laterosphenoid, (Madsen 1976) distinguishing it from that of *Ceratosaurus magnicornis* (Madsen and Welles 2000). *Ceratosaurus magnicornis* appears to have more pronounced medial ridges than either OMNH 1771 or *Allosaurus fragilis* as well (Madsen 1976; Madsen and Welles 2000). The postorbital of *Torvosaurus tanneri* possesses a ventral bar that is thinner than that of either species of *Allosaurus* or OMNH 1771 (Britt 1991; Chure and Loewen 2020; Madsen 1976). *Torvosaurus* also lacks the ridge on the medial surface of the posterior bar that is present in both OMNH 1771 and *Allosaurus fragilis* (Britt 1991; Madsen 1976). As such, OMNH 1771 can be assigned most parsimoniously to a large allosaurid.

As described above, there are some signs of taphonomic wear and overpreparation on the lateral surface of OMNH 1771, but we do not think this damage could explain the lack of cranial ornamentation. The toolmarks are not extensive enough to account for the lack of the raised rugosity that is typically present in specimens of both *Allosaurus fragilis* and *Allosaurus jimmdaseni* (Carpenter 2010; Chure and Loewen 2020; Madsen 1976). Some parts of OMNH 1771, including the lateral surfaces of the posterior and ventral bars, appear worn but other regions such as the medial surface and most of the lateral surface of the anterior bar seem to represent finished bone. The shape of OMNH 1771 in dorsal view is very similar to those of *Allosaurus* apart from the lack of cranial ornamentation (Chure and Loewen 2020; Madsen 1976), suggesting that it has not been altered by wear. As with the toolmarks, the wear does not seem extensive enough to completely erase the aforementioned cranial ornamentation. Ontogeny and allometry are also unlikely explanations as similarly sized *Allosaurus* postorbitals feature prominent rugosities (Carpenter 2010). Bone resorption that reduces cranial ornamentation in senescent individuals is a primitive trait of Dinosauria, but the most mature individuals of *Tyrannosaurus rex* still display prominent cranial ornamentation (Carr 2020). The holotype of *Meraxes gigas* (MMCh-PV 65) possesses extensive cranial ornamentation (Canale et al. 2022), but was confirmed to be skeletally mature and one of the oldest known theropod individuals (Cullen et al. 2020). Thus, advanced age is unlikely to explain the lack of cranial ornamentation in OMNH 1771. Cranial ornamentation has been shown to be positively correlated with the evolution of large body size in theropods

(Gates et al. 2016), making it notable that such a large allosaurid would lack the raised cranial ornamentation present in smaller specimens of both *Allosaurus fragilis* and *Allosaurus jimmdaseni* (Chure and Loewen 2020; Madsen 1976). All known postorbitals of both *A. jimmdaseni* and *A. fragilis* seem to bear some form of raised ornamentation on their lateral surfaces, so the lack of such ornamentation on OMNH 1771 cannot be explained by individual variation (Carpenter 2010; Chure and Loewen 2020; Gilmore 1920; Madsen 1976). Furthermore, Carpenter (2010) did not report any changes in cranial ornamentation within a sample of nine postorbitals recovered from a population of *Allosaurus*. We conclude that the lack of raised cranial ornamentation on the postorbital is an autapomorphy of the Quarry 1 allosaurid, in agreement with Chure and Loewen (2020).

The absence of the dorsolateral ridge and presence of a shallower lateral fossa on the posterior bar could be explained through taphonomy or overpreparation. It is possible that the dorsolateral ridge was broken off and the lateral fossa was reduced through wear or a localized thickening of the concretionary layer. However, as stated above, overpreparation and taphonomic wear on the lateral surface of this specimen is slight. Additionally, the broken squamosal process of the posterior bar provides a cross section of this part of the specimen and the visible concretionary layer appears to be negligible. We do not think that these features could be either the result of damage to the original specimen or taphonomic. In *Tyrannosaurus rex*, most ontogenetic changes in the postorbital occur in juveniles (Carr 2020). Given the size of the postorbital and its consistency with that of large specimens of *Allosaurus*, we find it unlikely that this specimen represents a juvenile (Madsen 1976). It is also consistent in size with that of the *Allosaurus fragilis* specimen described by Madsen (1976) which has both a prominent dorsolateral ridge and deep lateral fossa. Accordingly, we do not think these changes could be explained by ontogeny or allometry. Lastly, individual specimens of *Allosaurus fragilis* seem to vary in the depths of their lateral fossae, but universally possess a dorsolateral ridge (Carpenter 2010; Chure and Loewen 2020; Madsen 1976), though the relative height of the dorsal ridge appears to vary across specimens (Carpenter 2010). As such, we conclude that the lack of the dorsolateral ridge and a shallower lateral fossa on the posterior bar of the postorbital are viable autapomorphies of the Quarry 1 allosaurid.

The conspicuous protrusion on the posterior margin of the ventral bar may represent a unique feature. Bone surface in this region has been damaged, suggesting that this protrusion may have been larger than as preserved. Exposed trabecular bone is rough and uneven, suggesting that this damage is the result of overpreparation rather than taphonomic wear. If anything, this protruding structure has been reduced from its original size. Similar

knobs of bone are not seen in other postorbitals referred to *Allosaurus*, including elements of a similar size (Carpenter 2010; Madsen 1976), which suggests that ontogeny, allometry, and individual variation are unlikely to explain this condition. Thus, we suggest that a thickened bulge on the posteromedial surface of the ventral bar is a possible autapomorphy of the Quarry 1 allosaurid.

In conclusion, a lateral surface without any form of raised or rugose cranial ornamentation, a shallower fossa on the lateral side of the posterior bar, and the lack of the dorsolateral ridge are autapomorphies of the Quarry 1 allosaurid that distinguish it from both *Allosaurus fragilis* and *Allosaurus jimmdaseni*, in agreement with the previous evaluations (Chure 2000; Chure and Loewen 2020). The presence of a thickened bulge or knob of bone on the posteromedial margin of the ventral bar is also provisionally considered autapomorphic as well.

Quadrates

Two partial quadrates, a left (OMNH 2145) and a right (OMNH 1142) (Fig. 2) from the Kenton 1 Quarry are re-

ferred to *Saurophaganax maximus* (Chure 2000). Only the inferior part of the quadrate is preserved in both specimens. Although both specimens are broken at the level of the quadrate foramen, the anterior curvature of the shaft, as described in *Allosaurus*, is recognizable (Madsen 1976). The condyles of the right quadrate OMNH 1142 are flatter and less defined than those of the left quadrate OMNH 2145. Their condylar widths (113.29 mm and 116.12 mm, respectively) suggest they may be from the same individual. A patina normally associated with hyaline cartilage (Holliday and Witmer 2008) suggested that the condyles possess original articular surfaces and are not significantly worn. In both elements, the lateral condyle is larger than the medial condyle and overlaps with approximately half the width of the medial condyle in the anterior view, as is typical of *Allosaurus* (Chure and Loewen 2020; Madsen 1976). Both elements display a small ridge of bone in the anterior view that runs from the medial side of the lateral condyle to the contact with the quadratojugal; this feature is also seen in *Allosaurus fragilis* (Madsen 1976).

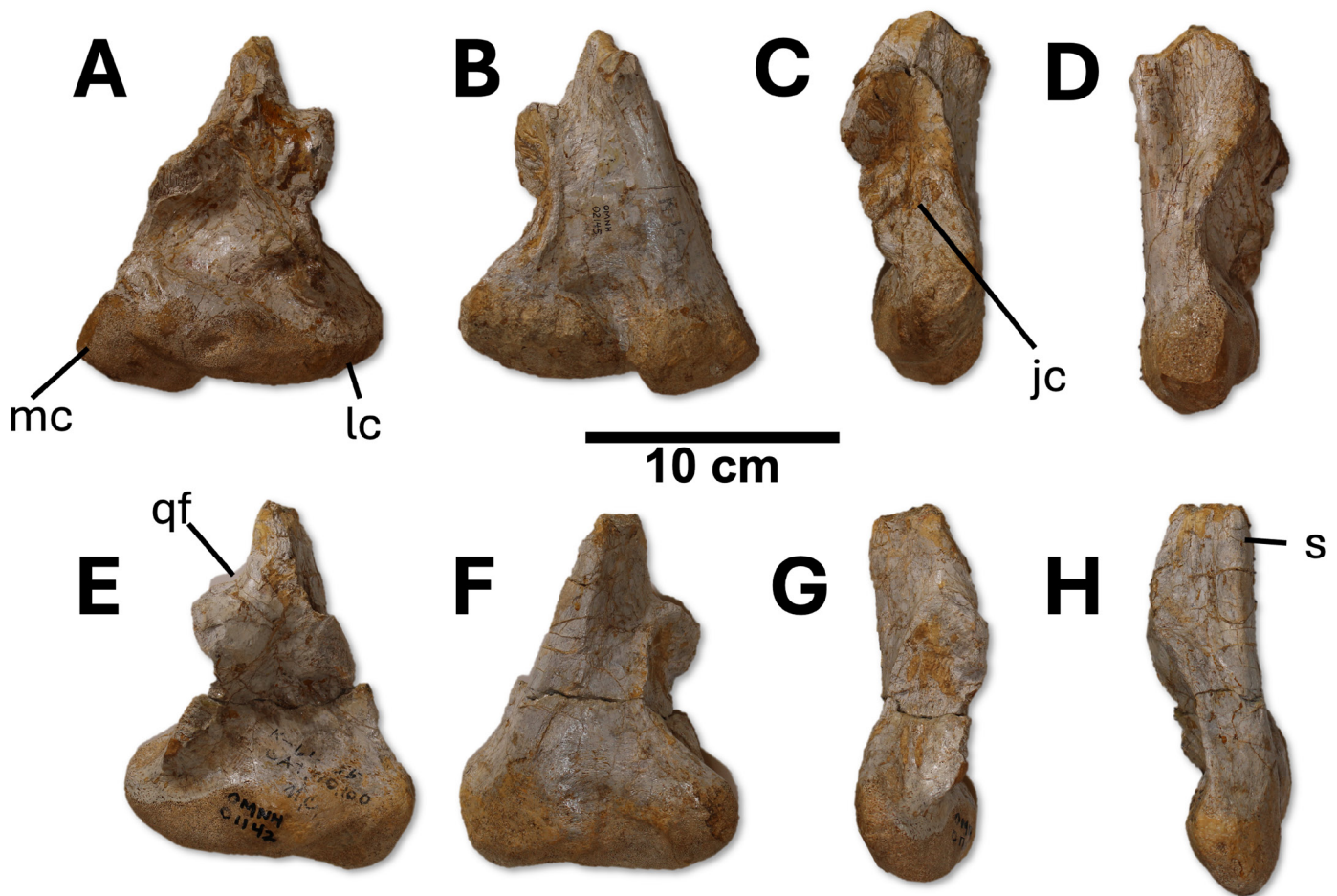


Figure 2. A–D, Left quadrate OMNH 2145; E–H, right quadrate OMNH 1142 referred to *Saurophaganax maximus* in anterior (A, E), posterior (B, F), lateral (C, G), and medial (D, H) views. Abbreviations: jc, contact with jugal; lc, lateral condyle; mc, medial condyle; qf, inferior margin of quadrate foramen; s, shaft of the quadrate.

OMNH 2145 and OMNH 1142 were previously described as indistinguishable from those of *Allosaurus* (Chure 2000). The inferior parts of the quadrates of diplodocids are distinct from those of OMNH 2145 and OMNH 1142 and *Allosaurus fragilis* in that they are anteroposteriorly longer (Holland 1906; Madsen 1976). The quadrates of diplodocids bend posteriorly while those of *Allosaurus*, OMNH 1142, and OMNH 2145 bend anteriorly (Holland 1906; Madsen 1976). The lateral condyles of the quadrates of *Torvosaurus tanneri* differ from OMNH 2145, OMNH 1142, and *Allosaurus fragilis* in that the lateral condyle is smaller than the medial condyle (Britt 1991; Madsen 1976). The quadrates of *Ceratosaurus magnicornis* differ from OMNH 1142, OMNH 2145, and *Allosaurus fragilis* in that they have smaller condyles and lack a quadrate foramen (Madsen and Welles 2000). In conclusion, both quadrates referred to *Saurophaganax* are indistinguishable from those of *Allosaurus* apart from their size, as previously reported (Chure 2000).

Atlas

The atlas OMNH 1135 (Fig. 3) referred to *Saurophaganax* is well preserved. The left neurapophysis is broken distally, the right neurapophysis is complete with a few glued breaks. The latter curves posteriorly and becomes progressively wider distally to articulate with the prezygapophysis of the axis. The anterior surfaces of both neurapophyses are smooth in the lateral view and lack conspicuous facets. In the anterior view, the atlantal intercentrum is slightly taller than it is wide. There is also a notch to accommodate the anteriorly projecting odontoid process of the axis. In lateral view, there is a clear anteroventral protrusion on the intercentrum that curves inferiorly. Two small pits are present on the posteroventral surface of the intercentrum. The atlas of *Saurophaganax* differs from that of *Allosaurus* in lacking facets for a proatlas, giving its neurapophyses a smooth anterior surface (Chure 1995, 2000). The presence of facets for the proatlas varies greatly across reptiles, including dinosaurs

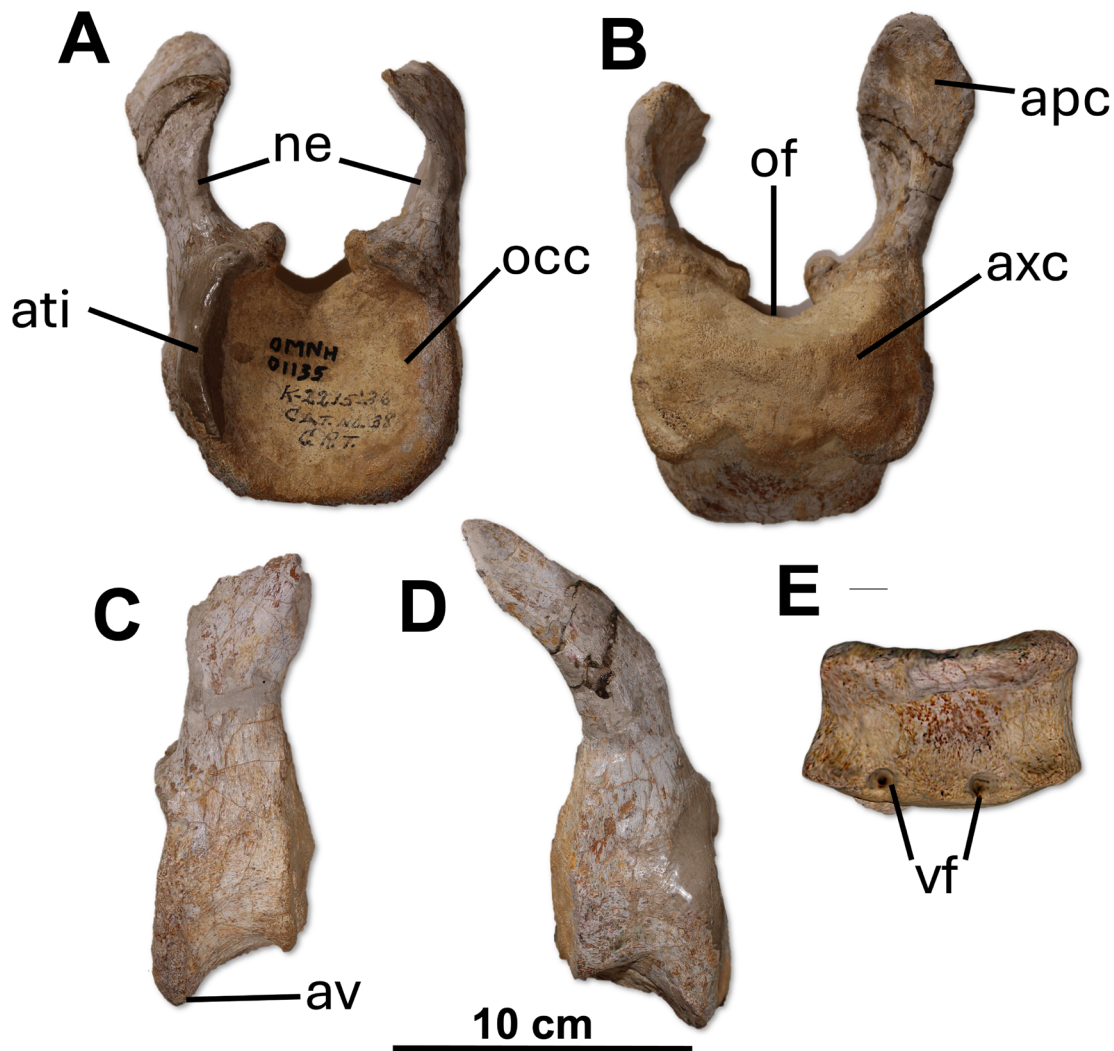


Figure 3. Atlas vertebra OMNH 1135 referred to *Saurophaganax maximus* in A, anterior; B, posterior; C, left lateral, D, right lateral; and E, ventral views (anterior toward the top). Abbreviations: apc, contact with axial prezygapophyses; ati, atlantal intercentrum; av, anteroventral protrusion; axc, contact with the axial intercentrum; ne, neurapophyses; occ, contact with occipital condyle; of, facet for the odontoid process of the axis; pvp, posterior ventrolateral process; vf, vascular foramina.

(Williston 1925). Atlas vertebrae are known in *Allosaurus fragilis*, *Sinraptor dongi*, and *Tyrannotitan chubutensis*, and each seem to possess facets for a proatlas represented by processes extending from the anterior surface of the neurapophyses (Canale et al. 2015; Madsen 1976; Novas et al. 2005; Zhao and Currie 1993). Facets for a proatlas also have been reported in *Dilophosaurus wetherelli*, *Ceratosaurus nasicornis*, and *Torvosaurus tanneri* (Britt 1991; Gilmore 1920; Marsh and Rowe 2020). Although *Diplodocus carnegii* possesses facets for a proatlas (Hatcher 1901; Holland 1906), they are absent from the atlas of *Apatosaurus louisae* (Gilmore 1936; Tschopp et al. 2015). Some specimens of *Camarasaurus* appear to approach this condition as well (Madsen et al. 1995). As such, the lack of facets for a proatlas in OMNH 1135 is more consistent with the condition seen in sauropods like *Apatosaurus* and *Camarasaurus*.

Chure (1995, 2000) also reported that OMNH 1195 differs from the atlas of *Allosaurus* in that its neurapophyses do not roof over the neural canal. *Allosaurus* atlases with neurapophyses preserved in articulation with the intercentrum indeed roof over the neural canal (Chure and Loewen 2020; Smith et al. 1999). This is also readily visible in the carcharodontosaurid *Tyrannotitan chubuten-*

sis (Canale et al. 2015). Conversely, the neurapophyses do not form a closed roof over the neural canal in the atlas of *Camarasaurus* (Madsen et al. 1995; Woodruff and Foster 2017), similar to OMNH 1135. This is the case in *Apatosaurus louisae* as well (Gilmore 1936).

The presence of a prominent anteroventral protrusion on the atlantal intercentrum of OMNH 1135 (Fig. 4) also suggests assignment to Sauropoda. A similar condition is present in numerous Jurassic sauropods, including *Camarasaurus* and *Apatosaurus* (Tschopp et al. 2015). In flagellicaudatans such as diplodocids and dicraeosaurids, this feature, termed an anteroventral lip (Tschopp et al. 2015; Tschopp and Mateus 2013, 2017), curves anteriorly, making the atlantal intercentrum anteriorly concave in lateral view. In other taxa like *Camarasaurus*, this structure does not curve anteriorly and the anterior border of the atlantal intercentrum is convex in lateral view (Tschopp et al. 2015; Woodruff and Foster 2017). The condition in OMNH 1135 is more similar to that of *Camarasaurus*, as the atlantal intercentrum is anteriorly convex in lateral view (Tschopp et al. 2015; Woodruff and Foster 2017). Similar structures are not present in known allosaurid atlases (Chure and Loewen 2020; Gilmore 1920; Madsen

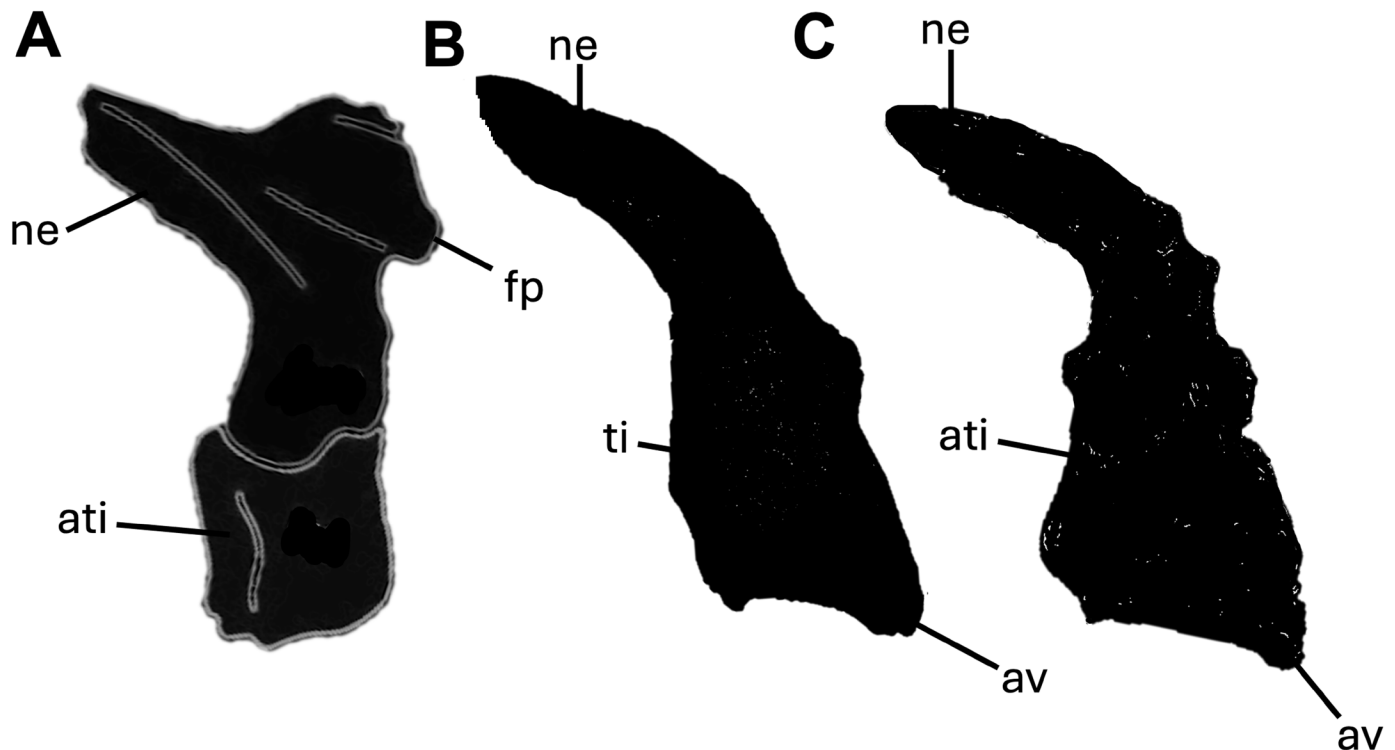


Figure 4. Comparison of the morphologies of select atlas vertebrae in right lateral view. A, cf. *Allosaurus jimmadnseni* MOR 693, modified from Chure and Loewen (2020: fig. 15); B, *Saurophaganax maximus* OMNH 1135; and C, *Camarasaurus* sp. UUVF 2983 (mirrored), adapted from Madsen et al. (1995: fig. 52). Abbreviations: ati, atlantal intercentrum; av, anteroventral protrusion; fp, facet for articulation with the proatlas; ne, neurapophysis. OMNH 1135 has been digitally modified so that the complete neurapophysis on the right side of the element was added to the mirrored left side of the atlantal intercentrum. Note that OMNH 1135 has a prominent anteroventral protrusion and lacks facets for a proatlas, similar to *Camarasaurus* but unlike *Allosaurus*. Elements are scaled to be of similar size.

1976), and appear to be absent in other theropods including *Tyrannotitan*, *Torvosaurus*, *Sinraptor*, *Ceratosaurus*, and *Dilophosaurus* (Britt 1991; Canale et al. 2015; Currie and Zhao 1993; Gilmore 1920; Madsen and Welles 2000; Marsh and Rowe 2020). Thus, this feature strongly supports the hypothesis that OMNH 1135 is a sauropod atlas, specifically suggesting a macronarian assignment.

OMNH 1135 was also previously noted to have two parasagittal pits on the ventral surface of its intercentrum (Fig. 3E) (Chure 2000). These small, widely separated holes on the ventral surface of OMNH 1135 are probably vascular foramina. Similar paired foramina have been documented in the Morrison diplodocoid *Smitanosaurus* (Whitlock and Wilson Mantilla 2020). A single foramen is present in a similar position in *Galeamopus* (Tschopp et al. 2015). To our knowledge, no similarly conspicuous ventral foramina have been reported on the atlas vertebrae of non-avian theropods (Brochu 2003; Canale et al. 2015; Currie and Zhao 1993; Gilmore 1920; Madsen 1976; Madsen and Welles 2000; Marsh and Rowe 2020). However, single or paired vascular foramina are variably present on the ventral surfaces of the vertebrae in lizards (Holder 1960), crocodylians (O'Connor 2006), and in birds the free (unfused) caudal vertebrae and pygostyle bear ventral grooves for the caudal aorta and caudal veins (Rashid et al. 2018). Thus, although it is not impossible that similar foramina could occur in the atlases of non-avian theropods as a result of the inherent variability of the vascular system, the documented presence of these foramina in sauropods renders the referral of OMNH 1135 to Sauropoda as most parsimonious.

OMNH 1135 does not feature the anterolateral processes seen in *Allosaurus*, *Tyrannotitan*, and *Sinraptor* (Juan Ignacio Canale pers. comm. 2024; Currie and Zhao 1993; Madsen 1976). As their name suggests, these processes project ventrolaterally from the anterior margin of the atlantal intercentrum. These processes may also be present in *Dilophosaurus*; ventrolateral ‘tubers’ were reported to project from its intercentrum (Marsh and Rowe 2020). *Ceratosaurus nasicornis* appears to have these structures on its atlantal intercentrum as well (Gilmore 1920). In contrast, sauropods such as *Apatosaurus*, *Camarasaurus*, and *Diplodocus* lack these processes (Holland 1906; Gilmore 1936; Madsen et al. 2015; Woodruff and Foster 2017). Sauropods often feature posterior ventrolateral processes on the posteroventral margin of their atlantal intercentra (Madsen et al. 2015; Tschopp et al. 2015; Woodruff and Foster 2017). OMNH 1135 displays posterior ventrolateral processes similar to those of *Camarasaurus* (Madsen et al. 1995; Woodruff and Foster 2017), further supporting a sauropod diagnosis. However, *Torvosaurus tanneri* may possess similar processes on the posteroventral margin of its atlas as well (Britt 1991).

In conclusion, the atlas OMNH 1135 that was referred to *Saurophaganax maximus* lacks facets for a proatlas and anterolateral processes, but has posterior ventrolateral processes, neurapophyses that do not roof over the neural canal, paired vascular foramina on its ventral surface, and an anteroventral protrusion. These features are more consistent with the condition in sauropods like *Camarasaurus* or *Apatosaurus* (Gilmore 1936; Madsen et al. 1995; Tschopp et al. 2015; Woodruff and Foster 2017), rather than *Allosaurus* or other closely related theropods (Canale et al. 2015; Currie and Zhao 1993; Madsen 1976), so we assign this element to Neosauropoda.

Post Atlas-axis Cervical Vertebra

OMNH 2146 is a cervical vertebra referred to *Saurophaganax maximus* (Chure 2000). Only the right side of the element is present: evidently it was cut in half during excavation (Fig. 5). The remnants of the neural arch and the centrum were evidently completely separated and have been glued together. The neural spine and diapophyses are missing from the neural arch, but an epipophysis and a postzygapophysis are both preserved. The epipophysis bears a smooth lamina on its dorsal surface. The centrum is noticeably opisthocoeleous with a patina on the anterior articular surface. Though cut in half, the centrum appears to have been heart-shaped in posterior view, as are many cervical centra of *Allosaurus fragilis* (Madsen 1976). The preserved parapophysis is prominent and has a single, crescent-shaped pneumatic foramen directly dorsal to it. A thin centropostzygapophyseal lamina is also partially prepared.

OMNH 2146 was reported to be distinct from the cervical vertebrae of *Allosaurus fragilis* in that it has nearly vertical postzygapophyses (Chure 2000). The relationship between the pneumatic foramen and the parapophysis, and the relative length and height of the centrum, are consistent with these conditions in *Allosaurus* (Madsen 1976; Snively et al. 2013). This suggests that at least the centrum belongs to the Quarry 1 allosaurid rather than to a diplodocid such as *Apatosaurus louisae* or *Diplodocus carnegii*, which tend to have proportionately longer centra and two pneumatic foramina that are not as closely associated with the parapophysis (Gilmore 1936; Holland 1906). In addition, the proportions of the epipophysis and postzygapophysis of OMNH 2146 are not consistent with those of the bifid cervicals of *Apatosaurus louisae* (Gilmore 1936). Although the cervical vertebrae of OMNH 2146 and *Allosaurus fragilis* (Gilmore 1920; Madsen 1976; Madsen and Welles 2000) are similar, those of *Ceratosaurus nasicornis* and *Ceratosaurus magnicornis* are distinct in having smaller epipophyses. Furthermore, unlike *Allosaurus* and OMNH 2146, the latter also appear to lack the pneumatic foramina associated with their parapophyses (Gilmore 1920; Madsen 1976; Madsen and Welles

2000). The cervical vertebrae of *Torvosaurus tanneri* are distinct from OMNH 2146 in that they have more prominent epiphyses (Britt 1991). Thus we conclude that this element is correctly referred to a large allosaurid.

As reconstructed, the postzygapophysis of OMNH 2146 is nearly vertical in orientation. The significance of this morphology is uncertain. The epiphyses and postzygapophyses of cervical vertebrae are frequently taphonomically deformed. In this case, while the epiphysis itself has not been conspicuously warped, it is possible that it was distorted and pushed dorsally, making it seem as though the postzygapophysis was more vertical than it was in life. However, there is no other evidence of taphonomic distortion in this element. The transverse cut between the fragmentary neural arch and centrum makes it possible that the angle of the epiphysis and postzygapophysis in OMNH 2146 is not representative of the original condition of the vertebra, but the break is subtle and the centrum and neural arch fit together well, suggesting that they pertain to a single vertebra, and that the orientation of the postzygapophysis has been reconstructed accurately. Another cervical vertebra, OMNH 2010, collected from the Kenton 6 Quarry is the only other element that preserves a complete epiphysis and postzygapophysis. This element does not display the nearly vertical postzygapophysis of OMNH 2146, but

instead more closely resembles the condition typically seen in *Allosaurus fragilis* (Madsen 1976). However, it is possible that serial variation could account for this change even within a single individual. As such, we cannot confidently invalidate the nearly vertical postzygapophyses of OMNH 2146 as the result of taphonomy, preparation, or individual variation, and we tentatively include this feature as an autapomorphy of the Quarry 1 allosaurid.

Dorsal Neural Arch

A dorsal neural arch OMNH 1123 (Fig. 6) is the holotype of *Saurophaganax maximus* (Chure 1995). It bears two prominent plates of bone which were previously described as accessory laminae (al) (Chure 1995, 2000). These structures emerge just dorsal to the prezygapophyses and extend beyond the diapophyses, but are broken posteriorly. These laminae appear to be laterally excavated, likely by pneumatic diverticula, creating a distinct fossa beneath each lamina (Chure 1995, 2000). The laminae become progressively wider and thicker posteriorly. OMNH 1123 is highly pneumatized with four diapophyseal laminae and six zygapophyseal laminae, a morphology typical of ancestral saurischian dorsal vertebrae (Wilson 1999), apart from the accessory laminae (al). The diapophyseal laminae include prezygodiapophyseal laminae

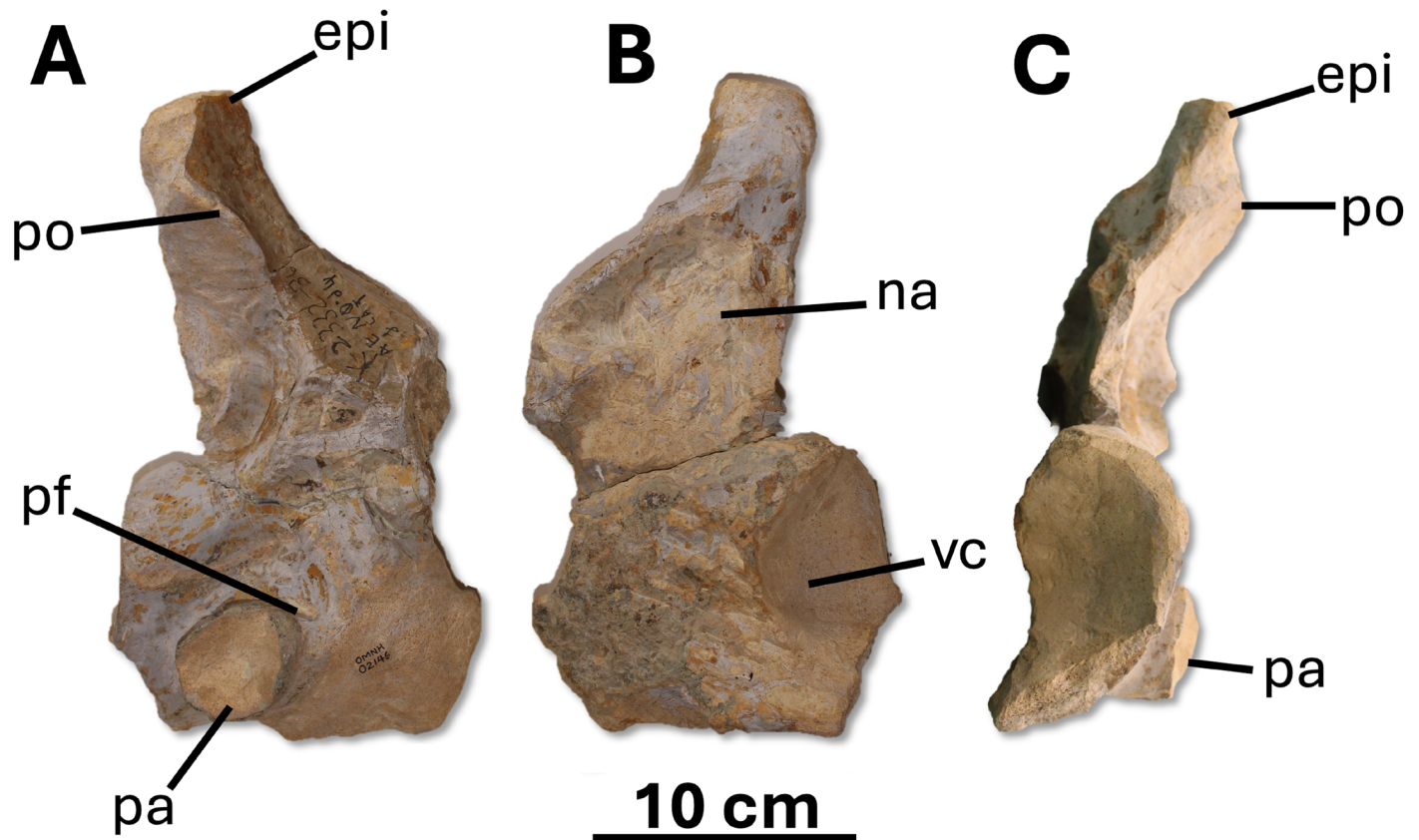


Figure 5. Cervical vertebra OMNH 2146 with nearly vertical postzygapophyses in A, lateral; B, medial; and C, posterior views. Abbreviations: epi, epiphysis; na, neural arch; pa, parapophysis; pf, pneumatic foramen; po, postzygapophysis; vc, vertebral centrum.

(prdl) extending from the lateral border of the prezygapophyses to the anterior border of the diapophyses, anterior centrodiaepophyseal laminae (acdl) and posterior centrodiaepophyseal laminae (pcdl) which both connect the centrum to the diapophysis, and postzygodiaepophyseal laminae (podl) which extend from the postzygapophyses. The prezygapophyseal laminae include the intraprezygapophyseal lamina (tprl) which connects the prezygapophyses, the centroprezygapophyseal laminae (cprl) which bilaterally extend from the centrum to the prezygapophyses, and possible spinoprezygapophyseal laminae (sprl) which appear worn and are only weakly present above the accessory laminae (al). The postzygapophyseal laminae include an intrapostzygapophyseal lamina (tpol) which connects the postzygapophyses, an undivided centropostzygapophyseal lamina (cpol), and paired spinopostzygapophyseal laminae (spol) which extend upwards from the postzygapophyses and create a deep elliptical fossa. The diapophyses, neural spine, and centrum are all broken. The hyposphene has been completely worn away and a

subtle hypantrum may be present. Partial parapophyses are present where the neural arch would have attached to the vertebral centrum, denoting this element as part of a dorsal vertebra.

Assignment of the holotype neural arch to either theropod or sauropod is difficult. While accessory lamination is more typical of sauropods than theropods (Wilson 1999), the element displays several features consistent with a theropod referral that would distinguish it from adult diplodocids, such as upturned diapophyses (Gilmore 1936; Madsen 1976). However, the diapophyses of juvenile diplodocid vertebrae are frequently upturned (Carpenter 2013; Hanik et al. 2017; Woodruff 2015), which suggests that this feature varies ontogenetically and is not reliably diagnostic. Some diplodocid dorsal vertebrae have bifid spinous processes (Gilmore 1936; Holland 1906; McIntosh 2005), but this is serially variable (Wedel and Taylor 2013), and also seems to vary ontogenetically (Woodruff 2015). The prezygapophyses of OMNH 1123 seem narrower than those of adult diplodocids like *Apatosaurus* and *Barosaurus* (Gilmore

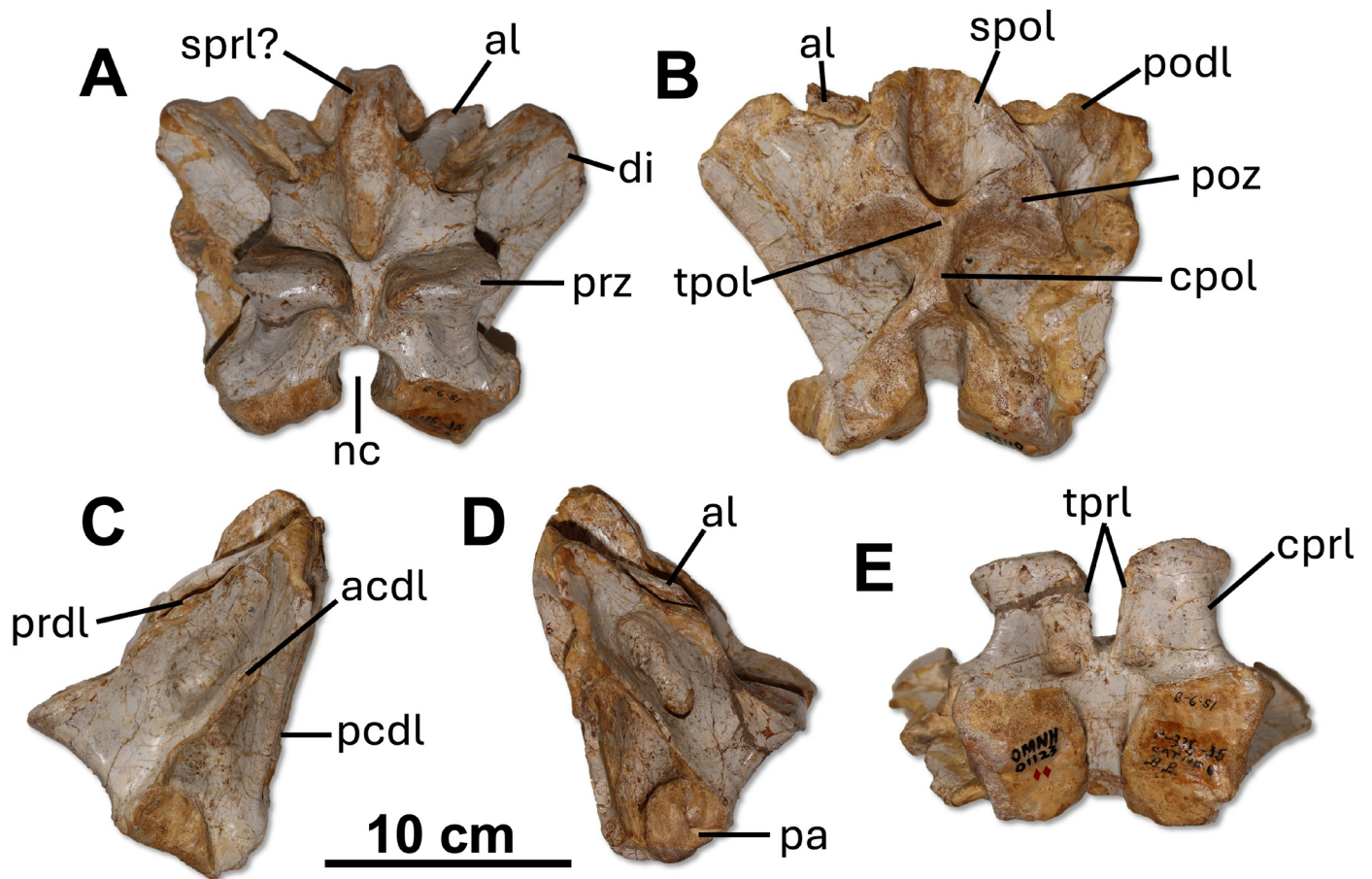


Figure 6. The holotype dorsal neural arch of *Saurophaganax maximus* OMNH 1123 in A, anterior; B, posterior; C, left lateral; D, right lateral; and E, ventral views. Abbreviations: acdl, anterior centrodiaepophyseal lamina; al, accessory lamina; cpol, centropostzygapophyseal lamina; cprl, centroprezygapophyseal lamina; di, diapophysis; nc, neural canal; pa, parapophysis; pcdl, posterior centrodiaepophyseal lamina; poz, postzygapophysis; prz, prezygapophysis; spol, spinopostzygapophyseal lamina; sprl?, possible spinoprezygapophyseal lamina; tpol, intrapostzygapophyseal lamina; tprl, intraprezygapophyseal lamina.

1936; McIntosh 2005), but the zygapophyses appear to vary across ontogeny as well (Hanik et al. 2017; McIntosh 2005; Melstrom et al. 2016). Apart from the accessory laminae (al), OMNH 1123 appears to display the ancestral pattern of saurischian lamination (Wilson 1999), lacking laminae such as the prespinal (prsl), postspinal (posl) and spinodiapophyseal laminae (spdl). However, these structures have also been reported to be ontogenetic (Carballido et al. 2012) and do not seem to be present on every dorsal vertebra within an individual (Gilmore 1936; Melstrom et al. 2016). The fragmentary nature of the holotype neural arch makes it difficult to confidently assess its characteristics, but the accessory laminae (al) of the holotype may themselves provide insight into its assignment.

To our knowledge, no other vertebra referred to *Saurophaganax maximus* from across the Kenton quarries displays similar accessory laminae (al), including cervical, dorsal, sacral, and caudal vertebrae. Accessory laminae (al) are not known in *Allosaurus* (Madsen 1976), but are known in the closely related carcharodontosaurids (Canale et al. 2015; Harris 1998; Malafaia et al. 2020). Some carcharodontosaurids such as *Acrocanthosaurus atokensis* and *Tyrannotitan chubutensis* display accessory laminae that connect the anterior centrodiapophyseal laminae (acd1) to the posterior centrodiapophyseal laminae (pcdl) (Canale et al. 2015; Harris 1998). However, to be of taxonomic value, laminae must be compared based on the landmarks they connect (Wilson 1999), and neither of these landmarks are shared by the accessory laminae (al) of OMNH 1123. *Lusovenator santosi* features laminae extending from the prezygapophyses to the postzygapophyses in its mid-caudal vertebrae (Malafaia et al. 2020). While the accessory laminae (al) of *Lusovenator* and *Saurophaganax* share a landmark, those of *Saurophaganax* extend beyond the diapophyses and do not approach the postzygapophyses. However, it is unknown whether similar laminae were present in the dorsal vertebrae of *L. santosi*. Thus, to our knowledge, no comparable laminae are known in theropods that could aid in the assignment of the holotype neural arch.

It is possible that OMNH 1123 belonged to a theropod with autapomorphic accessory laminae (al) as previously reported (Chure 1995, 2000). However, the Kenton 1 Quarry primarily yielded sauropod postcrania (Hunt and Lucas 1987), which commonly exhibit accessory lamination (Wilson 1999), so the possibility that OMNH 1123 may belong to a sauropod should be considered. Accessory lamination of the neural arch in dorsal vertebrae is a synapomorphy of Neosauropoda (Wilson 1999). However, the laminae of OMNH 1123 are highly complex and more prominent than the accessory laminae seen in other taxa (Canale et al. 2015; Gilmore 1936; Hanik et al. 2017; Harris 1998; Malafaia et al. 2020), and seem to be

free posteriorly (Chure 1995, 2000), so ‘accessory laminae’ may not be the best term to describe these structures. We examined the Kenton 1 Quarry sauropod material for comparison to OMNH 1123. Multiple elements referred to *Apatosaurus* sp. feature laminae with a similar orientation to OMNH 1123. One of these elements is OMNH 1366 (Fig. 7), a massive sauropod dorsal vertebra. However, the laminae on this element are raised spinoprezygapophyseal laminae (sprl) which become noticeable just above the prezygapophyses and are broken before reaching their other landmark, similar to OMNH 1123 (Fig. 8). While the laminae of OMNH 1366 are not as proportionately prominent as those of OMNH 1123, laminae are defined by the landmarks they connect (Wilson 1999) and develop throughout ontogeny (Carballido et al. 2012). A juvenile specimen of *Apatosaurus*, DFN 24, appears to display structures that are similar to the accessory laminae of OMNH 1123 (Carpenter 2013), possibly representing the spinoprezygapophyseal laminae (sprl) or spinous processes before they become strongly bifid in the adult (Gilmore 1936). As such, the structures previously described as accessory laminae (al) in the holotype of *Saurophaganax maximus* may be comparable to the spinoprezygapophyseal laminae (sprl) seen in sauropod vertebrae from the same site and may represent these structures at an early ontogenetic stage.

Chure (1995, 2000) noted that the laminae of OMNH 1123 appear to have had diverticula laterally penetrating into the accessory laminae (al). While the laminae of OMNH 1366 are too worn for comparison, those of OMNH 1440 (Fig. 9), another dorsal vertebra referred to *Apatosaurus* sp. preserve notable fossae laterally penetrating its spinoprezygapophyseal laminae (sprl) that resembles the condition of OMNH 1123. This appears to be the case in *Apatosaurus louisae* as well (Gilmore 1936). In both OMNH 1123 and OMNH 1440, these lateral fossae are best developed near the prezygapophyses and progressively narrow away from them. To our knowledge, similar excavation of the neural arch does not occur in theropods. Therefore, not only do the laminae that define *Saurophaganax maximus* resemble those of diplodocid elements from the same quarry, but both seem to have similar lateral fossae.

The lamination of the *Apatosaurus* sp. dorsal vertebra OMNH 1366 is largely consistent with that of OMNH 1123, displaying the same relationship between the anterior centrodiapophyseal lamina (acd1), the parapophysis, and the posterior centrodiapophyseal lamina (pcdl) that is typically seen in theropod dorsal vertebrae (Madsen 1976; Wilson 1999). This relationship between these landmarks has previously been described in diplodocids: the 4th and 5th dorsal vertebrae of *Barosaurus lentus* display this condition (McIntosh 2005), as do the 1st, 2nd, and 3rd dorsal vertebrae of *Apatosaurus louisae* (Gilmore 1936).

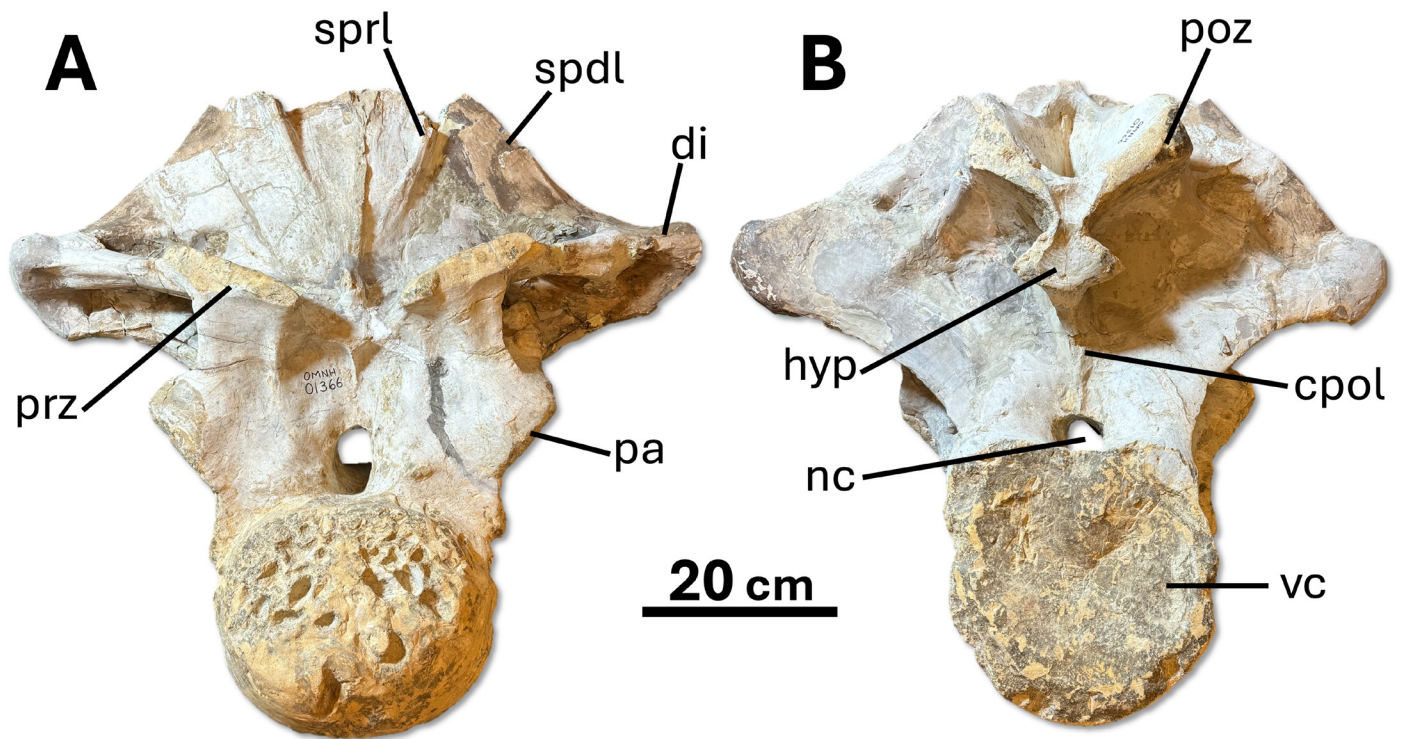


Figure 7. Dorsal vertebra OMNH 1366 referred to *Apatosaurus* sp. in A, anterior; and B, posterior views. Abbreviations: cpol, centropostzygapophyseal lamina; di, diapophysis; hyp, hyposphene; nc, neural canal; pa, parapophysis; prz, prezygapophysis; poz, postzygapophysis; spdl, spinodiapophyseal lamina; sprl, spinoprezygapophyseal lamina; vc, vertebral centrum. The prezygapophyses, while present, are completely worn down.

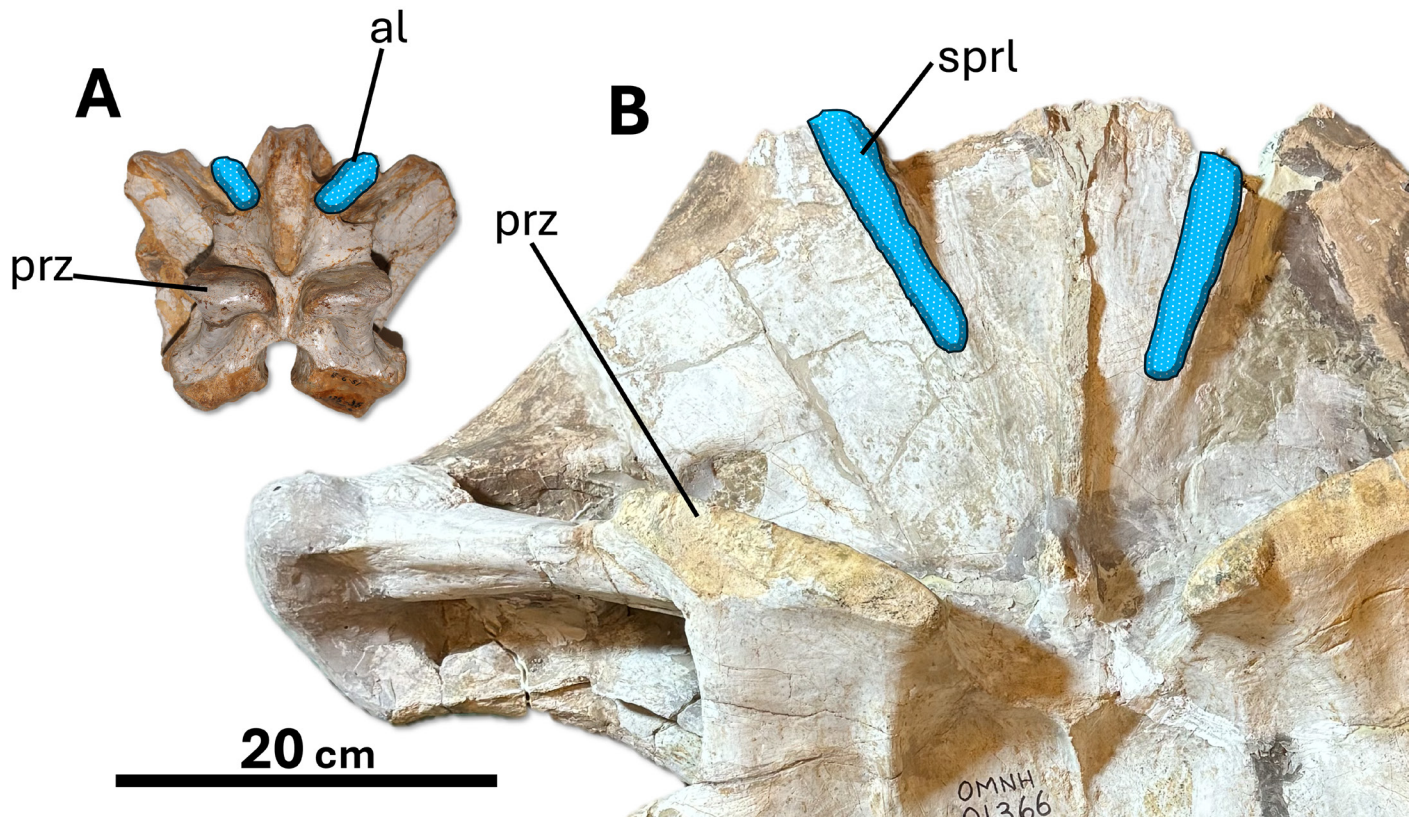


Figure 8. Comparison of the accessory laminae in OMNH 1123 (A) and the spinoprezygapophyseal laminae of OMNH 1366 (B) in anterior views. Abbreviations: al, accessory lamina; prz, prezygapophysis; sprl, spinoprezygapophyseal laminae.

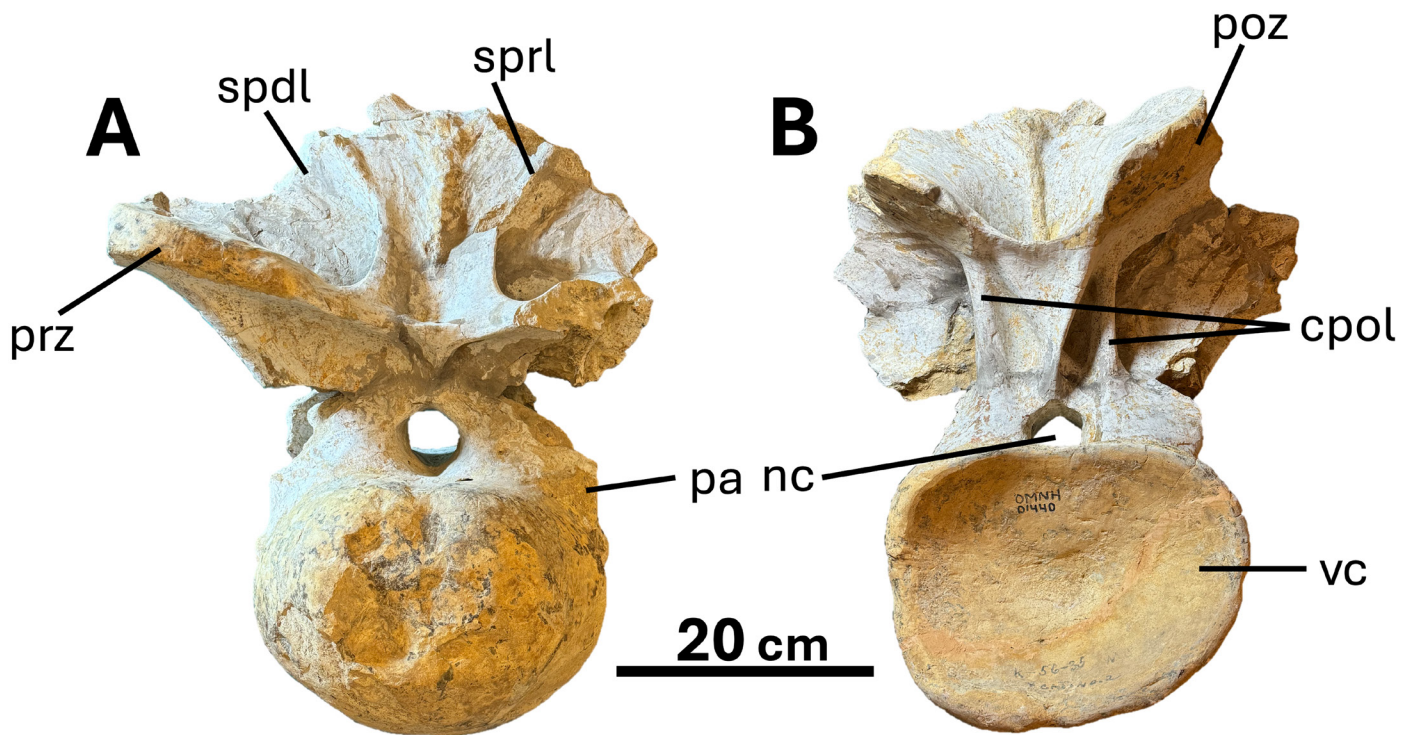


Figure 9. Dorsal vertebra OMNH 1440 referred to *Apatosaurus* sp. in A, anterior; and B, posterior views. Abbreviations: al, accessory laminae; cpol, centropostzygapophyseal lamina; nc, neural canal; pa, parapophysis; prz, prezygapophysis; poz, postzygapophysis; spdl, spinodiapophyseal lamina; vc, vertebral centrum. The diapophyses are broken on this element.

This relationship is present in *Allosaurus* as well (Gilmore 1920; Madsen 1976).

A diagnostic trait of Flagellicaudata is the presence of divided centropostzygapophyseal laminae (cpol) (Hanik et al. 2017). These are present in many of the large vertebrae referred to *Apatosaurus* sp. collected from the Kenton 1 Quarry, including OMNH 1440. This condition differs from that of theropods such as *Allosaurus* and OMNH 1123, which have a single centropostzygapophyseal lamina (cpol). However, OMNH 1366 similarly features a single centropostzygapophyseal lamina (cpol) and this varies serially in *Apatosaurus louisae* (Gilmore 1936). Additionally, a juvenile specimen of *Apatosaurus* appears to have a single centropostzygapophyseal lamina (cpol) (Carpenter 2013), while its serial homolog in the holotype of *Apatosaurus louisae* does not (Gilmore 1936). The wear on OMNH 1123 makes it impossible to evaluate the characteristics of the hyposphene or even if it was present, however, OMNH 1440 seems to lack a hyposphene and a hypantrum, while both are present on OMNH 1366. OMNH 1123 may have a slight hypantrum which is similar to the condition in *Allosaurus* (Madsen 1976). However, the condition of the hyposphene was not reported in the juvenile *Barosaurus* described by Melstrom et al. (2016) and the only hyposphene visible in the specimen described by Hanik et al. (2017) has a thin hyposphene similar to that of *Allosaurus* (Madsen 1976). The juvenile *Apatosaurus* described by

Carpenter (2013) also seems to have a similar hyposphene, but this specimen is worn so this may not be the case. Accordingly, characteristics such as the shape of the hyposphene and centropostzygapophyseal lamina (cpol) cannot be used to assess the taxonomic status of OMNH 1123.

The presence of similar laminae and lateral fossae present in OMNH 1123 and large diplodocid specimens recovered from the same quarry suggest that OMNH 1123 may have belonged to a sauropod. While relatively well-preserved, the fragmentary condition of this element and the lack of confident serial position makes assignment to either a sauropod or theropod difficult. These laminae (al) are present in nearly all other dorsal vertebrae referred to *Apatosaurus* sp. from the Kenton 1 Quarry, but none of the other vertebrae referred to *Saurophaganax*. Otherwise, the lamination of OMNH 1123 is comparable to the diplodocid dorsal vertebra OMNH 1366, especially if sauropod ontogenetic trends and serial variation are considered. We can be more confident in referral of this element with more complete comparative material. If the holotype of *Saurophaganax maximus* cannot be confidently assigned to either Sauropoda or Theropoda, then neither sauropod nor theropod material can be confidently assigned to this taxon, making it a *nomen dubium*.

Pneumatic Dorsal Centra

OMNH 1450 and OMNH 1906 (Fig. 10) are two isolated vertebral centra that have deep pneumatic fo-

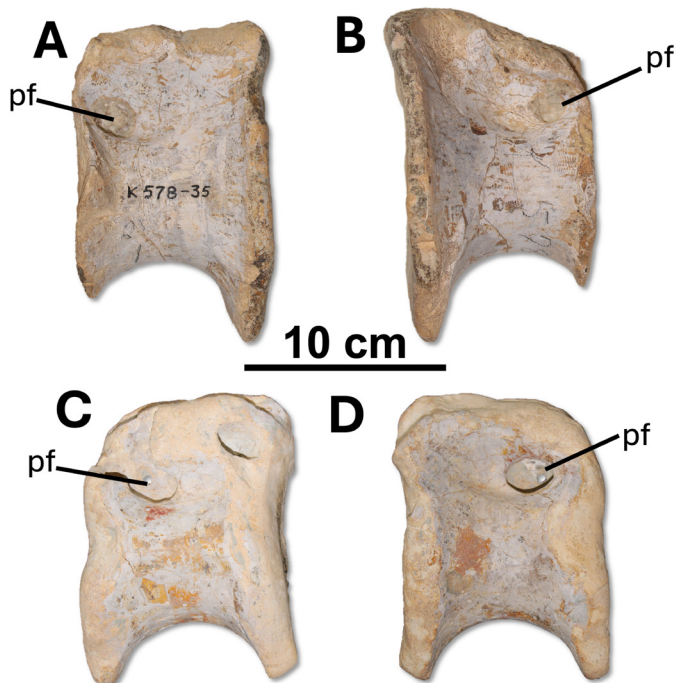


Figure 10. Dorsal centra with pneumatic foramina. A, B, OMNH 1906; C, D, OMNH 1450. Elements in left (A, C) and right (B, D) lateral views. Abbreviations: pf, pneumatic foramen.

ramina (Chure 2000). Both elements were interpreted to be anterior, post-pectoral dorsals (Chure 2000). They were considered to be too small to be from the same individuals that the massive theropod bones belong to, but were nevertheless referred to *Saurophaganax maximus* (Chure 2000). Both OMNH 1450 and OMNH 1906 are hourglass shaped and lack distinct ventral keels. Neither centrum has intact parapophyses. The articular surfaces of both centra are worn, but appear to have been relatively flat. OMNH 1450 has a complete pneumatic foramen preserved. Part of the neural canal is preserved dorsally. OMNH 1906 also displays a pneumatic foramen that is infilled with sediment.

The hourglass-shaped pectoral centra of *Allosaurus fragilis* and *Allosaurus jimmadseni* have not been reported to possess pneumatic foramina (Chure 2000; Gilmore 1920; Madsen 1976); dorsal centra with pneumatic foramina would be autapomorphic within *Allosaurus*. The presence of pneumatic foramina on hourglass-shaped centra distinguish OMNH 1450 and OMNH 1906 from *Ceratosaurus magnicornis* as well (Madsen and Welles 2020). The hourglass-shaped dorsal centra of *Torvosaurus tanneri* possess pneumatic foramina similar to those OMNH 1450 and OMNH 1906, though they are larger in *T. tanneri* (Britt 1991). *Apatosaurus louisae* has similarly shaped post-pectoral dorsal centra that have pneumatic foramina (Gilmore 1936). Additionally, ontogeny may play a role in the shapes of the centra: those in juvenile *Barosaurus* display similar pneumaticity (Hanik et al. 2017). Many juvenile sauropods are known from the Kenton 1 Quarry

from multiple individuals in a range of centrum heights that includes OMNH 1450 and OMNH 1906, so attributing these centra to a juvenile sauropod could be reasonable. However, OMNH 1450 and OMNH 1906 both appear to be more strongly hourglass-shaped in lateral view than those of juvenile *Barosaurus* (Hanik et al. 2017), which suggests that they may belong to a theropod; hourglass-shaped dorsal centra are a theropod synapomorphy (Carrano et al. 2012). The shape of the dorsal centrum seems to be entirely consistent with those of *Allosaurus fragilis* apart from the pneumatic foramen (Madsen 1976).

Hunt and Lucas (1987) indicated that *Saurophaganax maximus* is the only large theropod confidently known from the Kenton quarries. More extensive pneumaticity is also known in the closely related carcharodontosaurids (Canale et al. 2014; Harris 1998). There are larger dorsal centra in the collection, such as OMNH 1188 and OMNH 1189, that lack pneumatic foramina; additionally, OMNH 1905 lacks pneumatic foramina but is nearly identical in size to OMNH 1450 and OMNH 1906 (Fig. 11). These elements can be more confidently assigned to the Quarry 1 allosaurid because pneumatic foramina tend to develop only a few years after hatching and no dorsal vertebrae of *Apatosaurus louisae* lack pneumatic foramina (Gilmore 1936; Hanik et al. 2017). This suggests that either not all of the hourglass-shaped dorsal vertebrae of the Quarry 1 allosaurid had pneumatic foramina or that OMNH 1450 and OMNH 1906 belonged to another taxon. All of the postatlantal vertebrae of *Acrocanthosaurus atokensis* possess pneumatic foramina (Harris 1998). *Concavenator corcovatus* has pneumatic foramina in all of its cervicals but lacks them in all of its dorsals (Ortega et al. 2010). *Sinraptor dongi* has pneumatic foramina limited to its second, third, and fourth dorsal vertebrae, each of which is hourglass shaped (Currie and Zhao 1993). This pneumaticity does not seem to be strictly linked to centrum shape within Allosauroidea, making it a reasonable inference that the Quarry 1 allosaurid has an autapomorphic combination of an hourglass shaped centrum with a pneumatic foramen. Additionally, different specimens of *Allosaurus fragilis* and *Allosaurus jimmadseni* differ in the distribution of pneumatic foramina in their dorsal vertebrae (Chure 2000; Gilmore 1920; Madsen 1976). Pneumatic foramina are recorded to the 4th dorsal vertebra in *Allosaurus fragilis* while the 5th dorsal vertebra is the first to possess an amphiplatyan, hourglass-shaped centrum (Madsen 1976). However, two additional specimens referred to *Allosaurus fragilis*, USNM 8367 and USNM 4734, only bear pneumatic foramina up to the 3rd dorsal centrum (Gilmore 1920). Pneumatic foramina are only reported to the second dorsal in the holotype of *Allosaurus*

jimmadseni DINO 11541 (Chure 2000). While the extent of pneumatic foramina appears to vary across specimens of *Allosaurus*, to our knowledge, none display the previously proposed autapomorphic condition of hourglass-shaped centra with pneumatic foramina.

To further explore the taxonomic status of these centra, the midsection widths of these elements were compared (Fig. 11). OMNH 1450 and OMNH 1906 measured 59.0 mm and 62.4 mm wide at their midsection, respectively. The largest hourglass-shaped centra that lacked pneumatic foramina OMNH 1888 and OMNH 1889 measured 91.9 mm and 112.9 mm wide at their midsections, respectively. Thus, we agree with Chure (2000) that the pneumatic centra are too small to belong to the largest theropod found in the Kenton 1 Quarry. OMNH 1905 lacks a pneumatic

foramen and has a minimum width of 65.9 mm, which is nearly identical to the width of OMNH 1906, which has pneumatic foramina. No map for the Kenton 1 Quarry exists (Hunt and Lucas 1987), but the adjacent specimen numbers and similar widths suggest that OMNH 1905 and OMNH 1906 could belong to the same individual. This, in turn, suggests that this taxon had a mix of dorsal centra with and without pneumatic foramina, which is more typical of the theropods discussed above. Additionally, OMNH 1450 is of a similar size to OMNH 1905 and OMNH 1906 as well, which could suggest that all three centra belonged to the same individual. If this is true, and a condition similar to *Allosaurus fragilis* is assumed, pneumatic foramina in the Quarry 1 allosaurid would extend to at least the 6th dorsal vertebra, as opposed to the 4th as

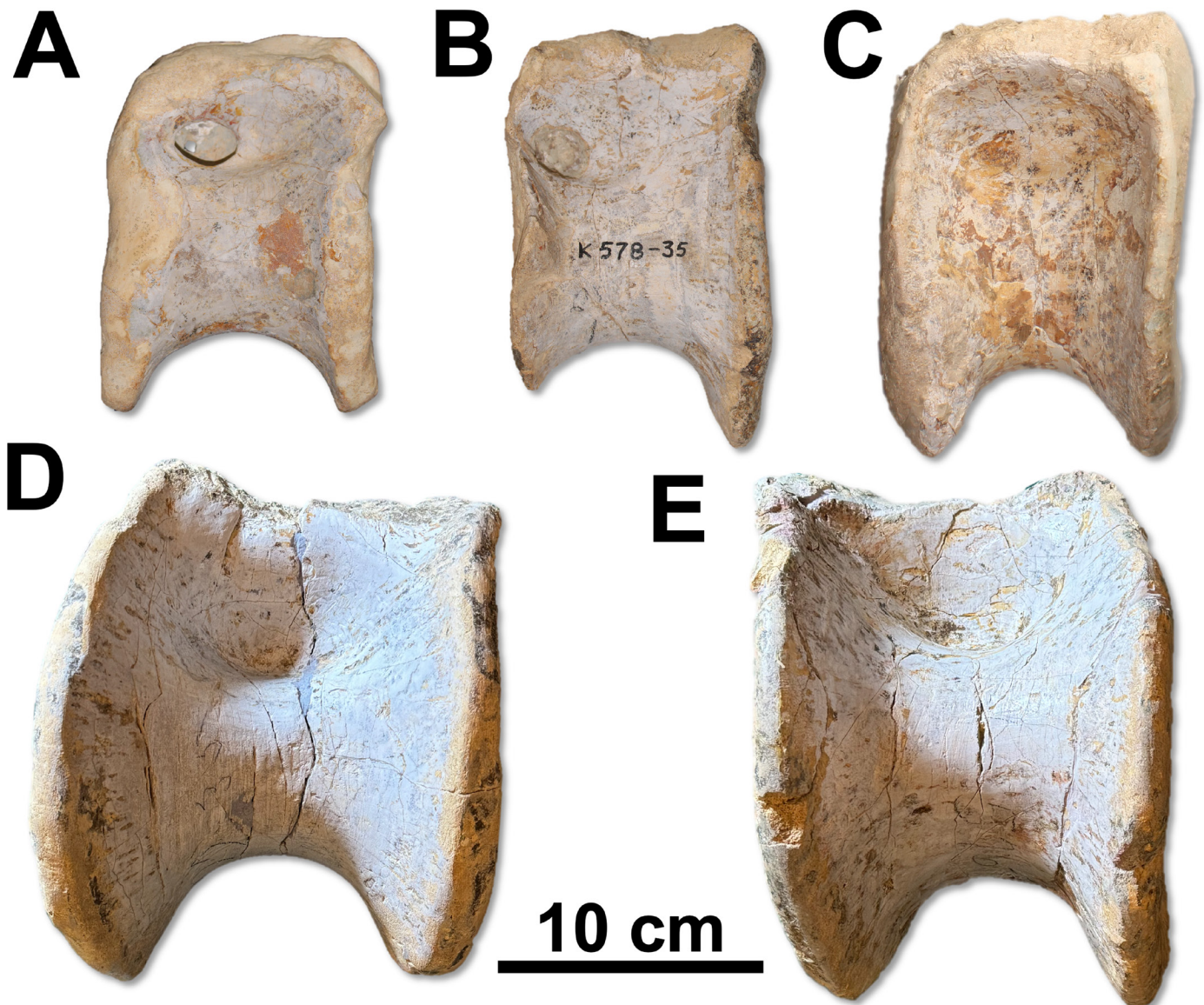


Figure 11. Centra referred to *Saurophaganax maximus* from the Kenton 1 Quarry in lateral view. A, OMNH 1450 (mirrored), B, OMNH 1906; C, OMNH 1905 (mirrored); D, OMNH 1188; and E, OMNH 1189.

described by Madsen (1976). This suggests that the Quarry 1 allosaurid may exhibit more extensive postcranial pneumaticity than both *A. fragilis* and *A. jimmadseni* (Chure 2000; Gilmore 1920; Madsen 1976). Although we acknowledge the possibility that these may belong to another taxon or represent an extreme case of individual variation, we suggest that the possession of hourglass-shaped dorsal centra in combination with prominent pneumatic foramina is an autapomorphy of the Quarry 1 allosaurid.

Chevrons

Several chevrons displaying two distinct morphologies have been referred to *Saurophaganax maximus*. One morphology, indistinguishable from that of *Allosaurus*, is represented by the proximal chevrons. The other morphology, previously described as ‘meat-chopper’ and considered to be autapomorphic (Chure 1995, 2000), is exhibited by the mid-caudal chevrons. For the purpose of this analysis, we will focus on the latter morphology as it displays the purportedly autapomorphic condition. Six of these chevrons (OMNH 1102, OMNH 1104, OMNH 1438, OMNH 1439, OMNH 1684, and OMNH 1685) are preserved in the collection (Fig. 12). All six are badly broken and none feature an intact ramus or a bony bridge connecting the articular surfaces and forming a roof over the haemal canal. The articular surfaces of these chevrons are ovoid and relatively flat in OMNH 1102, 1104, 1438, and 1685. Complete articular surfaces are not preserved in OMNH 1469 or OMNH 1684. They also lack any trace of the small cranial and caudal processes that appear on the

rami of *Allosaurus* (Madsen 1976). The bodies of the chevrons, the inferior rami, and the areas immediately around the articular surfaces are the only parts that are complete across these six chevrons. These chevrons, particularly OMNH 1102, OMNH 1104, and OMNH 1438, display an anterior spine, giving them a craniocaudally elongated body (Chure 1995, 2000). The rami seem to be somewhat curved, and the articular surfaces are flat and ovoid.

The presence of an anterior spine on mid-caudal chevrons resulting in a craniocaudally expanded body distinguishes these chevrons from those of *Allosaurus* (Chure 1995, 2000). The expanded bodies of the mid-caudal chevrons were originally thought to be an example of convergence with the condition in tyrannosaurids (Chure 1995). Bodies of mid-caudal chevrons of *Tyrannosaurus rex* have anterior processes (Brochu 2003). Apart from tyrannosaurids and putatively in *Saurophaganax*, this condition is largely absent among theropods, including *Allosaurus*, *Torvosaurus*, and *Ceratosaurus* (Britt 1991; Gilmore 1920; Madsen 1976). Although the mid-caudal ‘meat chopper’ chevrons are dissimilar to better-known large theropods from the Morrison Formation, a prominent anterior spine is typical in the mid- and posterior caudal chevrons of diplodocids such as *Apatosaurus louisae*, *Barosaurus lentus*, and *Diplodocus carnegii* (Gilmore 1936; Holland 1906; McIntosh 2005). This morphology can be described as ‘forked’ or ‘asymmetric’ in lateral view and are both typical of the mid-posterior caudal chevrons of diplodocids (Otero et al. 2012; Upchurch et al. 2007). As mentioned above, the Kenton

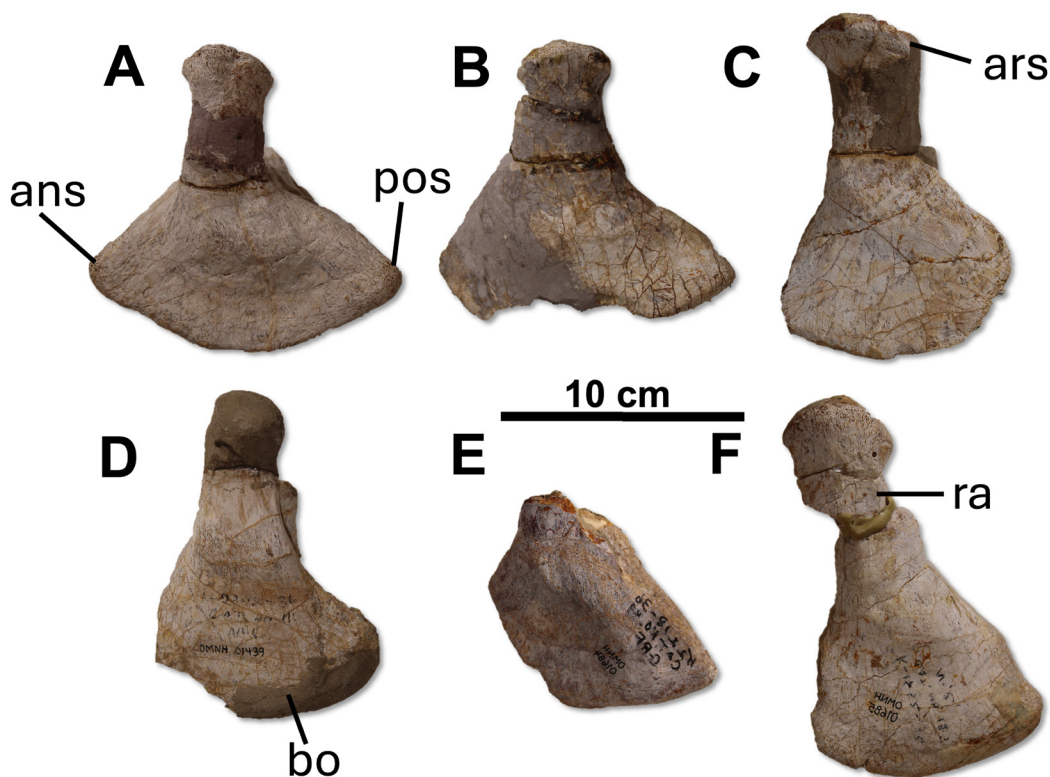


Figure 12. Apomorphic chevrons referred to *Saurophaganax maximus* in lateral view. A, OMNH 1102; B, OMNH 1104; C, OMNH 1438 (mirrored); D, OMNH 1439; E, OMNH 1684 (mirrored); and F, OMNH 1685 (mirrored). Abbreviations: ans, anterior spine or anterior process; ars, articular surface; bo, body of chevron; pos, posterior spine or posterior process; ra, ramus of chevron.

quarries are known for primarily yielding sauropod post-crania, including *Apatosaurus louisae*, *Barosaurus lentus*, and *Diplodocus carnegii* (Hunt and Lucas 1987), so the most parsimonious explanation for this material may be that these chevrons belong to the diplodocids found in the Kenton 1 Quarry. To investigate this hypothesis, a chevron referred to *Apatosaurus*, OMNH 1700, was examined from the Kenton 1 Quarry (Fig. 13). Like the autapomorphic ‘meat chopper’ chevrons described above, OMNH 1700 displays an apparent anterior spine which supports the above hypothesis.

As stated above, there is no trace of a bony bridge or roof over the haemal canal that connects the articular surfaces in any of the elements listed above (Fig. 14). This could be the result of taphonomy or overpreparation but is consistent across all four *Saurophaganax* chevrons with complete articular surfaces. Known theropods, including *Allosaurus* and *Tyrannosaurus*, consistently have a bony bridge that encloses the haemal canal throughout their caudal chevrons, with the sole exception of the proximal-most chevrons of *Spinosaurus aegyptiacus* in FSAC-KK 11888 (A.D. pers. obs.; Brochu 2003; Ibrahim et al. 2020; Madsen 1976). Some mid-posterior diplodocid chevrons lack a bony bridge, giving them an ‘open v-shape’ in cranial view (Otero et al. 2012). While none of the three chevrons referred to *Apatosaurus* from the Kenton 1 Quarry preserve two complete rami, OMNH 1700 lacks any trace of a bony bridge like the chevrons referred to *S. maximus*. Because this is a trait typical of diplodocids rather than allosaurids, this further supports the hypothesis that the purportedly autapomorphic chevrons referred to *Saurophaganax* belong to a diplodocid (Chure 1995; Otero et al. 2012; Madsen 1976).

A quantitative analysis (Tab. 2) was performed to compare the shape of the articular surfaces preserved in the chevrons of *Saurophaganax maximus* and *Apatosaurus* sp. to further evaluate possible sauropod chimerism (Fig.

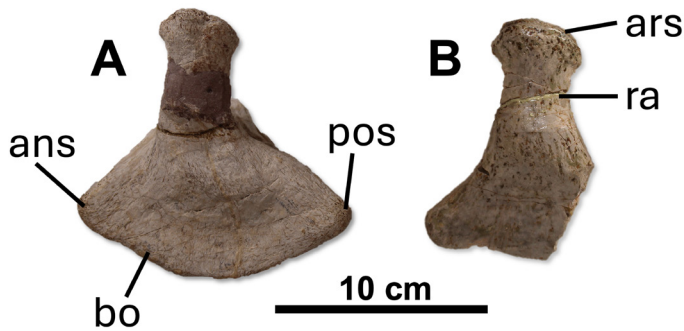


Figure 13. Comparison of a chevron referred to *Saurophaganax maximus* OMNH 1102 (A) to a chevron referred to *Apatosaurus* sp. OMNH 1700 (B). OMNH 1700 was mirrored to align with OMNH 1102. Abbreviations: ans, anterior spine or anterior process; bo, body of chevron; pos, posterior spine or posterior process.

15). Four chevrons referred to *S. maximus* have complete articular surfaces: OMNH 1102, OMNH 1104, OMNH 1438, and OMNH 1685. Of those referred to *Apatosaurus* with a similar morphology, only OMNH 1700 preserves a complete articular surface.

The length to width ratio of the chevron OMNH 1700 referred to *Apatosaurus* sp. is only 0.06 above the mean length to width ratio of the chevrons referred to

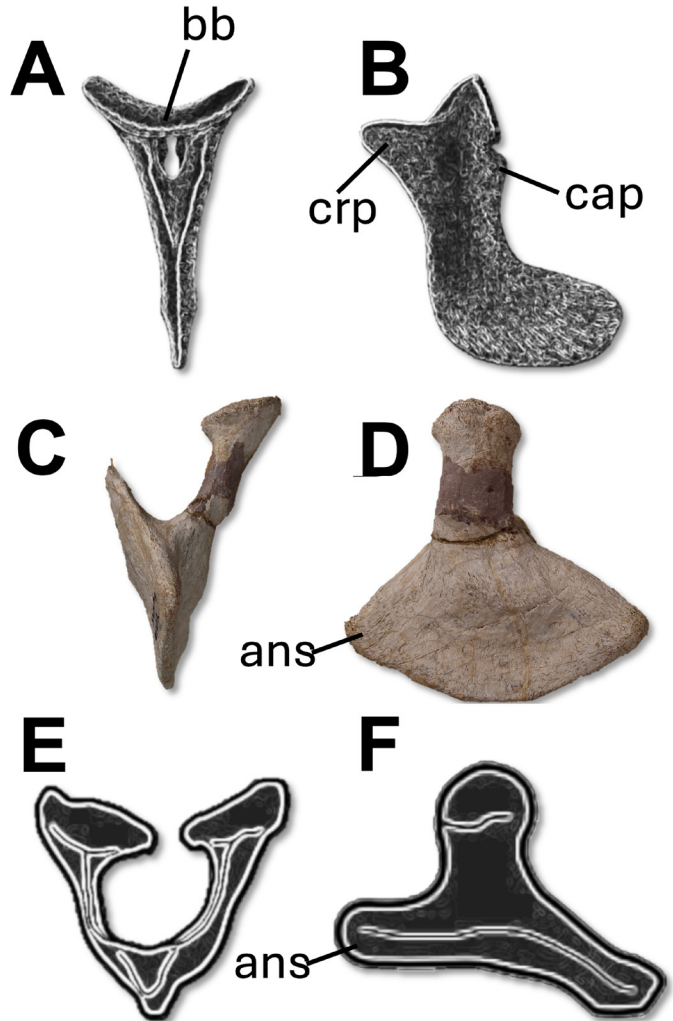


Figure 14. Comparison of chevron referred to *Saurophaganax maximus* OMNH 1102 (C, D) to the mid-caudal chevrons of *Allosaurus fragilis* (A, B) adapted from Madsen (1976, plate 37) and *Diplodocus carnegii* (E, F) modified from Otero et al. (2011, Figure 2). Elements are displayed in posterior (A, C, E) and lateral (B, D, F) views. Abbreviations: ans, anterior spine; bb, bony bridge; cap, caudal process of ramus; crp, cranial process of the ramus; pos, posterior spine. Note that OMNH 1102 lacks any evidence of a bony bridge, cranial processes, or caudal processes similar to the mid-caudal chevrons of *Diplodocus* but dissimilar to the condition in the mid-caudal chevrons of *Allosaurus*. Additionally, OMNH 1102 and the mid-posterior caudal chevrons of *Diplodocus* both have cranial processes which are absent in *Allosaurus*.

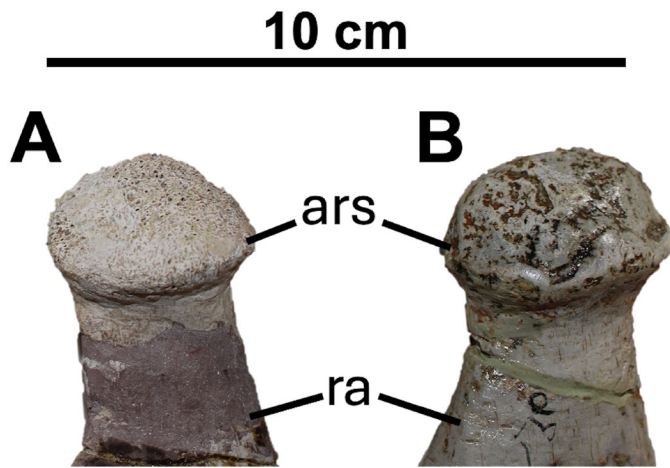


Figure 15. Comparison between the articular surface of a chevron referred to *Saurophaganax* OMNH 1102 (A) and the articular surface of a chevron referred to *Apatosaurus* sp. OMNH 1700 (B). Abbreviations: ars, articular surface; ra, ramus of chevron. Note the reflective concretionary layer on OMNH 1700 that is absent from OMNH 1102. Additionally, the ramus of OMNH 1700 is nearly complete except for a single repaired break while the ramus of OMNH 1102 has been restored with plaster, with neither showing signs of the anterior and posterior processes present in most theropods.

Saurophaganax, and falls well within the measurements of these chevrons, further supporting the suggestion that they all belong to the same taxon. The chevron rami of theropods seem to universally possess cranial processes and caudal processes (A.D. pers. obs.; Brochu 2003; Cuesta et al. 2019; Madsen 1976; Madsen and Welles 2000; Malafaia et al. 2019). However, the mid-posterior caudal chevrons of diplodocids frequently lack them (Holland 1906; Otero et al. 2012). The complete ramus of OMNH 1700 lacks any trace of either of these processes and is complete except for a single small break, supporting the hypothesis that all nine of the chevrons discussed above belong to a diplodocid.

In conclusion, the mid-caudal chevrons OMNH 1102, OMNH 1104, OMNH 1438, OMNH 1439, OMNH

1684, and OMNH 1685 from the Kenton 1 Quarry and referred to *Saurophaganax maximus* bear craniocaudal expansions that were used to distinguish them from those of *Allosaurus*, and are much more typical of the diplodocids that were recovered from the same site. The lack of a bony bridge over the haemal canal and comparison to *Apatosaurus* chevrons recovered from the same quarry support this interpretation, so we conclude that the chevrons referred to *Saurophaganax* could be most confidently assigned to a diplodocid rather than a theropod.

Humerus

A complete left humerus OMNH 1935 (Fig. 16) collected from the Kenton 1 Quarry was also referred to *Saurophaganax maximus* (Chure 1995, 2000). Two other humeri (OMNH 1517 and OMNH 1693) were recovered from the same locality and referred to *S. maximus*, but are too fragmentary for confident taxonomic referral. The deltopectoral crest of OMNH 1935 is well defined and curves medially. Both the proximal and distal articular surfaces are wider than the midshaft but are somewhat taphonomically worn. A large nutrient foramen is present on the posterior surface of the midshaft. The continuation of associated structures across three breaks along the body of the element, including a possible attachment site for the m. humeroradialis (Madsen 1976), suggests that the original orientation of these structures is preserved.

OMNH 1935 is distinct from the humerus of *Apatosaurus excelsus* in that it has a much more pronounced deltopectoral crest and is strongly bowed in anterior view (Gilmore 1936). It can also be distinguished from both *Apatosaurus* and *Diplodocus* by being relatively short (Gilmore 1936; Osborn and Granger 1901). The humeri of both *Ceratosaurus* and *Torvosaurus* are not as prominently bowed as OMNH 1935 (Galton and Jensen 1979; Madsen and Welles 2000). The deltopectoral crest is also more prominent in the lateral view than that of *Torvosaurus tanneri* (Galton and Jensen 1979). Apart from its size, OMNH

Table 2. Measurements of articular surfaces of chevrons from the Kenton 1 Quarry.

Specimen Number	Taxon Referral	Length of Articular Surface (mm)	Width of Articular Surface (mm)	Length:Width
1102	<i>Saurophaganax maximus</i>	35.44	30.30	1.17
1104	<i>Saurophaganax maximus</i>	36.14	24.92	1.45
1438	<i>Saurophaganax maximus</i>	42.43	32.78	1.29
1685	<i>Saurophaganax maximus</i>	42.09	39.47	1.07
1700	<i>Apatosaurus</i> sp.	40.49	30.97	1.31
			L:W Median	1.23
			L:W Mean	1.25

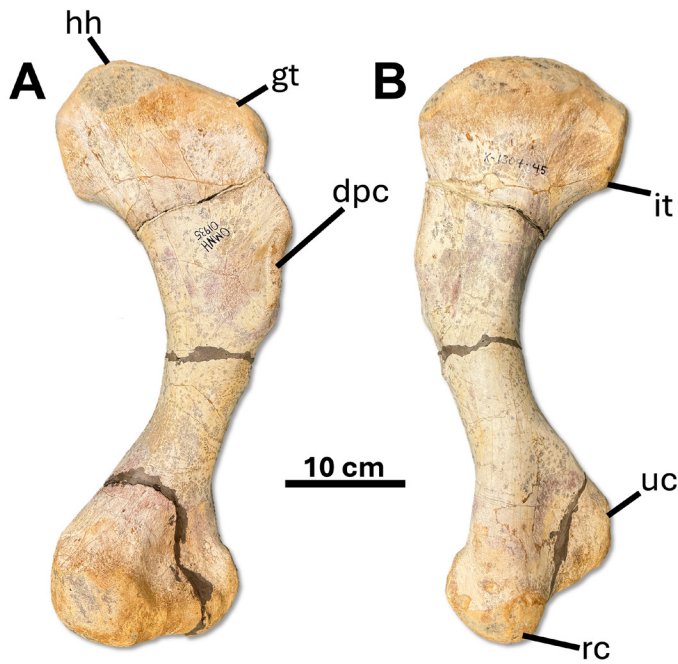


Figure 16. Left humerus OMNH 1935 referred to *Saurophaganax maximus* in anterior (A) and posterior (B) views. Abbreviations: dpc, deltopectoral crest; gt, greater tuberosity; hh, head of the humerus; it, internal tuberosity; uc, ulnar condyle; rc, radial condyle.

1935 is indistinguishable from that of *Allosaurus fragilis* and *Allosaurus jimmadseni* (Chure 1995, 2000; Madsen 1976). Thus, we can be confident that this humerus belongs to a large allosaurid from the Kenton 1 Quarry.

Femora

Three large femora (OMNH 1371, OMNH 1708, and OMNH 2114) were collected from the Kenton 1 Quarry (Fig. 17), and referred to *Saurophaganax maximus* (Chure 1995, 2000). OMNH 1708 has been broken transversely and repaired, while OMNH 2114 has an intact diaphysis. OMNH 1371 has a damaged diaphysis that has been repaired with plaster. OMNH 1708 and OMNH 2114 (right and left femora, respectively) have nearly identical mid-diaphyseal circumferences, so we suspect they belong to the same individual; OMNH 1371, a left femur, has a greater mid-diaphyseal circumference.

Mass estimates of all three femora were calculated following Campione et al. (2014). The circumferences for OMNH 1371, OMNH 1708, and OMNH 2114 are 47.4 cm, 44.4 cm, and 44.0 cm, respectively. The masses of the individuals that OMNH 1371, OMNH 1708, and OMNH 2114 belonged to are estimated as 4,634 kg, 3,871 kg, and 3,776 kg respectively.

The femora bow anteriorly, as is the case in both species of *Allosaurus* (Chure 2000; Gilmore 1920; Madsen 1976), but are noticeably more laterally bowed than is typically reported for *Allosaurus fragilis* (Chure 1995, 2000; Madsen

1976). OMNH 1371 has been crushed anteroposteriorly and the distal condyles are missing. Most of the greater trochanter is lost in this element, but OMNH 2114 and OMNH 1708 have complete greater trochanters that are consistent with *Allosaurus* (Madsen 1976). The lesser trochanter in OMNH 2114 is broken. The fourth trochanter is worn in OMNH 1371 and broken in OMNH 2114, but that of OMNH 1708 is intact. The blocky protuberance on the posterior surface of the fibular condyle is worn in OMNH 1708 but complete in OMNH 2114. The greater,

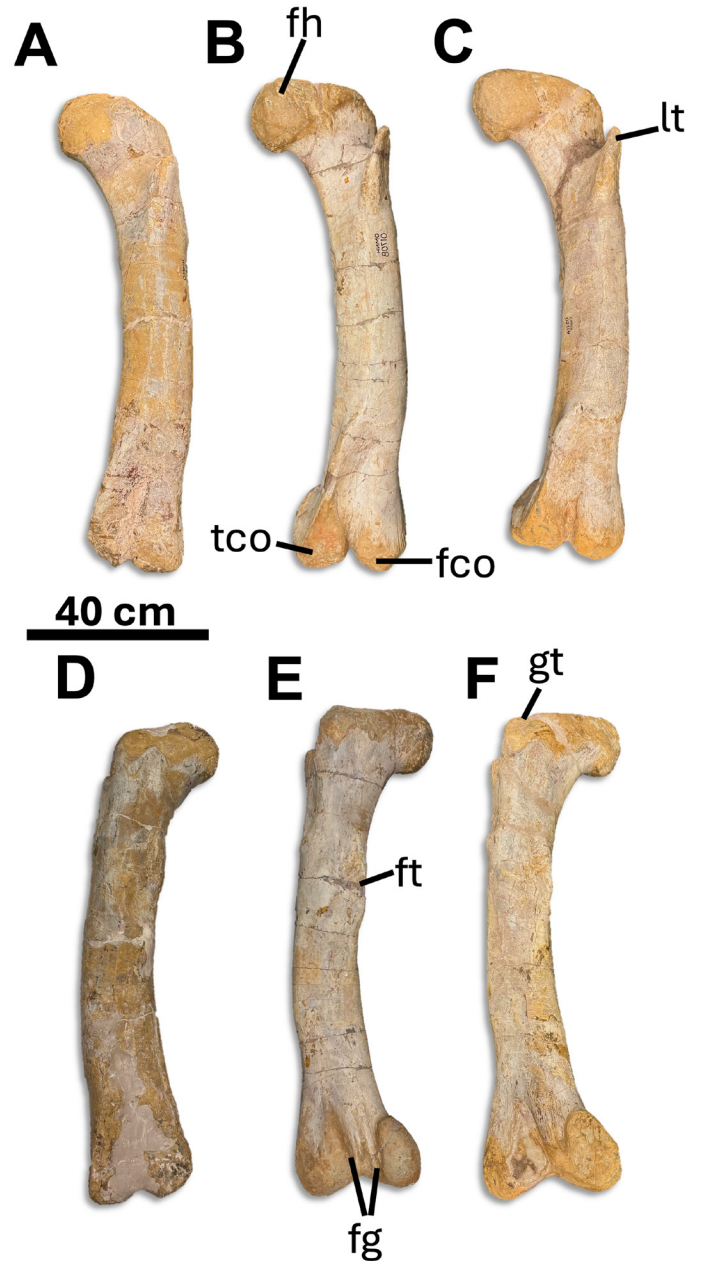


Figure 17. Femora referred to *Saurophaganax maximus*. Left femur OMNH 1371 (A, D), right femur OMNH 1708 (mirrored) (B, E), and left femur OMNH 2114 (C, F) in anterior (A, B, C) and posterior (D, E, F) view. Abbreviations: fco, fibular condyle; fg, flexor groove; fh, femoral head; ft, fourth trochanter; gt, greater trochanter; lt, lesser trochanter; tco, tibial condyle.

lesser, and fourth trochanters of OMNH 1708 are identical in shape to those of *Allosaurus* (Madsen 1976). The extensor groove in both OMNH 1708 and OMNH 2114 is narrow and deep. The flexor groove is notably shallower and wider, containing parasagittal ridges for ligament attachment. Together, these grooves separate the tibial and fibular condyles.

The relatively gracile proportions in anterior view and the presence of a distinct, wing-like lesser trochanter (Gilmore 1936; Hatcher 1901; Madsen 1976), clearly indicates that all three femora pertain to a large theropod. The lesser trochanter preserved in OMNH 1708 is much more prominent than that of *Ceratosaurus magnicornis* (Madsen and Welles 2000) but resembles that of *Allosaurus fragilis* (Madsen 1976). The fourth trochanter is relatively more defined in *Ceratosaurus* than is seen in *Allosaurus* or OMNH 1708 (Madsen 1976; Madsen and Welles 2020). The lone femur described for *Torvosaurus* was recovered from Portugal with only the distal end preserved (Hendrickx and Mateus 2014). This femur lacks the distal ridge that arises from the tibial condyle in anterior view present in *Allosaurus* and OMNH 1708 (Hendrickx and Mateus 2014; Madsen 1976). Thus, we most confidently attribute these femora to a large allosaurid distinct from either of the *Allosaurus* species recorded at this locality.

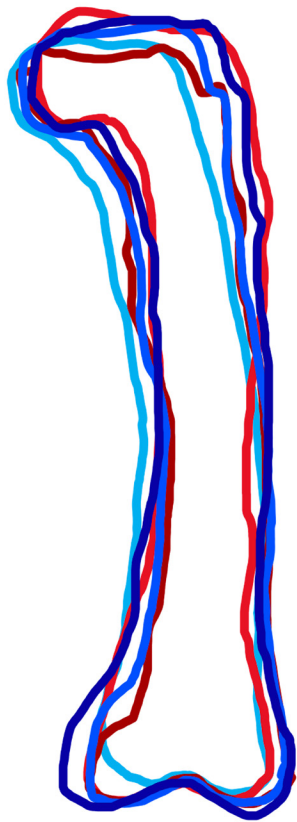


Figure 18. Björk superposition of femora referred to *Saurophaganax maximus* and *Allosaurus* adapted from Madsen (1976) and Chure (2000). The left femur of *Allosaurus fragilis* described by Madsen (1976) is outlined in light red, while that of right femur of DINO 11541 is highlighted in dark red. The left femur OMNH 1371 is outlined in light blue, the right femur OMNH 1708 is outlined in royal blue, while the left femur OMNH 2114 is outlined in navy blue. The right femora were mirrored to align with the left. While the femora of *Saurophaganax maximus* appear to be on average more laterally bowed than those of *Allosaurus fragilis*, DINO 11541 is similarly laterally bowed almost identically to OMNH 1708 and more bowed than OMNH 2114. The intercondylar sulcus was used as a consistent landmark to ground comparisons.

All three Quarry 1 allosaurid femora are laterally bowed at a consistent angle greater than that of *Allosaurus fragilis* (Chure 1995, 2000; Madsen 1976). In contrast, the right femur of DINO 11541, the holotype of *A. jimmadnseni*, seems to be similarly laterally bowed (Fig. 18) (Chure 2000). However, it is worth noting that much of DINO 11541 is taphonomically distorted (Chure 2000; Chure and Loewen 2020), so it is possible that the bowed appearance of the femur is not representative of its original condition. If this is the case, the lateral bowing of the Quarry 1 allosaurid femora may be autapomorphic.

Tibia

Four tibiae were recovered from the Kenton 1 Quarry. OMNH 1369 is a proximal tibia, OMNH 1370 is a complete tibia, OMNH 1949 is a proximal tibia fragment, and OMNH 2149 is a distal tibia fragment (Fig. 19). We primarily focus on OMNH 1370 because it is the most complete, while OMNH 1949 was considered too fragmentary for analysis. The diaphysis of OMNH 1370 has been broken transversely into three approximately equal pieces. A prominent ridge passing from the inferior margin of the fibular crest to the distal articular surface shows consistent orientation across these breaks, indicating that the tibia has been accurately restored, and that no significant portion of the shaft is missing. Holes that were drilled into both proximal and distal articular surfaces to accommodate rod have been repaired. Both the distomedial and distolateral crests of OMNH 1370 have also been restored. It bears a fibular crest on its lateral surface. The cnemial crest is prominent. All the articular surfaces show some sign of wear, but the rest of the surface is intact.

These tibiae were previously indicated to have more prominent distomedial crests than *Allosaurus fragilis* and differ from *A. fragilis* in lacking an astragalar buttress (Chure 2000). Their proportions, the more prominent cnemial crests, and the laterally compressed distal surfaces all distinguish them from those of *Apatosaurus louisae* (Gilmore 1936; Madsen 1976) and support their assignment to Theropoda. OMNH 1370 and *Allosaurus fragilis* both have much more pronounced cnemial crests and much thicker distal articular surfaces (Hatcher 1901; Madsen 1976) than *Diplodocus carnegii*. The proximal articular surface of OMNH 1370 is much wider than that of *Ceratosaurus magnicornis* and is not anteroposteriorly compressed as in *Ceratosaurus magnicornis* (Gilmore 1936; Madsen 1976). None of them are as robust as those referred to *Torvosaurus*, and the distomedial crest is less prominent than in *Torvosaurus tanneri* (Britt 1991; Carrano et al. 2012; Hendrickx and Mateus 2014; Madsen 1976). The proportions of the tibiae referred to *S. maximus* are most consistent with those of *Allosaurus*, so we attribute these tibiae to an allosaurid (Madsen 1976).

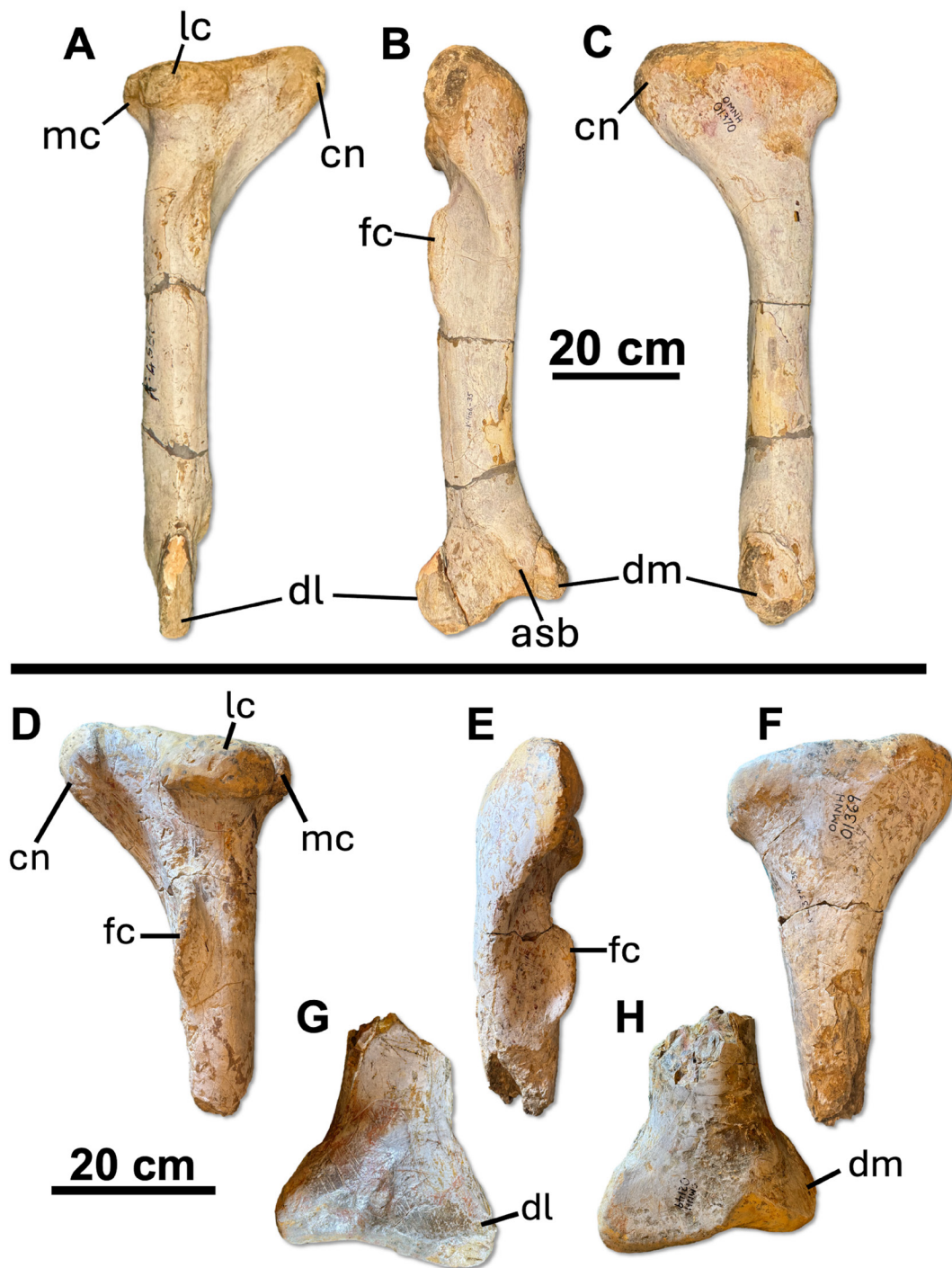


Figure 19. Tibiae referred to *Saurophaganax maximus*. The complete right tibia OMNH 1370 in lateral (A), anterior (B), and medial (C) views. The proximal tibia left OMNH 1369 in lateral (D), anterior (E), and medial (F) views. The distal left tibia fragment OMNH 2149 in anterior (G) and posterior (H) views. Abbreviations: asb, astragalar buttress; cn, cnemial crest; dl, distolateral crest; dm, distomedial crest; fc, fibular crest; lc, lateral condyle; mc, medial condyle. Note the different scale bars between OMNH 1370 and the fragmentary tibiae OMNH 1369 and OMNH 2149.

The distomedial crests of OMNH 1370 and OMNH 2149 do not appear to be more prominent than that of *Allosaurus fragilis* as previously reported (Fig. 20) (Chure 2000; Madsen 1976), although the articular surfaces are worn, so it is difficult to assess the original state of these features. As with many elements in the Kenton Quarry, OMNH 1370 had a hole drilled into its distal articular surface to support the insertion of a metal rod for stabilization. One of these was drilled directly between the distomedial and distolateral crests of OMNH 1370, which may have made the crests appear more pronounced by deepening

the sulcus between them. However, the shape of the distal surface of the tibia preserved in OMNH 2149 appears to be more similar to the condition Madsen (1976) reported in *Allosaurus fragilis*. As such, we cannot conclude that a more prominent distomedial crest is an autapomorphy of the Quarry 1 allosaurid.

Both OMNH 2149 and OMNH 1370 show evidence of postmortem abrasion. Although OMNH 2149 does not appear to possess an astragalar buttress, OMNH 1370 exhibits a subtle astragalar buttress similar to that present in *Allosaurus fragilis* (Madsen 1976), conflicting with previous

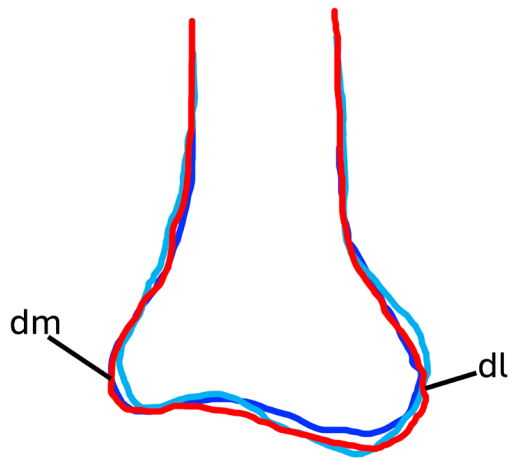


Figure 20. Björk superimposition of distal tibiae in anterior view referred to *Saurophaganax maximus* and *Allosaurus fragilis* adapted from Madsen (1976). The diaphyses were used as congruent structures to ground comparison of the distal articular surfaces. The right tibia OMNH 1370 was mirrored to align with the left tibia OMNH 2149 and the left tibia described by Madsen (1976). OMNH 1370 is outlined in light blue and OMNH 2149 is outlined in dark blue, while the distal tibia of *Allosaurus fragilis* is outlined in red. Abbreviations: dl, distolateral crest; dm, distomedial crest.

descriptions (Chure 2000). The lack of this structure in OMNH 2149 is most likely the result of taphonomic wear, so we do not consider the lack of an astragalar buttress to be a viable autapomorphy for the Quarry 1 allosaurid.

OMNH 1370 differs from the tibia of *Allosaurus fragilis* in that its fibular crest is more laterally oriented so that it is not visible in a medial view (Madsen 1976). However, Chure (2000) reported that the fibular crest in the holotype of *Allosaurus jimmadsemi* (DINO 11541) has an identical orientation to those of OMNH 1369 and OMNH 1370. As such, we cannot conclude that a more laterally oriented fibular crest is a unique feature of the Quarry 1 allosaurid relative to other species of *Allosaurus*, but it may be a useful character for establishing the relationships among these taxa.

Fibulae

Three fibulae referred to *Saurophaganax maximus* were recovered from the Kenton 1 Quarry: OMNH 1426, OMNH 1694, OMNH 1695 (Fig. 21) (Chure 2000). All have been broken transversely and repaired. OMNH 1694 preserves more of the diaphysis than OMNH 1426 and OMNH 1695, but all three lack distal articular surfaces. They all have smooth lateral surfaces and somewhat worn proximal articular surfaces. The medial surface of the diaphysis is shallowly excavated. The head of the fibula bears three small fossae on its medial surface.

These fibulae can all be distinguished from those of *Apatosaurus louisae* in that they have proportionately wider

proximal articular surfaces in relation to their diaphyses (Gilmore 1936). They are distinct from *Ceratosaurus nasicornis* and *Ceratosaurus dentisulcatus* in that the tibial flanges are reduced in size or absent (Gilmore 1920; Madsen and Welles 2000). Additionally, the medial surface of the fibula referred to *Ceratosaurus dentisulcatus* lacks the excavated diaphyseal groove visible on the fibulae referred to *S. maximus* (Madsen and Welles 2000). Restoration of the *Torvosaurus* fibula BYUVP 9620 makes it difficult to assess the anatomy of its medial surface (Britt 1991), but like *C. dentisulcatus* lacks this excavation (Britt 1991). Nevertheless, the fibulae described here have proportions more consistent with those of other large Morrison Formation theropods (*Ceratosaurus*, *Torvosaurus*, and *Allosaurus*) than those of *Apatosaurus louisae* (Britt 1991; Gilmore 1936; Madsen 1976; Madsen and Welles 2000). Thus, we are confident that they belong to a theropod.

OMNH 1426, OMNH 1694, and OMNH 1695 differ from the fibulae of *Allosaurus fragilis* in that the latter have more deeply excavated fossae on the medial surfaces of their diaphyses and do not display additional fossae on their medial surfaces (Madsen 1976), suggesting that they may be autapomorphic. However, the fibulae of DINO 11541, the holotype of *Allosaurus jimmadsemi*, are reported to be less medially concave than Madsen (1976) observed in *Allosaurus fragilis* (Chure 2000). A shallower fossa is visible on the medial surface of the fibular diaphysis in both *Allosaurus jimmadsemi* and the Quarry 1 allosaurid. OMNH 1426, OMNH 1694, and OMNH 1695 show signs of taphonomic wear at the proximal articular surface and are broken at their diaphyses. The medial surfaces of these fibulae are largely intact, without signs of overpreparation or taphonomic wear, so this cannot explain the additional proximal fossae or the shallowly excavated diaphyseal fossae present on these elements. Ontogeny or allometry are unlikely to explain the possibly autapomorphic condition because the fibula described by Madsen (1976) lacks proximomedial fossa, but has a larger maximum proximal width than OMNH 1426, the smallest fibula referred to *Saurophaganax* (14.8 cm and 14.5 cm, respectively). Because this putative autapomorphic condition is observed in all three theropod fibulae recovered from the Kenton 1 Quarry, individual variation is also unlikely to explain this condition. Thus, we tentatively conclude that the presence of three shallow fossae on the proximomedial surface of the fibula is an autapomorphic character of the Quarry 1 allosaurid, but we note that further comparison to *A. jimmadsemi* may change this diagnosis. Additionally, both *Allosaurus jimmadsemi* and the Quarry 1 allosaurid exhibit less pronounced medial fossae on the diaphyses of their fibulae (Chure 2000).



Figure 21. Fibulae referred to *Saurophaganax maximus*. Left proximal fibula OMNH 1426 (A, B), left proximal fibula OMNH 1694 (C, D) and right proximal fibula OMNH 1695 (E, F) in lateral (A, C, E) and medial (B, D, and F) views. Abbreviations: hf, head of the fibula; mf, medial fossae.

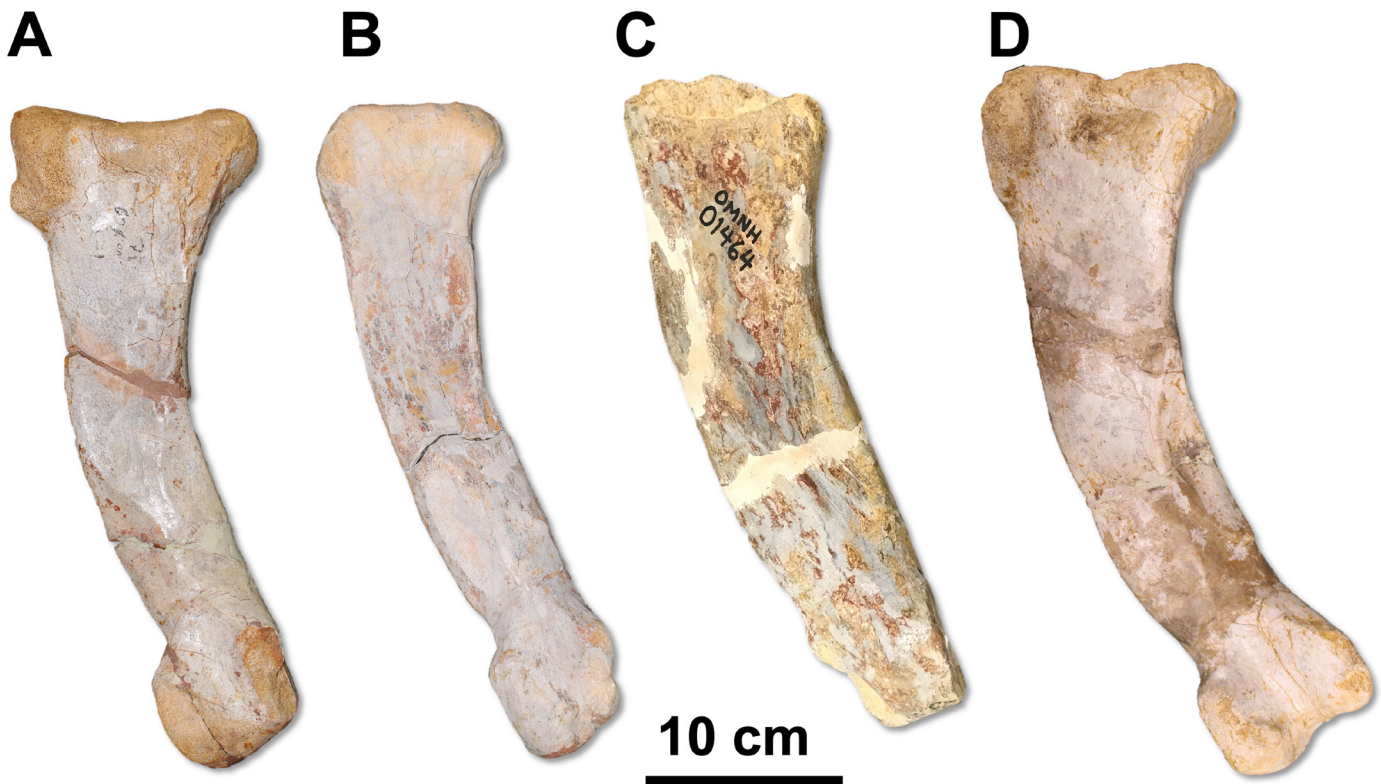


Figure 22. Fourth metatarsals referred to *Saurophaganax maximus* in posterior view. A, right fourth metatarsal OMNH 1193; B, left fourth metatarsal OMNH 1306 (mirrored); C, right fourth metatarsal OMNH 1464; D, left fourth metatarsal OMNH 1936 (mirrored).

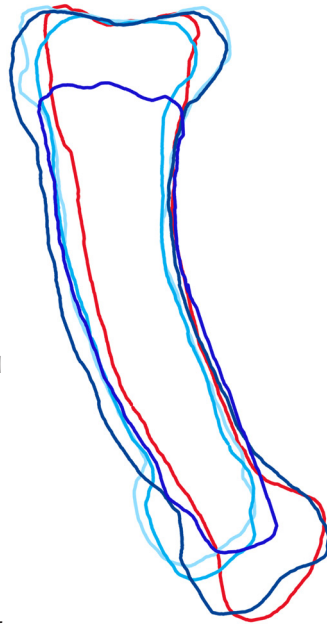
Fourth Metatarsals

Four fourth metatarsals have been referred to *Saurophaganax maximus*: OMNH 1193, OMNH 1306, OMNH 1464, and OMNH 1936 (Fig. 22) (Chure 2000). Each of these elements is laterally bowed and preserves two articular facets on its diaphysis. OMNH 1193 has two breaks along its diaphysis and the distolateral epiphysis is broken. OMNH 1306 features two breaks along its diaphysis as well. OMNH 1464 has broken epiphyses and the diaphysis is broken but has been repaired. OMNH 1936 is the most complete of these elements, though has also been broken along its diaphysis.

Each of these metatarsals is easily distinguishable from those of sauropods such as *Apatosaurus louisae* by their proportions, curvature, and articular facets (Gilmore 1976; Madsen 1976), and more similar to those of *Allosaurus* (Madsen 1976), and are notably curved laterally in anterior view, which distinguishes them from those of both *Torvosaurus* and *Ceratosaurus* (Gilmore 1920; Hanson and Mackovicky 2013; Madsen and Welles 2000).

OMNH 1193, OMNH 1306, OMNH 1464, and OMNH 1936 were previously noted to be less bowed than those of *Allosaurus fragilis* (Chure 2000). However, we cannot verify this claim because the lateral surfaces of these elements align well with that of *Allosaurus fragilis* in posterior view (Fig. 23)

Figure 23. Björk superimposition of *Saurophaganax maximus* fourth metatarsals to that of *Allosaurus fragilis* adapted from Madsen (1976). The size of the metatarsals has been adjusted so that they are roughly equal and left metatarsals were mirrored. OMNH 1193 is outlined in the lightest blue, OMNH 1306 is outlined in electric blue, OMNH 1464 is outlined in dark blue, and OMNH 1936 is outlined in navy blue. The specimen of *Allosaurus fragilis* described by Madsen (1976) is outlined in red. The proximal articular surface was used as a consistent landmark for all of the metatarsals except for OMNH 1464, which lacks a complete proximal surface. OMNH 1464 was oriented using the lateral surface of the diaphysis. Note that the metatarsals referred to *Saurophaganax* are more robust with wider articular surfaces and diaphyses than that of the *Allosaurus fragilis* described by Madsen (1976), but do not appear to be less laterally bowed than those of *Allosaurus*. Indeed, OMNH 1464 and OMNH 1936 appear to be more laterally bowed than the specimen described by Madsen (1976).



(Madsen 1976). In conclusion, although we can confidently refer these metatarsals to an allosaurid, we cannot confirm that they are more laterally bowed than the fourth metatarsal of *Allosaurus fragilis* and therefore do not consider this feature an autapomorphy of the Quarry 1 allosaurid.

Paleohistology

The right fourth metatarsal OMNH 1464 displays regions of dense Haversian bone and plexiform fibrolamellar bone (Fig. 24A). The cortex preserves 12–14 lines of arrested growth (LAGs). One region of dense Haversian bone features Sharpey's fibers just deep to the external cortex and likely represents an enthesis. This enthesis, which is on the posterolateral surface of the diaphysis at what would be the facet for articulation with the fifth metatarsal, likely represents the attachment site of an intermetatarsal ligament connecting metatarsals IV and V. A similar enthesis is exhibited by *Gorgosaurus libratus* and other coelurosaurs (Surring et al. 2022). The plexiform bone extends to the outer cortex. The element is diagenetically modified in some regions, particularly anterolaterally, and the external cortex has been slightly worn. However, there is a structure in the outermost cortex that resembles an external fundamental system (EFS) (Fig. 24B–D). An EFS is a poorly vascularized superficial layer of lamellar bone (also known as the outer circumferential lamellae) that indicates a substantial reduction in appositional growth and reflects skeletal maturity assuming isometric growth (Francillon-Vieillot et al. 1990; Horner et al. 1999).

DISCUSSION

A comparative analysis of the elements previously used to distinguish *Saurophaganax maximus* from *Allosaurus* suggests that some of the purportedly diagnostic material is more parsimoniously assigned to diplodocids than the large Kenton 1 Quarry allosaurid. Additionally, we find that the holotype neural arch currently cannot be confidently assigned to a theropod or sauropod, making *Saurophaganax maximus* a *nomen dubium*. Chimerism would explain why some elements, such the humerus OMNH 1935, are wholly consistent with those of *Allosaurus* apart from size (Smith 1998; Chure 1995, 2000), while others, such as the atlas OMNH 1135, are starkly different from known specimens of *Allosaurus* (Chure 1995, 2000; Madsen 1976). Whether the holotype of *Saurophaganax maximus* can be more confidently assigned to a sauropod or theropod will be the subject of future analyses. Our findings highlight the need for increased understanding of serial, ontogenetic, and other individual variation within the axial skeletons of both Morrison Formation sauropods and theropods, given the possibility of convergent or plesiomorphic morphologies that render taxonomic identification difficult, particularly

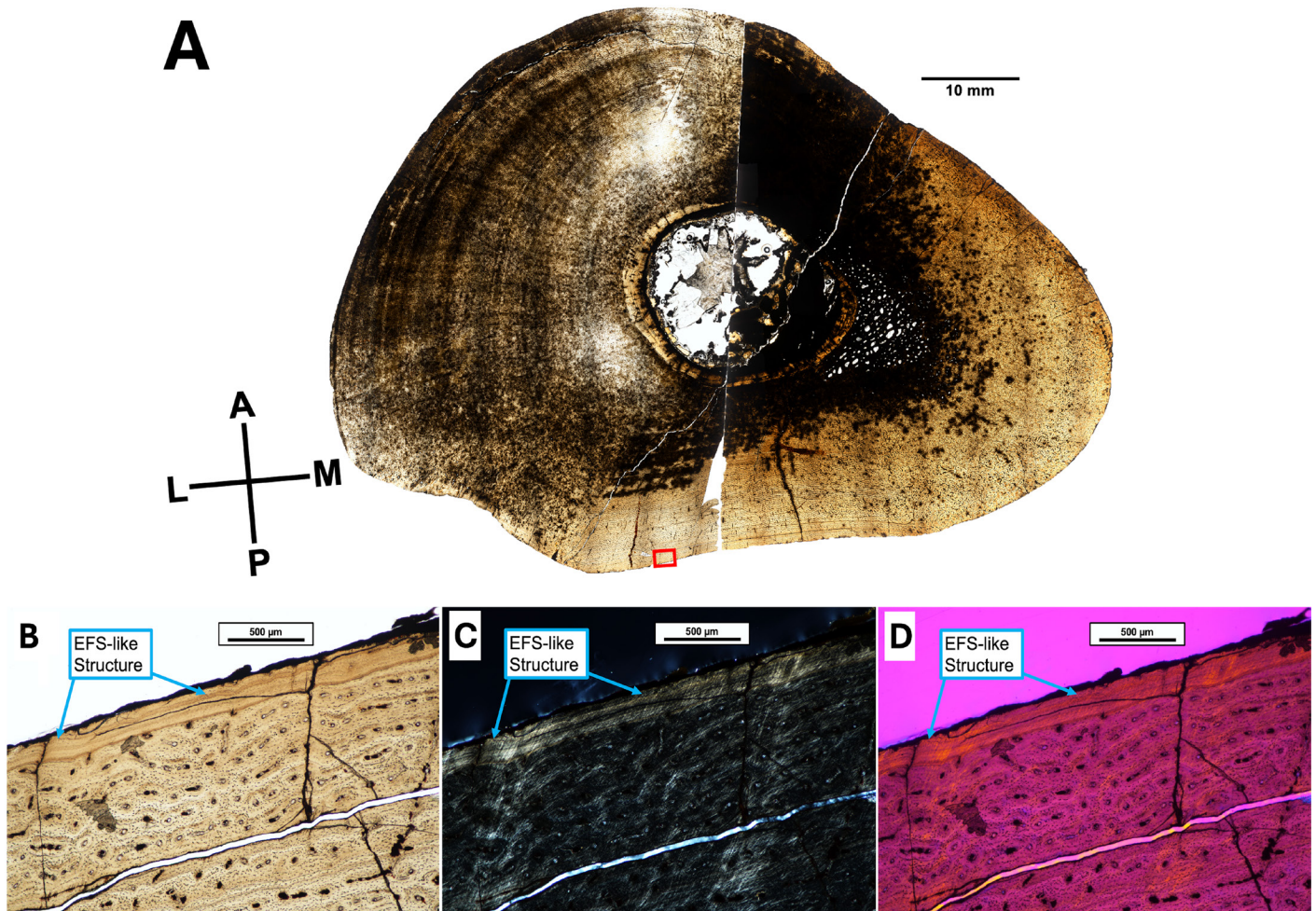


Figure 24. Thin section of a left fourth metatarsal OMNH 1464 referred to *Saurophaganax maximus*. A, Complete mid-diaphyseal thin section of OMNH 1464 under plane polarized light (PPL). Location of B, C, and D is highlighted in red. B, EFS-like structure under plane polarized light (PPL); C, EFS-like structure under circular polarized light (CPL); D, EFS-like structure under cross polarized light with full wave plate compensator (CXPL).

when disarticulated remains are comingled.

The ambiguity of the holotype element of *Saurophaganax maximus* leaves the Kenton 1 Quarry theropod without a taxonomically valid name. Chure (1995) tentatively gave the material a new generic name (consistent with its past, preoccupied name), noting its similarity to *Allosaurus*. With our analysis eliminating many of the previously reported autapomorphies that distinguished the Quarry 1 allosaurid from *Allosaurus*, we do not consider a distinct genus warranted. The Quarry 1 allosaurid was previously described as *Allosaurus maximus* (Smith 1998). However, that analysis also designated OMNH 1123 as the holotype. This makes *Allosaurus maximus* a junior synonym of *Saurophaganax maximus* because Chure (1995) conformed to ICZN standards. Therefore, the name *Allosaurus maximus* should also be considered a *nomen dubium* as well. Despite disagreements over whether the Quarry 1 allosaurid warrants a distinct genus, previous analyses of the elements that we recognize as pertaining to the Quarry 1 allosaurid have

maintained it as distinct from other species of *Allosaurus* (Chure 1995, 2000; Chure and Loewen 2020; Smith 1998; Smith et al. 1999). We agree, for example, that the postorbital OMNH 1771, while almost certainly referable to an allosaurid, is distinct from those of both *Allosaurus fragilis* and *Allosaurus jimmadseni* (Chure and Loewen 2020). Thus, we give the Kenton 1 Quarry theropod the new name *Allosaurus anax*. Large theropod material from the Kenton 1 Quarry that does not have any autapomorphies distinguishing it from other species of *Allosaurus* is referred to *Allosaurus* sp., but likely belongs to the same taxon (Tab. 3). It is possible that future studies will show that the holotype neural arch of *Saurophaganax* belongs to a theropod, in which case *Allosaurus anax* will be considered a junior synonym of the former.

Specific identification of non-avian dinosaurs relies largely on cranial apomorphies (Brusatte et al. 2008; Carrano et al. 2012; Danison et al. 2023); as previously noted little cranial material of *A. anax* is known (Chure 1995, 2000). Therefore,

Table 3. Revised referrals of specimens referred to *Saurophaganax maximus* from the Kenton 1 Quarry.

Specimen no.	Element	Initial Referral	Revised Referral	Justification
OMNH 1771	Postorbital	<i>Saurophaganax maximus</i>	<i>Allosaurus anax</i> (holotype)	Autapomorphies including the lack of a postorbital boss, absence or significant reduction of the dorsolateral crest and lateral fossa on the posterior bar of the postorbital, the lack of a ridge extending from the anterior bar of the postorbital down the anterior margin of the ventral bar distinguish this specimen from both <i>Allosaurus fragilis</i> and <i>Allosaurus jimmadseni</i> .
OMNH 1142	Quadrate	<i>Saurophaganax maximus</i>	<i>Allosaurus</i> sp.	Referable to <i>Allosaurus</i> but indistinguishable from the quadrates of other <i>Allosaurus</i> species.
OMNH 2145	Quadrate	<i>Saurophaganax maximus</i>	<i>Allosaurus</i> sp.	Referable to <i>Allosaurus</i> but indistinguishable from the quadrates of other <i>Allosaurus</i> species.
OMNH 1135	Atlas	<i>Saurophaganax maximus</i>	Neosauropoda	Anteroventral protrusion, lack of anterolateral processes, and lack of facets for a proatlas are more consistent with sauropods than <i>Allosaurus</i> . Lack of proatlas is present in <i>Apatosaurus</i> and possibly <i>Camarasaurus</i> as well.
OMNH 2146	Cervical Vertebra	<i>Saurophaganax maximus</i>	<i>Allosaurus anax</i>	Tentatively referred to <i>A. anax</i> as nearly vertical postzygopophyses are distinct from both other species of <i>Allosaurus</i> . Deformation is possible but not evident.
OMNH 1123	Dorsal Neural Arch	<i>Saurophaganax maximus</i> (holotype)	<i>Saurophaganax maximus</i> (<i>nomen dubium</i>)	Accessory laminae (al) are complex and more typical of sauropods, theropod characteristics found in juvenile sauropods, and this element is fragmentary, preventing confident assignment to a theropod.
OMNH 1450	Dorsal Centrum	<i>Saurophaganax maximus</i>	<i>Allosaurus anax</i>	Tentatively referred to <i>A. anax</i> as the presence of a pneumatic foramina on an hourglass-shaped dorsal centrum is not seen in any other specimen of <i>Allosaurus</i> .
OMNH 1906	Dorsal Centrum	<i>Saurophaganax maximus</i>	<i>Allosaurus anax</i>	Tentatively referred to <i>A. anax</i> as the presence of a pneumatic foramina on an hourglass-shaped dorsal centrum is not seen in any other specimen of <i>Allosaurus</i> .
OMNH 1102	Chevron	<i>Saurophaganax maximus</i>	Diplodocidae	Previously reported autapomorphic morphology and lack of bony bridge is typical of diplodocids, similarity of articular surface proportions of confidently referred diplodocid chevrons from the same quarry.
OMNH 1104	Chevron	<i>Saurophaganax maximus</i>	Diplodocidae	Previously reported autapomorphic morphology and lack of bony bridge is typical of diplodocids, similarity of articular surface proportions of confidently referred diplodocid chevrons from the same quarry.
OMNH 1438	Chevron	<i>Saurophaganax maximus</i>	Diplodocidae	Previously reported autapomorphic morphology and lack of bony bridge is typical of diplodocids, similarity of articular surface proportions of confidently referred diplodocid chevrons from the same quarry.
OMNH 1439	Chevron	<i>Saurophaganax maximus</i>	Diplodocidae	Previously reported autapomorphic morphology and lack of bony bridge is typical of diplodocids, similarity of articular surface proportions of confidently referred diplodocid chevrons from the same quarry.

Table 3. continued

Specimen no.	Element	Initial Referral	Revised Referral	Justification
OMNH 1684	Chevron	<i>Saurophaganax maximus</i>	Diplodocidae	Previously reported autapomorphic morphology and lack of bony bridge is typical of diplodocids, similarity of articular surface proportions of confidently referred diplodocid chevrons from the same quarry.
OMNH 1685	Chevron	<i>Saurophaganax maximus</i>	Diplodocidae	Previously reported autapomorphic morphology and lack of bony bridge is typical of diplodocids, similarity of articular surface proportions of confidently referred diplodocid chevrons from the same quarry.
OMNH 1371	Femur	<i>Saurophaganax maximus</i>	<i>Allosaurus</i> sp.	Similar lateral bowing seen in <i>Allosaurus jimmadseni</i> holotype DINO 11541, so is not autapomorphic.
OMNH 1708	Femur	<i>Saurophaganax maximus</i>	<i>Allosaurus</i> sp.	Similar lateral bowing seen in <i>Allosaurus jimmadseni</i> holotype DINO 11541, so is not autapomorphic.
OMNH 2114	Femur	<i>Saurophaganax maximus</i>	<i>Allosaurus</i> sp.	Similar lateral bowing seen in <i>Allosaurus jimmadseni</i> holotype DINO 11541, so is not autapomorphic.
OMNH 1369	Tibia	<i>Saurophaganax maximus</i>	<i>Allosaurus</i> sp.	Fibular crest orientation consistent with <i>Allosaurus jimmadseni</i> holotype DINO 11541, so is not autapomorphic.
OMNH 1370	Tibia	<i>Saurophaganax maximus</i>	<i>Allosaurus</i> sp.	Astragalar buttress weakly present, fibular crest orientation consistent with <i>Allosaurus jimmadseni</i> holotype DINO 11541, and the distomedial crest are all comparable to other specimens of <i>Allosaurus</i> .
OMNH 1949	Tibia	<i>Saurophaganax maximus</i>	<i>Allosaurus</i> sp.	Too fragmentary to be certain of its status.
OMNH 2149	Tibia	<i>Saurophaganax maximus</i>	<i>Allosaurus</i> sp.	Astragalar buttress weakly present, distomedial crest comparable to other specimens of <i>Allosaurus</i> .
OMNH 1426	Fibula	<i>Saurophaganax maximus</i>	<i>Allosaurus anax</i>	Referred to <i>A. anax</i> as additional proximomedial fossae are not reported in <i>A. fragilis</i> or <i>A. jimmadseni</i> .
OMNH 1694	Fibula	<i>Saurophaganax maximus</i>	<i>Allosaurus anax</i>	Referred to <i>A. anax</i> as additional proximomedial fossae are not reported in <i>A. fragilis</i> or <i>A. jimmadseni</i> .
OMNH 1695	Fibula	<i>Saurophaganax maximus</i>	<i>Allosaurus anax</i>	Referred to <i>A. anax</i> as additional proximomedial fossae are not reported in <i>A. fragilis</i> or <i>A. jimmadseni</i> .
OMNH 1193	Metatarsal IV	<i>Saurophaganax maximus</i>	<i>Allosaurus</i> sp.	Metatarsals do not appear to be consistently less bowed than those of <i>Allosaurus</i> .
OMNH 1306	Metatarsal IV	<i>Saurophaganax maximus</i>	<i>Allosaurus</i> sp.	Metatarsals do not appear to be consistently less bowed than those of <i>Allosaurus</i> .
OMNH 1464	Metatarsal IV	<i>Saurophaganax maximus</i>	<i>Allosaurus</i> sp.	Metatarsals do not appear to be consistently less bowed than those of <i>Allosaurus</i> .
OMNH 1936	Metatarsal IV	<i>Saurophaganax maximus</i>	<i>Allosaurus</i> sp.	Metatarsals do not appear to be consistently less bowed than those of <i>Allosaurus</i> .

our referrals of allosaur postcranial bones that match neither those of *Allosaurus fragilis* nor *Allosaurus jimmadseni* to *Allosaurus anax* are necessarily tentative. The future discovery of articulated or associated elements that include the diagnostic postorbital will corroborate our referrals of the associated postcranial elements and likely provide additional apomorphic features of *A. anax*. Thus, fully assessing the taxonomic status of *Allosaurus anax* is difficult without additional material. Further excavation of the Kenton quarries may be required to further assess the taxonomic status of the material, but the Kenton 1 Quarry that yielded the *A. anax* holotype has been closed due to the structural instability of the outcrop (Anne Weil pers. comm. 2024).

The estimated mass of *A. anax* (4,634 kg, 3,871 kg, and 3,776 kg), based on circumferences of the three femora that likely belong to the species (OMNH 1371, OMNH 1708, and OMNH 2114 respectively) exceeds the maximum asymptotic body size that Prondvai (2017) estimated for *Allosaurus fragilis* by more than 1,500 kg. A mass estimate for the femur AMNH FARB 680 referred to *Allosaurus fragilis* using this method yielded a mass of 2,681 kg which exceeds this asymptote as well (Campione et al. 2014). However, each of the Kenton 1 *Allosaurus* specimens still exceed this estimate by more than 1,000 kg or 40%. For reference, each of the Kenton 1 *Allosaurus* femora exceed the estimate provided for the *Acrocanthosaurus atokensis* specimen NCSM 14345 as well (Campione et al. 2014). Mass estimation via minimum femoral circumference often provides lower estimates than volumetric estimates (Campione et al. 2014), so these individuals may have been even heavier. Size alone is not of particular taxonomic value (Chure 1995; Loewen 2009), but it may support hypotheses of taxonomic identity based on skeletal autapomorphies when combined with the known ontogenetic stage of a specimen (Atkins-Weltman et al. 2024; Sander et al. 2006).

Paleohistology of a fourth metatarsal that likely belonged to *Allosaurus anax* revealed a structure resembling an external fundamental system (EFS). We cannot fully confirm that this structure extended completely around the external cortex due to diagenetic modification, so we refrain from describing it as a true EFS. However, the poor vascularity, tightly compressed lamellae, and moderate thickness are all consistent with an EFS (Chinsamy 1990; de Ricqlès et al. 2003; Erickson et al. 2004; Horner et al. 1999; Köhler and Moyà-Solà 2009; Lee and O'Connor 2013; Sander et al. 2006; Woodward et al. 2011). It is unlikely to represent an annulus as part of a zone-annulus annual complex because the deeper cortex displays no evidence of annuli. The EFS-like structure suggests that this metatarsal was attaining or had attained skeletal maturity, further suggesting that the individual it belonged to was similarly mature. As such, we conclude that at least one large theropod represented in the

Kenton 1 Quarry is sufficiently mature for taxonomic analysis and comparison. A more detailed analysis comparing the paleohistology of material likely belonging to *Allosaurus anax* to other species of *Allosaurus* will be the subject of future research.

Variation within *Allosaurus* warrants further exploration because the number of referred specimens allows for detailed analyses of individual variation (Carpenter 2010). It is possible that further analyses may indicate that the proposed autapomorphies of *Allosaurus anax* fall within the realm of individual variation within *Allosaurus*. In particular, some external morphological traits appear to correlate with size (Griffin and Nesbitt 2016) and may account for some differences between specimens of different size. *Allosaurus europaeus* was described as the sole representative of the genus outside of North America (Mateus et al. 2006). However, it may lack valid autapomorphies that distinguish it from other species of *Allosaurus*, so a re-assessment of *Allosaurus* material from Europe is required (Evers et al. 2020). A broader review exploring variation across specimens of *Allosaurus* and Allosauroidea would be valuable to parse the specific relationships between these taxa and will be the subject of future work. Additionally, *Allosaurus* may have had highly varied growth strategies that resulted in individuals reaching dramatically different maximum sizes (Bybee et al. 2006; Campione et al. 2014; Ferrante et al. 2021; Griffin and Nesbitt 2016; Prondvai 2017; Myhrvold 2013; Riley Sombathy pers. comm. 2024). This may be correlated with ontogenetic niche partitioning within the population in which size classes performed different ecological roles, much as has been proposed for tyrannosaurs, but further analysis will be required to test this hypothesis (Holtz 2021; Woodward et al. 2020).

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