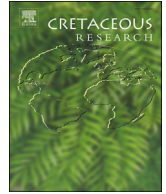




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Dinosaur remains from the Upper Cretaceous (Campanian) of the Western Desert, Egypt

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ABSTRACT

Upper Cretaceous dinosaur remains from Afro-Arabia are rare and mainly restricted to pre-Turonian horizons. Consequently, the discovery of new fossils from Upper Cretaceous deposits in the Western Desert, central Egypt is significant because it adds to the meager record of dinosaurs described from this landmass. The oases of Kharga and Dakhla, Western Desert, Egypt, expose the Quseir Formation (Campanian), with the titanosaurian sauropod *Mansourasaurus shahinae* as the only currently named dinosaur from strata of this age in the entire region. Numerous (~80) other non-avian dinosaur fossils have also been collected from the Quseir Formation, including material that can be referred to Somphospondyli, Titanosauriformes/Titanosauria, and non-avian Theropoda. Among the discoveries from the Dakhla Oasis are the proximal ends of an associated sauropod tibia and fibula and several sauropod caudal vertebrae representing both sub-adult and adult individuals. Middle caudal vertebrae can be referred to Titanosauria on the basis of procoelous centra and anteriorly displaced neural arches. One caudal vertebra even exhibits pneumatic internal structures rarely observed outside of the Upper Cretaceous South American saltasaurines. Dinosaur fossils recovered from the Kharga Oasis include a partial femur and partial cervical vertebra of a sauropod dinosaur and an isolated proximal fibula of a non-avian theropod dinosaur. Taken together, these findings indicate that Late Cretaceous North African ecosystems supported a diversity of non-avian dinosaurs, some demonstrating affinities with South American forms and others (e.g., *Mansourasaurus*) with Eurasian groups. Additional exploration of the uppermost Cretaceous units in southern Egypt offers promise for the discovery of important fossils to better characterize Afro-Arabian biotas generally while also providing important perspectives on non-avian dinosaur faunas near the close of the Mesozoic Era.

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1. Introduction

The terminal Late Cretaceous (Campanian–Maastrichtian) is recognized by geographically distinct non-avian dinosaur faunas, particularly when compared to faunas from earlier in Earth history (e.g., during the breakup of Laurasia and Gondwana in the mid Mesozoic; Bonaparte, 1986; Bonaparte and Kielan-Jaworowska, 1987; Sereno, 1997; Weishampel et al., 2004; Ezcurra and Agnolín, 2012). Recent studies focused on post-Cenomanian

paleobiogeography indicate the presence of potential connections and faunal dispersals between Laurasia and Gondwana, likely via islands and/or intermittently exposed lowstand emergent terrains connecting landmasses (Ezcurra and Agnolín, 2012; Csiki-Sava et al., 2015; Gorscak and O'Connor, 2016; Sallam et al., 2018; Krause et al., 2019). Such paleobiogeographic studies are incomplete due to the restricted sampling of terminal Cretaceous fossils from the African continent by comparison with the fossil record from other Gondwanan landmasses (Jacobs et al., 1996; Krause et al., 2006, 2019; O'Connor et al., 2006). Efforts to address such sampling deficiencies, particularly in northern Africa, reveal that intensified field efforts in historically under-sampled areas hold great promise for yielding important new information (Gorscak et al., 2014, 2017; Sallam et al., 2016, 2018; Longrich et al., 2017; Gorscak and O'Connor, 2019).

For over the last decade, the Mansoura University Vertebrate Paleontology (MUVP) Center has conducted paleontological explorations in the central and southern regions of the Egyptian Western Desert, in the areas near the Dakhla and Kharga oases. The primary purpose of these efforts is to identify fossil-bearing strata, collect vertebrate fossils, and when possible, provide robust age assessments and paleoenvironmental reconstructions for strata in historically under-sampled areas in central and southern Egypt. Work has thus far identified numerous fossil-bearing localities (Fig. 1), yielding dinosaur (e.g., *Mansourasaurus shahinae*; Sallam et al., 2018), crocodyliform (e.g., *Wahasuchus egyptensis*; Saber et al., 2018, 2020), fish (e.g., Claeson et al., 2014; Holloway et al., 2017) and other vertebrate remains (Sallam et al., 2016). These efforts have also increased the total number of other specimens, ranging from fragmentary to complete cranial and postcranial elements from a variety of taxa.

The Upper Cretaceous, and in particular the Campanian–Maastrichtian, dinosaur fossil record from Egypt is restricted to a handful of discoveries represented by isolated remains of mainly titanosaurian sauropods and abelisaurid theropods (Buffetaut et al., 1990; Rauhut and Werner, 1997; Wiechmann, 1999a, 1999b; Smith and Lamanna, 2006). However, the recently described titanosaurian sauropod *Mansourasaurus shahinae* (Sallam et al., 2018), excavated from the Campanian Quseir Formation in the Dakhla Oasis, is represented by both cranial and postcranial remains, making this specimen the most complete dinosaur yet discovered from the terminal Late Cretaceous of Afro-Arabia.

In this contribution, we describe additional sauropod and non-avian theropod dinosaur remains from the Quseir Formation recovered near the villages of Tineida (Dakhla Oasis) and Baris (Kharga Oasis). All fossils yield from distinct localities spanning a large area in the Western Desert (Fig. 1). Although the fossils described here preserve only a limited number of diagnostic features (i.e., they can only be referred to relatively high taxonomic ranks), they exhibit features that are known in select Laurasian and Gondwanan non-avian dinosaurs and add information that representative members of various non-avian dinosaur clades were present in northern Africa near the close of the Cretaceous.

2. Geologic setting

The uppermost Cretaceous (Campanian and Maastrichtian) succession exposed throughout central and southern Egypt in Dakhla and Kharga oases reflects a variety of depositional environments that range from fluvial to brackish and variable marine facies (Klitzsch and Schandelmeier, 1979; Hendriks et al., 1984; Hermina, 1990; Klitzsch and Squyres, 1990; Tantawy et al., 2001; Mahmoud, 2003; O'Connor et al., 2010a). This succession is represented by four major rock units (from oldest to youngest): the Taref,

Qusier, Duwi, and Dakhla formations. These units are accessible in multiple areas near both the Kharga and the Dakhla oases.

All of the non-avian dinosaur materials in the present study were recovered from the Quseir Formation. Localities preserving fossils in this rock unit span from the Dakhla Oasis (near the town of Tineida) in the west to the Kharga Oasis (in the Baris area) to the east and south. The Quseir Formation (lower–middle Campanian) was identified by Youssef (1957) as a unit consisting of alternating variegated claystone, siltstone, and sandstone beds. It overlies the fluvial Taref Formation and is conformably overlain by the shallow marine Duwi Formation. This Quseir Formation was later divided by Hermina (1990) into two formal members: the lower brick-red mudstone and shale dominated Mut Member that contains relatively fewer fossils when compared to the upper variegated shale-dominated El Hindaw Member. Most of the vertebrate fossils were collected from the lower part of the El Hindaw Member, including, fish, turtle, crocodyliform, and dinosaur (e.g., *Mansourasaurus shahinae*) remains, in addition to numerous isolated and moderately preserved indeterminate sauropod and non-avian theropod postcranial axial and appendicular elements (Claeson et al., 2014; Sallam et al., 2016, 2018; Saber et al., 2018). Facies containing fossils represent nearshore-marine to fluvial environments, some of which also include the preservation of petrified wood (Sallam et al., 2016; fig. 3). Moreover, charcoal remains collected from the Quseir Formation in the area gives direct evidence for the occurrence of paleo-wildfires during the Campanian of northern Africa (El Atfy et al., 2016).

3. Materials and methods

All fossils described herein were recovered from the Quseir Formation as isolated elements, except for an associated sauropod tibia and fibula noted below. Sauropods (Figs. 2–3) include one partial cervical vertebra (MUVP 213) and two caudal vertebrae (MUVP 209 and MUVP 206) from the axial skeleton, with an isolated partial left femur (MUVP 181) and the associated proximal ends of a right tibia and fibula (MUVP 182) representing the appendicular skeleton. Non-avian theropod dinosaurs (Fig. 4) are represented by one caudal vertebra (MUVP 199) and a proximal left fibula (MUVP 187). The material described in this contribution was collected as part of the Mansoura University Vertebrate Paleontology Center initiative, in collaboration with Ohio University, University of Southern California, and the Denver Museum of Nature & Science. All specimens are permanently housed at the Mansoura University Vertebrate Paleontology Center (MUVP), Mansoura University, Mansoura, Egypt.

4. Results

4.1. Sauropod dinosaurs

Sauropods are among the most common dinosaurs recovered from the area, with several isolated specimens representing both the postcranial axial and appendicular portions of the skeleton.

4.1.1. Postcranial axial skeleton

MUVP 213 (Fig. 2A–B) is an anterior-to-middle cervical vertebra represented by the isolated left half of the centrum; it is here referred to Somphospondyli/Titanosauriformes. The anterior surface is convex and the posterior surface is concave (i.e., opisthocelous). The centrum is longer (anteroposteriorly) than high (dorsoventrally) (Table 1). Although the posterior half and right side of the centrum are incomplete due to erosion, this damage exposes the camellate internal morphology. Camellate internal organization is consistent with the condition known in most

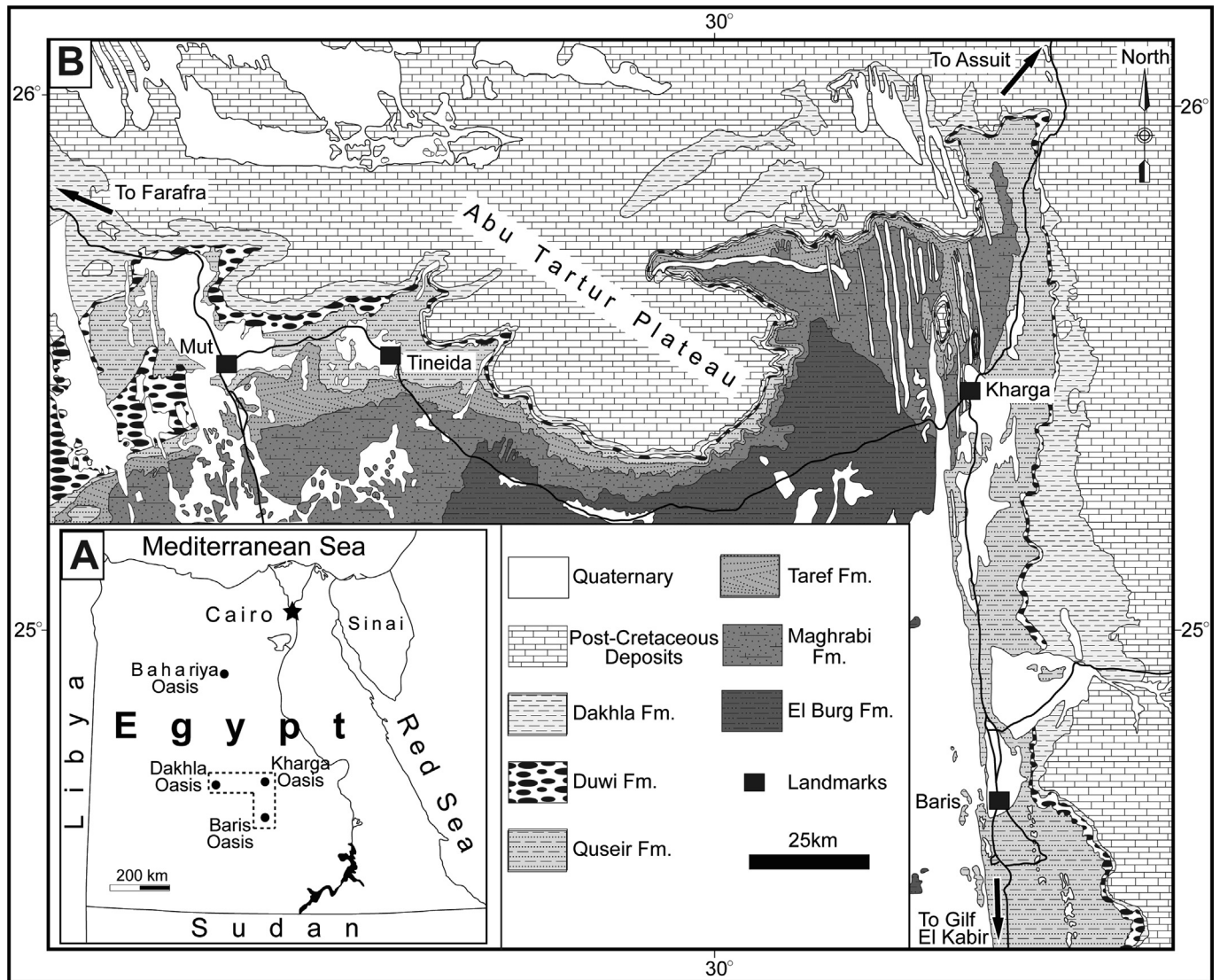


Fig. 1. Location (A) and geologic map (B) of the Dakhla and Kharga oases in the Western Desert, central Egypt, to illustrate main lithological units of the Upper Cretaceous–Paleogene succession. After Sallam et al. (2016).

titanosauriforms (Wilson, 2002), and specifically, as exhibited by Somphospondyli more broadly (D’Emic, 2012). The neural arch is incomplete. The neurocentral suture is not visible between the preserved pedicles and the centrum, indicating that the specimen likely represents a skeletally mature individual. Due to the poor preservation, there is no evidence of pneumatic or other surface features (e.g., vertebral laminae). Comparisons to the Upper Cretaceous Galula Formation titanosaurs of Tanzania, *Rukwatictan bisepultus* and *Shingopana songwensis*, are limited as most of their recovered cervical vertebrae are from the posterior region of the series with preserved portions of the neural arch which MUV 213 lacks (Gorscak et al., 2014, 2017). The partial anterior cervical

vertebra of *Shingopana* generally resembles MUV 213 yet both lack any distinguishing traits for further assessments. A similar situation is present with Late Cretaceous European taxa as the anterior cervical vertebra of *Lohuecotitan, pandafilandi* (Díez Díaz et al., 2016) and *Ampelosaurus ataxis* (Le Loeuff, 2005) are generally similar but with no significant comparable/preserved traits or also too incompletely preserved, respectively, for further definite statements.

MUV 209 (Fig. 2C-F) is an isolated, poorly preserved middle caudal centrum of a titanosaurian sauropod. The centrum is procoelous and is longer (anteroposteriorly) than high (dorsoventrally) (Table 1), with the latter dimension being larger than the transverse

Table 1

Measurements of dinosaur vertebrae are illustrated in Figs. 2 and 4; measurements are in mm.

Element		Centrum length	Centrum width (anterior)	Centrum height (anterior)	Centrum width (posterior)	Centrum height (posterior)
Titanosauria	MUV 213	250.0	50.0	80.0	–	140.0
	MUV 209	75.6	–	–	37.7	42.8
	MUV 206	~58.4	~50.6	~41.4	~50.0	~42.1
Theropoda	MUV 199	69.3	56.4	64.4	~53.0	~57.6

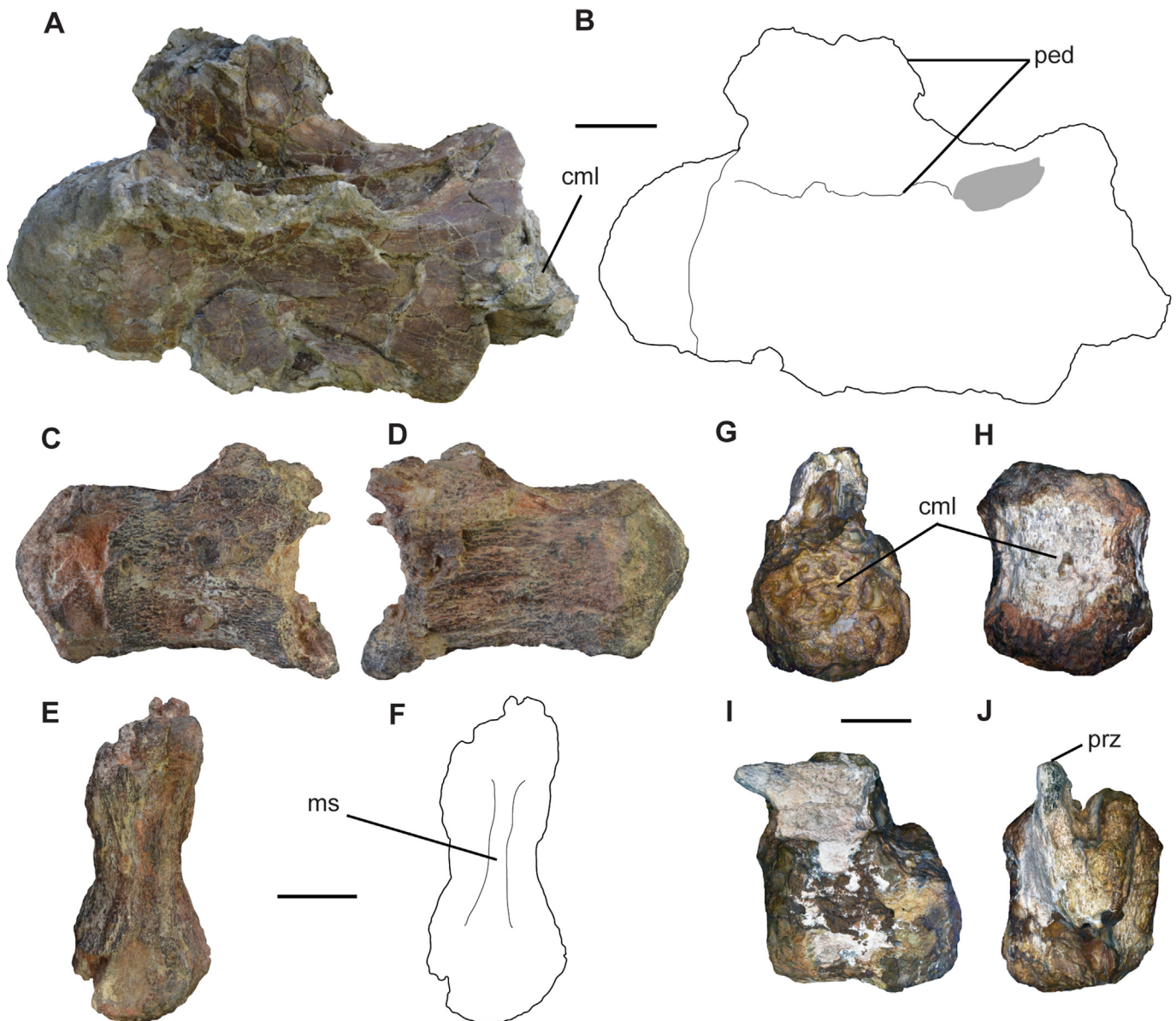


Fig. 2. Titanosaurian cervical vertebra (MUV P 213) in left lateral view (A) with corresponding line drawing (B); titanosaurian caudal vertebra (MUV P 209) in right lateral (C), left lateral (D) and ventral (E) views, with corresponding line drawing of ventral view (F); titanosaurian caudal vertebra (MUV P 206) in posterior (G), ventral (H), left lateral (I), and dorsal (J) views. **Abbreviations:** **cml**, camellate texture, **ms**, midline sulcus, **prz**, prezygapophysis, **ped**, pedicles. Scale bars = 2 cm.

width. The neurocentral suture is not visible, suggesting that the specimen represents a skeletally mature element. No chevron facets are preserved. The ventral and lateral surfaces are slightly concave, with the centrum transversely compressed at mid-length and the ventral surface exhibiting a narrow midline sulcus, a feature absent in the titanosaurian *Rukwatitan bisepultus* from the Upper Cretaceous (potentially Campanian) Namba Member of the Galula Formation of Tanzania (Gorscak et al., 2014), *Atsinganosaurus velauciensis* from the Upper Cretaceous Begudian sandstones of France (Díez Díaz et al., 2018), and *Lirainosaurus astibiae* from the Upper Cretaceous Laño Quarry of Spain (Díez Díaz et al., 2013). These features support the referral of MUV P 209 to Titanosauria (Wilson, 2002; D'Emic, 2012). There is no evidence of pneumatic or other surface features.

MUV P 206 (Fig. 2G–J) (Table 1) is another procoelous middle caudal vertebra with eroded surfaces. The centrum is quadrangular in shape with slight lateral compression and a nearly flat ventral

surface with no ventrolateral ridges or midline sulcus, similar to *Atsinganosaurus*, *Lirainosaurus*, and *Rukwatitan* but differs from MUV P 209 mentioned above. The centrum has camellate internal texture, a feature only known in a limited number of saltasaurine titanosaurs from the Upper Cretaceous (Campanian–Maastrichtian) of South America (e.g., *Saltasaurus*, *Rocasaurus*; Cerda et al., 2012; Zurriaguz and Cerda, 2017) but the specimen described here differs from saltasaurine titanosaurs in being poorly procoelous and in lacking the deep ventral excavation and dorsoventrally restricted vertebral centrum. This appears to be the first record of this otherwise rare titanosaurian trait in an Afro-Arabian form. The left prezygapophysis is mostly preserved and projects anteriorly with an elliptical facet that faces medially. The specimen is relatively short compared to other African titanosaurs (e.g., *Rukwatitan*, *Malawisaurus*). The neurocentral suture is not visible, suggesting that the specimen represents a skeletally mature element. The neural arch is mostly incomplete, preserving

only the pedicles. The pedicle is attached only along the anterior half of the centrum, consistent with a referral to titanosauriforms (Wilson, 2002). There is no evidence of external pneumatic or other surface features as preserved. A camellate caudal vertebra may indicate either the presence of a taxon that exhibits close affinities with South American titanosaurs or merely reflects a product of convergence; due to the absence of additional skeletal material associated with this single vertebra, neither hypothesis can be further evaluated at present.

4.1.2. Appendicular skeleton

A fragmentary left femur (MUVP 181; Fig. 3A-B) consists of a shaft with incomplete proximal and distal ends (Table 2). Although the specimen was altered through gypsum replacement, it is apparent that both proximal and distal ends were transversely expanded. The anterior and posterior surfaces are smooth and gently curved longitudinally. The lateral margin forms a smooth S-shape with the proximal end of the curve approaching the proximolateral bulge, or medial deflection, commonly exhibited by titanosauriforms (e.g., Wilson, 2002; D'Emic, 2012; Mannion et al., 2013); however, the lateral margin of the femora of *Atsinganosaurus*, *Lirainosaurus*, *Lohuecotitan* appear straighter than MUVP 181 (Diez Díaz et al., 2013, 2016, 2018). The cross section of the femur at midshaft is elliptical with the long axis oriented transversely and a width (153.5 mm) nearly twice the anteroposterior dimension (76.7 mm), another feature supporting a titanosauriform referral (Wilson, 2002; Mannion et al., 2013). The poorly preserved fourth

trochanter is barely noticeable on the posterior surface of the shaft, close to the medial edge. The proximal and distal ends are not preserved, preventing referral of MUVP 181 to lower taxonomic levels (e.g., Titanosauria) within titanosauriforms; indeed, key features like the shape of femoral head (Curry Rogers 2009), elevation of the abductor crest and beveling of the femoral distal condyles (Wilson, 2002; D'Emic, 2012; and; Mannion et al., 2013) cannot be evaluated in MUVP 181. For comparison, MUVP 181 is approximately half the size of the femur recovered from the Maastrichtian section of the Ammonite Hill Member of the Dakhla Formation (Rauhut and Werner, 1997), and suggests for the presence of different size sauropods within the region.

MUVP 182 consists of the associated proximal ends of a right tibia (Fig. 3C-E) and fibula (Fig. 3F-H). The tibia and fibula are interpreted as belonging to the same individual based on in-situ associations and relative size of the elements (Table 2). The tibia is transversely compressed and missing the shaft and the distal end. The proximal end is slightly eroded. The anteriorly-directed cnemial crest is represented by an expanded, rounded ridge that gently slopes distally from the proximal articular surface. The medial surface is smooth and gently convex with no evidence of other surface features. The cnemial crest also delimits a shallow, laterally oriented concavity (i.e., the lateral fossa) that accommodates the anteromedial surface of the proximal end of the associated fibula. The fibular crest, which articulates with the fibula, occupies the lateral surface immediately posterior to the lateral fossa. The right fibula is preserved, but the bone is missing along most of the shaft

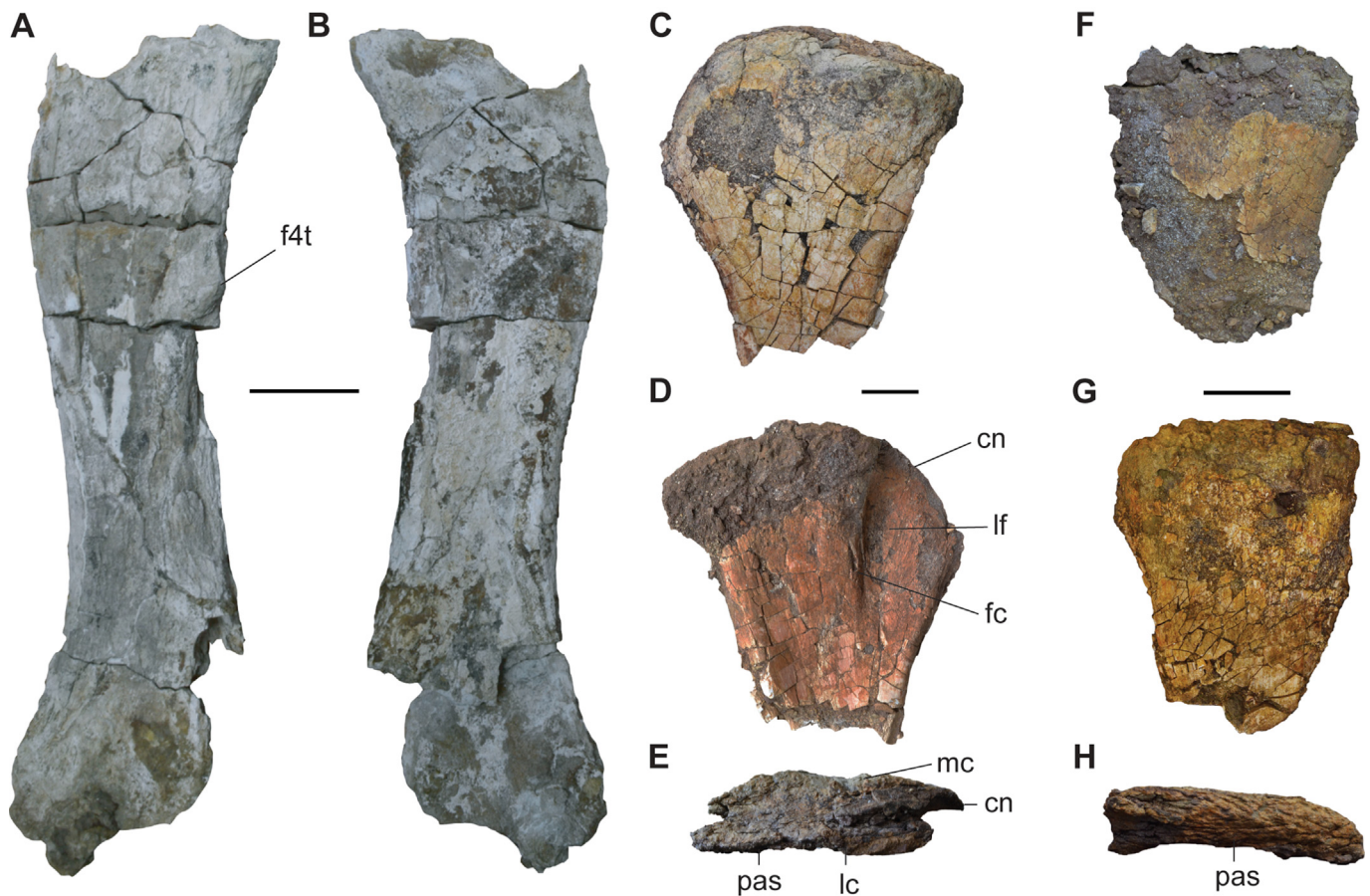


Fig. 3. Titanosauriform left femur (MUVP 181) in posterior (A) and anterior (B) views; titanosaurian right tibia (MUVP 182) in medial (C), lateral (D) and proximal (E) views; titanosaurian right fibula (MUVP 182) in medial (F), lateral (G) and proximal (H) views. **Abbreviations:** **cn**, cnemial crest; **fc**, fibular crest; **f4t**, fourth trochanter; **lc**, lateral condyle; **lf**, lateral fossa; **mc**, medial condyle; **pas**, proximal articular surface. Scale bars = 5 cm.

and the distal end; its condition parallels the preservation of the tibia. The proximal articular surface is transversely compressed. The medial and proximal surfaces are poorly preserved, preventing conservation of the fibular knob on the anteromedial surface (Silva Junior and Marinho, 2019). The lateral surface is slightly convex with no other surface features visible, whereas the medial surface appears rugose posteriorly, where the fovea ligamentosa inserted. As the tibia lacks an additional articular ridge with the fibula (the second cnemial crest as described in Bonaparte et al., 2000), MUVP 182 is here conservatively referred to Somphospondyli with a possibility that it represents a titanosaurian sauropod (Mannion et al., 2013). Although compressed and partially preserved, MUVP 182 resembles the same elements recovered for *Ampelosaurus*, *Atsinganosaurus*, *Lirainosaurus*, and *Lohuecotitan* of Late Cretaceous Europe (Le Loeuff, 2005; Díez Díaz et al., 2013, 2016, 2018), but no meaningful characters are preserved or present to confidently suggest a close association or deviation away from the general titanosaurian condition.

4.2. Non-avian theropod dinosaurs

4.2.1. Postcranial axial skeleton

MUVP 199 (Fig. 4A-E; Table 1) is a well-preserved caudal vertebra of a theropod dinosaur. The majority of the centrum is intact, with the posterior articular surface and the posterior portion of the right side with damaged surface bone. The centrum is amphicoelous–amphiplatyan (i.e., the anterior surface is slightly concave, whereas the posterior surface is slightly less so), with striations along both lateral and ventral surfaces. The centrum is spool-shaped, longer (anteroposteriorly) than high (dorsoventrally) and taller (dorsoventrally) than wide. The neural arch is mostly incomplete, being represented only by the ventral-most portions of the pedicles. Although the neural arch is incomplete, it appears that the neurocentral suture is closed and barely visible, suggesting that the specimen represents a skeletally mature element. There is no evidence of pneumatic or other surface features.

4.2.2. Appendicular skeleton

MUVP 187 (Fig. 4F-J; Table 2) is the proximal portion of a left fibula. It is a moderately well preserved specimen, though covered in a thin layer of gypsum. The bone is incomplete distally, with a lateral surface that is smooth and gently curved. On the anterior surface just below the proximal end, there is an elevated protuberance that serves as the attachment site for the iliofibularis muscle and is prominent as in *Majungasaurus*, *Xenotarsosaurus*, *Genusaurus*, *Rajasaurus*, and *Aucasaurus* (Carrano, 2007). Also, a proximally placed ridge serves as the attachment for the interosseous membrane. It passes from anterolateral then gradually extends to the center of the medial surface where it stops proximal to the insertion tubercle of the iliofibularis muscle. The well-defined medial fossa is present posterior to the ridge of attachment of the

interosseous membrane. It is a wide, slightly deep fossa that closely resembles the condition in the abelisaurid *Majungasaurus* (Carrano, 2007). The anterior and posterior edges of the shaft are acute, with the medial surface being concave and suitable for contact with the lateral surface of the tibia. The medial surface of the shaft also exhibits a small groove that serves as a contact for the lateral surface of the tibia (i.e., it forms a tibial facet).

5. Discussion

Afro-Arabia was once part of the supercontinent of Gondwana and became increasingly isolated from other southern landmasses by the end of the Cretaceous. How such landmass separation influenced resident biotas during the Late Cretaceous is not entirely resolved. Afro-Arabia preserves rare deposits that represent the uppermost Cretaceous, no doubt contributing to the apparent low diversity of dinosaurian taxa during this time when compared with other Gondwanan landmasses (e.g., South America) with relatively more complete fossil records. Several attempts have been made to recover vertebrate fossils from the Upper Cretaceous of Africa in order to address the lack of knowledge, with some success to date (e.g., Buffetaut et al., 1990; Jacobs et al., 1996; Rauhut and Werner, 1997; Schulp et al., 2000, 2008; O'Connor et al., 2006, 2010a, 2010b, 2019; Gorscak et al., 2014, 2017; Sertich et al., 2006, 2013; Sertich and O'Connor, 2014; Sallam et al., 2016, 2018; Longrich et al., 2017, 2020; Saber et al., 2018).

The Dakhla and Kharga oases, Western Desert, Egypt preserve abundant Upper Cretaceous exposures, providing the potential to better sample this important temporal interval on the African continent. Ongoing efforts document that these units now yield the taxonomically most diverse continental vertebrate fauna yet known from the latest Cretaceous of the Middle East, with dinosaur and other vertebrate materials derived from the Campanian–Maastrichtian Quseir and Duwi formations. In addition to the new materials described herein, other important discoveries from the area include one partial skeleton described to date (*Mansourasaurus shahinae*: Sallam et al., 2018) and two other partial titanosaurian skeletons currently under study (Gorscak et al., 2020; Salem et al., 2020).

To this record, we now add (Table 3) one cervical vertebra (MUVP 213), two caudal vertebrae (MUVP 209 and MUVP 206), one femur (MUVP 181), and an associated tibia and fibula (MUVP 182) referable to different taxonomic levels within Sauropoda, and one caudal vertebra (MUVP 199) and one fibula (MUVP 187) referable to non-avian Theropoda. All specimens were recovered from localities near Dakhla and Kharga oases. Most of the dinosaur fossils from the Quseir Formation were recovered from the El Hindaw Member, except for the associated sauropod tibia and fibula (MUVP 182) that are here considered the first dinosaur remains to be recovered from the Mut Member. The new materials constitute some of the first identifiable dinosaur materials from southern Egypt and pertain to somphospondylia/titanosauriform/titanosaurian sauropods (e.g.,

Table 2
Measurements of dinosaur limb bones are illustrated in Figs. 3 and 4; measurements are in mm.

Element		Maximum breadth				Shaft
		Proximal		Distal		
		Transverse	Ant-post.	Transverse	Ant-post.	
Sauropoda	MUVP 181	90.0	–	80.0	–	190.0
Titanosauria	MUVP 182 (tibia)	65.0	250.0	–	–	–
	MUVP 182 (fibula)	30.0	140.0	–	–	–
Theropoda	MUVP 187	5.0	25.0	–	–	130.0

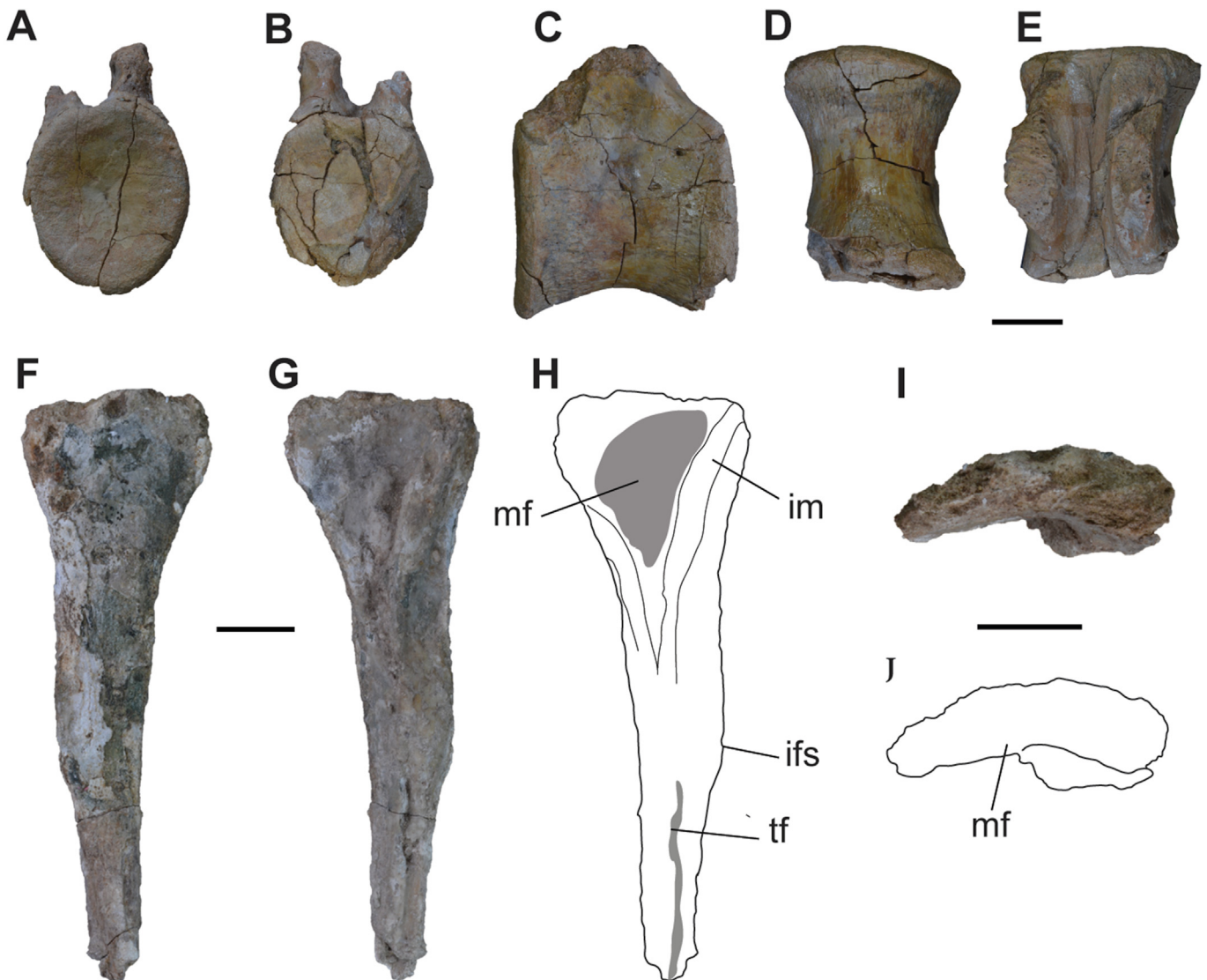


Fig. 4. Theropoda *indet.* caudal vertebra (MUV 199) in anterior (A), posterior (B), left lateral (C), ventral (D) view, and dorsal (E) views; Left theropod fibula (MUV 187) in lateral view (F), medial view (G) with corresponding line drawing (H), and in proximal view (I) with corresponding line drawing (J). **Abbreviations:** **ifs**, scar for iliofemoralis muscle; **im**, attachment for interosseus membrane; **mf**, medial fossa; **tf**, tibial facet. Scale bars = 2 cm.

procoelous centra with anteriorly displaced neural arches on the caudal vertebrae, lack of second cnemial crest on the tibia) and non-avian theropods.

The dinosaur remains recovered during MUV 199 field excavations were found along with other vertebrate fossils (e.g., turtles, crocodiles, fishes). Although most fossils are fragmentary, mainly isolated, and no doubt belong to different individuals (e.g., specimens are from different field localities), they still hold paleontological significance. Documenting the presence of non-avian theropods and titanosaurs, the latter of which includes a caudal vertebra exhibiting camellate internal morphology that is otherwise only known from a limited number of saltasaurine titanosaurs (e.g., *Saltasaurus*, *Rocasaurus*; Cerda et al., 2012; Zurriaguz and Cerda, 2017) from the Upper Cretaceous of Patagonia, among dinosaurs from the uppermost Cretaceous of Africa is consistent with a degree of general faunal similarity between Africa and South America (Serenó et al., 2004; Smith and Lamanna, 2006 and Longrich et al., 2017). This perhaps weakens the idea of African faunal isolation, a scenario involving only the persistence of relatively older lineages

into the latest Cretaceous. It seems, to some extent, that northern African faunas may have included some taxa more closely related to Eurasian forms (e.g., *Mansourasaurus*, potentially MUV 182), in addition to others exhibiting affinities with South American forms (e.g., MUV 206: camellate titanosaurian caudal vertebra similar to Upper Cretaceous South American saltasaurine titanosaurs), and eastern African forms (e.g., MUV 206: middle caudal vertebrae lacking ventrolateral ridges and a midline sulcus as in *Rukwatitan*; yet this trait is variable within titanosaurs and also present in some European forms). Whether this inference of an apparent mixed biogeographic signal holds is dependent on the recovery of more complete, phylogenetically informative fossil material for a more rigorous evaluation.

Somphospondyli specimens including an associated tibia-fibula, a titanosauriform femur, and titanosaurian caudal vertebrae are documented herein and described confidently for the first time from central Egypt. The proximal left fibula (MUV 187) of a non-avian theropod exhibits some affinities with abelisaurids, a group now documented in the southern Western Desert for the first time.

Table 3

Faunal list of dinosaur fossils discovered from the Upper Cretaceous (Campanian –Maastrichtian) of Egypt and their different taxonomic representatives.

Reference	Material	Taxon	Locality	Formation	Stage	
Hendriks et al., 1984	Bone remains	Dinosaur	Abu Tartur Plateau (Dakhla Oasis)	Quseir Fm.	Campanian	
Rauhut and Werner, 1997	Left femur	Sauropod, ?Brachiosaurid	Ammonite Hill Member (Dakhla Oasis)	Dakhla Fm.	Maastrichtian	
Churcher and De Iuliis, 2001	Bone remains	Cf. <i>Spinosaurus</i> , theropod	Wadi el-Battikh (Gebel Abu Tartur)	Quseir Fm.	Campanian	
Smith and Lamanna, 2006	Tooth	Theropod, Abelisaurid	Near Idfu (Nile Vally)	Duwi Fm.	Maastrichtian	
Moawad et al., 2008	Jaw with teeth & disk bones	?Dinosaur	Dakhla Oasis	Dakhla Fm.	Maastrichtian	
Sallam et al., 2016	Isolated axial and appendicular remains	Sauropods & Theropods	Dakhla & Kharga oases	Quseir Fm.	Campanian	
Sallam et al., 2018	Partial skeleton	Titanosauria: <i>Mansourasaurus shahinae</i>	Dakhla Oasis	Quseir Fm.	Campanian	
Present Study	MUVP 213	anterior-middle cervical vertebra	Somphospondyli/ Titanosauriform	Baris (Kharga Oasis)	Hindaw Member, Quseir Fm.	Campanian
	MUVP 209	middle caudal vertebral centrum	Titanosaurian indet, Sauropod	Tineida (Dakhla Oasis)		
	MUVP 206	middle caudal vertebra	Titanosauria, saltasaurine	Tineida (Dakhla Oasis)		
	MUVP 181	Left femur	Sauropod	Baris (Kharga Oasis)		
	MUVP 182	Associated proximal ends of a right tibia and fibula	Titanosauriform, Sauropod	Tineida (Dakhla Oasis)	Mut Member, Quseir Fm.	
	MUVP 199	caudal vertebra	Theropod	Tineida (Dakhla Oasis)	Hindaw Member, Quseir Fm.	
	MUVP 187	left fibula	Cf. Abelisaurid, Theropod	Baris (Kharga Oasis)		

The only other occurrence of Abelisauridae from the entire region is a single tooth noted from the Duwi Formation in the Eastern Desert (Smith and Lamanna, 2006). Abelisauridae are poorly recorded from the Upper Cretaceous of the African continent, represented by isolated teeth from Morocco (phosphates of the Ouled Abdoun Basin; Buffetaut et al., 2005), Saudi Arabia (Adaffa Formation; Kear et al., 2013), and Tanzania (Galula Formation, Rukwa Rift Basin; O'Connor et al., 2006), a partial left dentary with three teeth (phosphates of the Ouled Abdoun Basin; Longrich et al., 2017), and a partial, yet undescribed skull (Sertich et al., 2013).

The growing collection of dinosaur (and other vertebrate) material from the Dakhla and Kharga oases in Egypt helps to illuminate global faunal changes and dinosaur evolution during the latest Cretaceous. Ongoing work focused on describing a partial sauropod skeleton from the Quseir Formation, with continued exploration of the areas surrounding Dakhla and Kharga oases, offer great promise for better developing and formally assessing paleobiogeographic models/hypotheses during the latter stages of the Cretaceous.

6. Concluding remarks

New fossils from Upper Cretaceous deposits in the Western Desert, central Egypt constitute some of the first identifiable dinosaur materials that pertain to somphospondyli/titanosauriform/titanosaurian sauropods and non-avian theropods. Interestingly, one caudal vertebra exhibits camellate internal morphology that is otherwise only known from a limited number of saltasaurine titanosaurs (e.g., *Saltasaurus*, *Rocasaurus*; Cerda et al., 2012; Zurriaguz and Cerda, 2017) from the Upper Cretaceous of Patagonia whereas other sauropod fossils bear some superficial similarities to other African and/or European taxa from this era. Overall these findings indicate that Late Cretaceous North African ecosystems supported a diversity of non-avian dinosaurs, some demonstrating affinities with South American forms and others (e.g., *Mansourasaurus*) with Eurasian groups, with a faunal composition seemingly distinct from other Late Cretaceous African ecosystems (e.g., Galula Formation of Tanzania).

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