

Original Article

NEW TITANOSAURIFORM SAUROPOD DINOSAUR MATERIAL FROM THE CENOMANIAN OF MOROCCO: IMPLICATIONS FOR PALEOECOLOGY AND SAUROPOD DIVERSITY IN THE LATE CRETACEOUS OF NORTH AFRICA

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Abstract: Titanosauriform sauropod dinosaurs are widely regarded as the most diverse and abundant large herbivores in Cretaceous paleoecosystems of Gondwanan landmasses. Nevertheless, remains of these animals are scarce in Late Cretaceous deposits of continental Africa and the then-conjoined Arabian Peninsula. Here we describe two new titanosauriform fossils from the lower Upper Cretaceous (Cenomanian) ‘Kem Kem beds’ of Morocco that improve our understanding of the morphology and paleoecology of Afro-Arabian members of this clade. One specimen is a nearly complete, well-preserved anterior dorsal vertebra that pertains to a large-bodied member of Somphospondyli, possibly to a basal titanosaurian. The second specimen is a partial ischium that is not identifiable beyond Somphospondyli; nevertheless, the element is significant in exhibiting numerous tooth marks that we attribute to a very large carnivorous dinosaur, probably a carcharodontosaurid or *Spinosaurus*. These feeding traces constitute direct evidence that sauropods were a food source for at least one African Late Cretaceous theropod. It is presently uncertain whether or not the new titanosauriform elements pertain to any of three named genera from the early Late Cretaceous of Africa (*Aegyptosaurus*, *Paralititan*, and *Angolatitan*), or whether they represent previously undescribed taxa.

Key Words : Dinosauria, Sauropoda, Titanosauriformes, Somphospondyli, Late Cretaceous, Cenomanian, Africa, Morocco, ‘Kem Kem beds,’ paleoecology

INTRODUCTION

Titanosauriform sauropod dinosaurs were extraordinarily diverse and abundant in Cretaceous paleoecosystems of the former Gondwanan supercontinent (Curry Rogers, 2005; Wilson, 2005, 2006; González Riga, 2011; Mannion and Calvo, 2011; D’Emic, 2012). Nevertheless, the fossil record of the clade in the Late Cretaceous of continental Africa and the then-conjoined Arabian Peninsula (‘Afro-Arabia’) is meager compared to those of most other Gondwanan landmasses (Mannion, 2009), including Australia (Molnar, 2001; Molnar and Salisbury, 2005; Salisbury *et al.*, 2006; Hocknull *et al.*, 2009), Indo-Pakistan (Huene and Matley, 1933; Jain and Bandyopadhyay, 1997; Wilson and Upchurch, 2003; Wilson *et al.*, 2005, 2009, 2011a; Malkani, 2006), Madagascar (Curry Rogers and Forster, 2001, 2004; Curry Rogers, 2009; Curry Rogers *et al.*, 2011), and especially South America (Huene, 1929; Bonaparte, 1996; Powell, 2003; Martínez *et al.*, 2004; Salgado and Coria, 2005; Salgado and Bonaparte, 2007; Novas, 2009; Carballido *et al.*, 2011; González Riga, 2011). Only three titanosauriform taxa—the non-titanosaurian somphospondylan or titanosaurian *Angolatitan* (Mateus *et al.*, 2011) and the titanosaurians *Aegyptosaurus* (Stromer, 1932) and *Paralititan* (Smith *et al.*, 2001)—have been named from the Afro-Arabian Late Cretaceous. The former taxon is based on a well-preserved right scapula and forelimb from the Turonian Itombe Formation of northwestern

Angola, whereas the latter two are definitively known only from partial postcranial skeletons from the Cenomanian Bahariya Formation of Egypt’s Bahariya Oasis; that of *Aegyptosaurus* was destroyed during World War II along with all other dinosaurian material that had been recovered from Bahariya by that time (Dehm, 1956; Sereno *et al.*, 1996; Nothdurft *et al.*, 2002; Smith *et al.*, 2006). Another incomplete titanosauriform skeleton has been collected from the Campanian Baris Formation of the Kharga Oasis, Egypt (Brinkmann and Buffetaut, 1990; Wiechmann, 1999a, b; MCL, pers. obs.) but has yet to be formally described. Furthermore, a titanosauriform hindlimb lacking the tarsus and pes is known from Maastrichtian nearshore marine sediments in Morocco (Pereda Suberbiola *et al.*, 2004). Other, mostly isolated and fragmentary titanosauriform or probable titanosauriform body fossils have been reported from the Cenomanian of Egypt (Stromer, 1932, 1936; Schweitzer *et al.*, 2003), Morocco (Russell, 1996; Sereno *et al.*, 1996; Kellner and Mader, 1997; Cavin *et al.*, 2010; Mannion and Barrett, 2013), Niger (Lapparent, 1960; Sereno *et al.*, 2004), and Sudan (Buffetaut *et al.*, 1990; Rauhut, 1999), the Coniacian (Broin *et al.*, 1974) and Maastrichtian (Lapparent, 1954; Taquet, 1976) of Niger, the Santonian of South Africa (Kennedy *et al.*, 1987; Buffetaut, 1988), the Campanian (Churcher and Russell, 1992; Churcher, 1995, 1999) and Maastrichtian (Rauhut and Werner, 1997) of Egypt, the Campanian-Maastrichtian of Saudi Arabia (Hughes *et al.*, 1999; Hughes and Johnson, 2005; Kear *et al.*,

2008, 2009, 2013), the Maastrichtian of Jordan (Wilson *et al.*, 2006; D'Emic and Wilson, 2012; O'Connell *et al.*, 2012) and Oman (Schulp *et al.*, 2008), and the Upper Cretaceous (?Turonian-early Campanian; O'Connor *et al.*, 2011) of Kenya (Arambourg and Wolff, 1969; Sertich *et al.*, 2006). Additional titanosauriform remains, including a semi-articulated partial skeleton, have been recovered from the Galula Formation of Tanzania (O'Connor *et al.*, 2006; Gorscak *et al.*, 2012, in press); nevertheless, the precise age of these deposits within the 'middle' Cretaceous (Aptian-Turonian, ~126-90 Ma according to Walker *et al.* [2012]) remains unresolved (Roberts *et al.*, 2004, 2010; O'Connor *et al.*, 2010).

Here we describe two new, isolated titanosauriform skeletal elements recovered from the Cenomanian 'Kem Kem beds' of Morocco: a nearly complete anterior dorsal vertebra and a partial ischium. The former specimen is important in that it is among the best-preserved, most morphologically informative titanosauriform elements yet recovered from the Upper Cretaceous of Afro-Arabia, whereas the latter is significant in that it constitutes direct evidence that African Late Cretaceous titanosauriforms were a food source for at least one contemporaneous large theropod.

Institutional Abbreviations

BSP, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **CGM**, Egyptian Geological Museum, Cairo, Egypt; **FMNH**, Field Museum of Natural History, Chicago, USA; **GMNH-PV**, Gunma Museum of Natural History, Tomioka, Japan; **OCP**, Laboratoire de Paléontologie, Office Chérifien des Phosphates, Khouribga, Morocco; **PMU**, Palaeontological Museum, Uppsala, Sweden; **TUB**, Technische Universität Berlin, Berlin, Germany.

Anatomical Abbreviations

acdl, anterior centrodiapophyseal lamina; **apcdl**, accessory posterior centrodiapophyseal lamina; **cd**, anterior articular condyle; **cdf**, centrodiapophyseal fossa; **cpof**, centropostzygapophyseal fossa; **cpol**, centropostzygapophyseal lamina; **cprf**, centroprezygapophyseal fossa; **cprfl**, centroprezygapophyseal fossa lamina; **cpri**, centroprezygapophyseal lamina; **ct**, posterior articular cotyle; **dpc**, deltopectoral crest; **epri?**, epipophyseal-prezygapophyseal lamina?; **fh**, femoral head; **hy?**, hyposphene?; **mc**, medial condyle; **ml**, median lamina; **nc**, neural canal; **ns**, neural spine; **pcdl**, posterior centrodiapophyseal lamina; **pcpl**, posterior centroparapophyseal lamina; **pf**, pneumatic fossa; **plb**, proximolateral

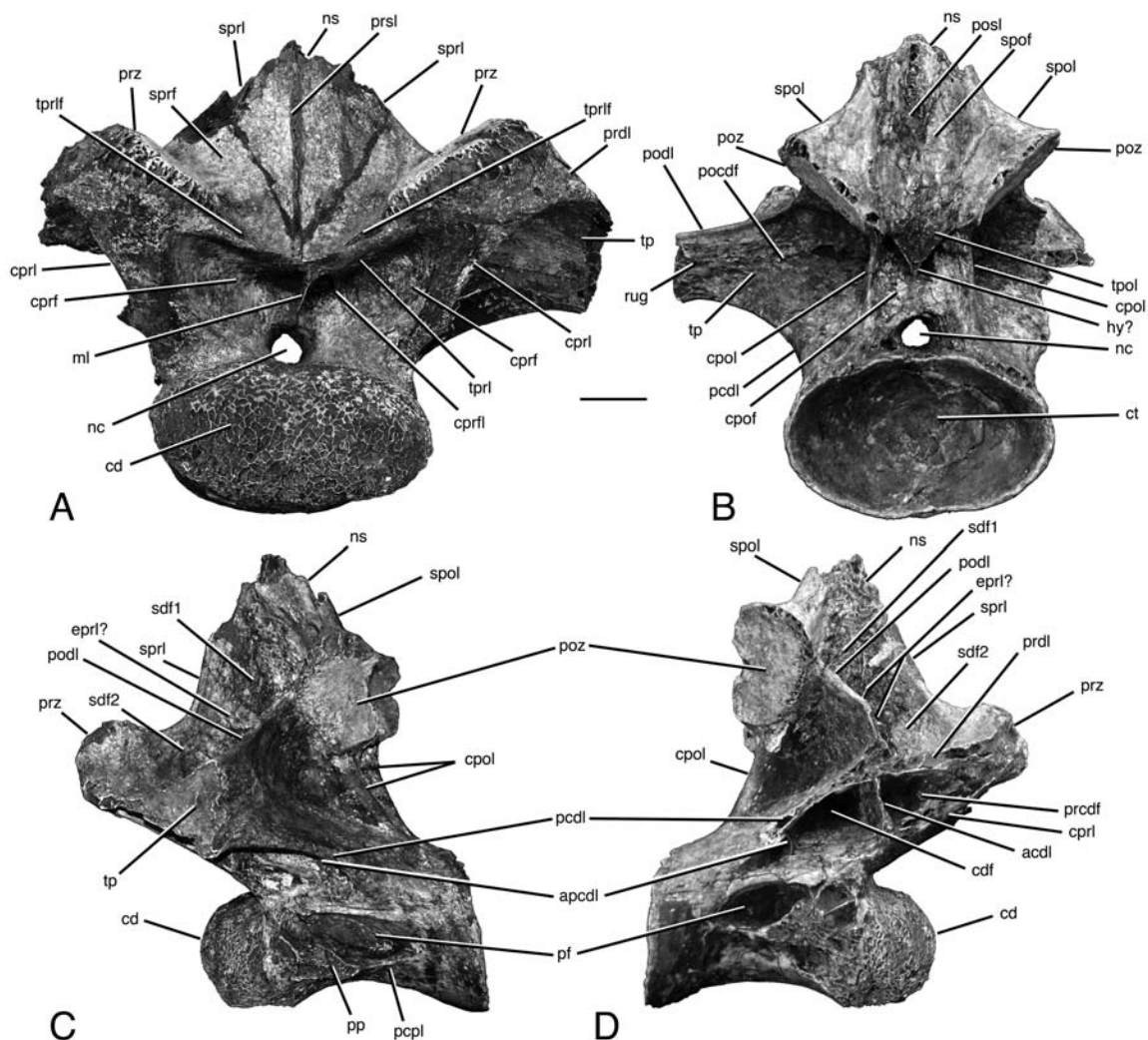


FIGURE 1. Titanosauriform anterior dorsal vertebra (GMNH-PV 2399) in (A) anterior; (B) posterior; (C) left lateral; (D) right lateral; (E) dorsal; (F) ventral; (G) left dorsolateral; and (H) right dorsolateral views. Scale bars equal 10 cm. Abbreviations see text.

‘bulge’; **plc**, proximolateral corner; **pmp**, proximomedial process; **pocdf**, postzygapophyseal centrodiapophyseal fossa; **podl**, postzygodiapophyseal lamina; **posl**, postspinal lamina; **poz**, postzygapophysis; **pp**, parapophysis; **prcdf**, prezygapophyseal centrodiapophyseal fossa; **prdl**, prezygodiapophyseal lamina; **prsl**, prespinal lamina; **prz**, prezygapophysis; **rug**, rugosities; **sdf1**, spinodiapophyseal fossa 1; **sdf2**, spinodiapophyseal fossa 2; **spof**, spinopostzygapophyseal fossa; **spol**, spinopostzygapophyseal lamina; **sprf**, spinoprezygapophyseal fossa; **sprl**, spinoprezygapophyseal lamina; **tp**, transverse process; **tpol**, intrapostzygapophyseal lamina; **tprl**, intraprezygapophyseal lamina; **tprlf**, intraprezygapophyseal lamina fossa.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1887

SAUROPODA Marsh, 1878

TITANOSAURIFORMES Salgado, Coria, and Calvo, 1997

SOMPHOSPONDYLI Wilson and Sereno, 1998

Referred Specimens—GMNH-PV 2399, a nearly complete, well-preserved anterior dorsal vertebra (Figs. 1-3, 5); GMNH-PV 2314, a partial right ischium (Fig. 4).

Locality—Kem Kem region, southeastern Morocco. More precise locality information is not available, as the specimens

were commercially collected and purchased by one of us (YH) in 2008 for the GMNH-PV collection at the Tucson Gem and Mineral Show in Tucson, Arizona (USA). As far as we are aware, the specimens were not associated in the field and as such should be regarded as belonging to separate titanosauriform individuals.

Horizon and Age—Despite our incomplete understanding of their geographic provenance, GMNH-PV 2399 and GMNH-PV 2314 can be attributed to the continental, predominantly red sandstones informally known as the ‘Kem Kem beds’ (i.e., the Ifezouane and Aoufous formations of Cavin *et al.*, 2010). These strata are generally regarded as early Late Cretaceous (Cenomanian) in age based on their vertebrate fossil (especially ichthyofossil) content and their relationship to stratigraphically overlying upper Cenomanian-Turonian limestones (see Cavin *et al.*, 2010 and references therein).

DESCRIPTION AND COMPARISONS

Anterior Dorsal Vertebra

GMNH-PV 2399 is a large (see Table 1 for measurements), nearly complete, well-preserved titanosauriform sauropod presacral vertebra that is missing only the lateral end of the left transverse process, most of the right transverse process, and the apex of the neural spine (Fig. 1). The centrum and neural arch are firmly coossified, leaving no trace of the neurocentral su-

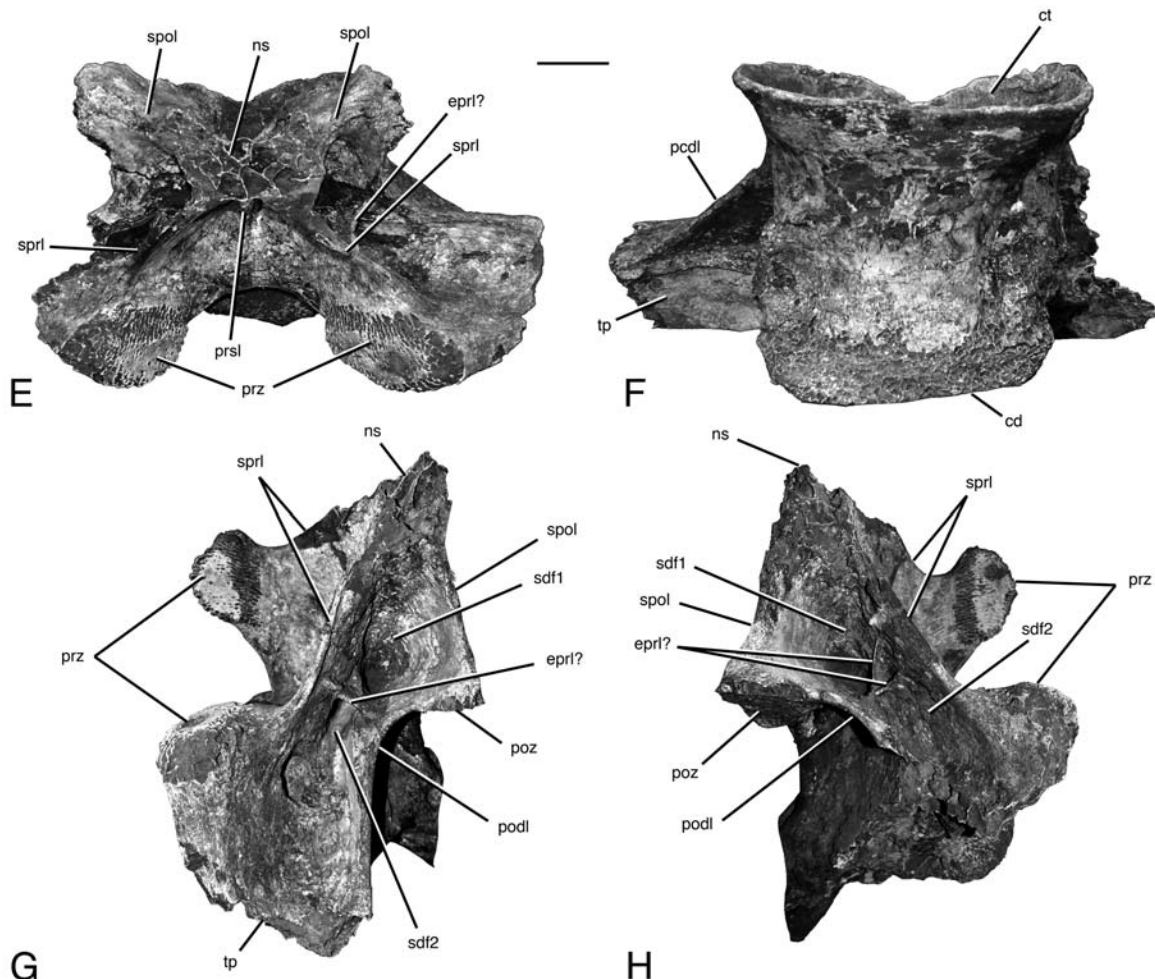


FIGURE 1. Continued.

ture, suggesting that the individual to which this vertebra pertained was skeletally mature at death.

The vertebra clearly occupied a position within the ‘cervico-dorsal transition’ of the sauropod to which it belonged. In titanosauriforms (e.g., *Euhelopus*), distinguishing between the posteriormost cervical and anteriormost dorsal vertebrae can be a challenge, especially in the absence of associated ribs, as is the case here (Wilson and Upchurch, 2009). Based, however, on the anteroposteriorly compact proportions of the centrum, the position of the parapophysis (which lies near, but not on, the ventral margin of the centrum), the substantial height of the neural arch, and comparisons with nearly complete presacral series of other titanosauriforms (e.g., *Giraffatitan* [Janensch, 1950], *Euhelopus* [Wiman, 1929; Wilson and Upchurch, 2009], *Overosaurus* [Coria *et al.*, 2013], *Rapetosaurus* [Curry Rogers, 2009], *Trigonosaurus* [Campos *et al.*, 2005]), we believe that the element occupied a very anterior position in the dorsal column, probably corresponding to the first dorsal vertebra.

Breakage and loss of surface bone in several areas of the vertebra (e.g., the anterior articular condyle of the centrum, the zygapophyses, and the neural spine) reveal that these regions are composed of highly camellate (i.e., ‘cancellous,’ ‘somphospondylous,’ or ‘spongy’) bone. The morphology of the camellae differs appreciably between different areas (Fig. 2). For example, the camellae that comprise the anterior con-

dyle of the centrum have no obvious alignment (Fig. 2B), whereas those that make up the prezygapophyses are clearly oriented anterolaterally-posteromedially and considerably longer anteroposteriorly than wide mediolaterally (Fig. 2C). The interior of the neural spine is composed of much larger chambers that are generally polygonal in dorsal view (Fig. 2D).

The centrum is strongly opisthocoelous, with a convex anterior articular condyle and a deeply concave posterior cotyle. It is significantly wider than tall (Table 1), such that the condyle and cotyle are elliptical in anterior and posterior views, respectively (Fig. 1A-B). The ventral surface is smooth and saddle-shaped, markedly concave anteroposteriorly but gently convex transversely (Fig. 1F). Each lateral surface is excavated by a large, deep, well-defined pneumatic fossa (‘pleurocoel’) that is deepest anteriorly and elliptical in lateral view (Fig. 1C-D), with the long axis of the ellipse oriented anterodorsally-posteroventrally. Anteriorly, the left fossa is partially subdivided by low ridges that arise from its dorsal and ventral surfaces. The parapophysis, better preserved on the left side, is positioned immediately ventral to the anterior end of the pneumatic fossa. Posteriorly, it merges with the remainder of the centrum via an incipient posterior centroparapophyseal lamina (*sensu* Wilson, 1999).

The neural arch is inclined anterodorsally with respect to the centrum, such that the prezygapophyses project well beyond the anterior edge of the centrum and the postzygapophyses are posi-

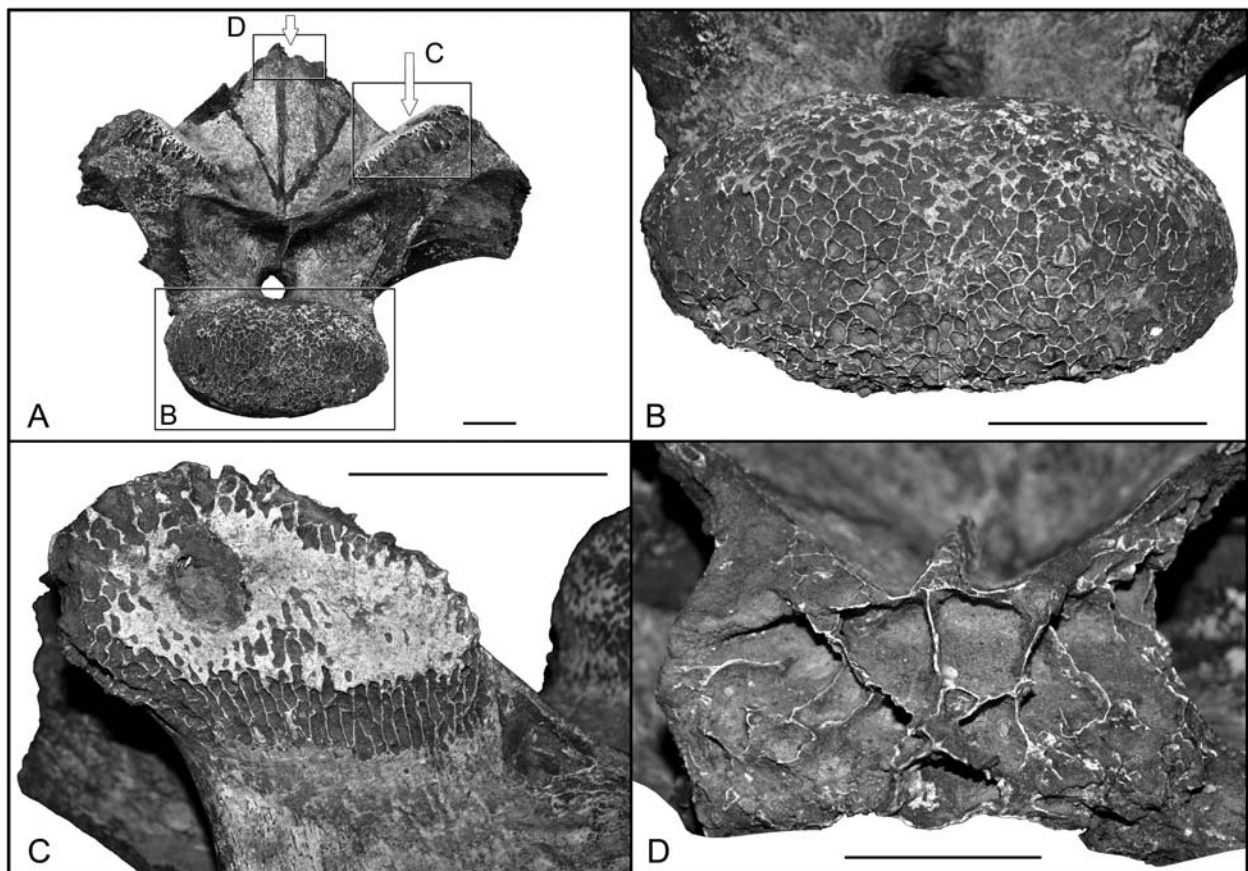


FIGURE 2. Details of internal bony structure in selected areas of titanosauriform anterior dorsal vertebra (GMNH-PV 2399). (A) vertebra in anterior view. (B) anterior articular condyle of centrum in anterior view, showing camellate tissue. (C) left prezygapophysis in dorsal view, showing anterolaterally-oriented, ‘honeycomb-like’ camellae. (D) neural spine in dorsal view, showing large, polygonal chambers. Boxes in (A) indicate approximate areas shown in (B) - (D); arrows indicate approximate viewing angle. Scale bars equal 10 cm in (A) - (C); 5 cm in (D).

TABLE 1. Measurements (mm) of titanosauriform anterior dorsal vertebra GMNH-PV 2399. * = specimen incomplete, measurement as preserved; † = measurement estimated. Abbreviations see text.

Total dorsoventral height	680*
Anteroposterior length, centrum	380 †
Transverse width, centrum, anterior	305
Dorsoventral height, centrum, anterior	140*, 150 †
Transverse width, centrum, posterior	345
Dorsoventral height, centrum, posterior	205
Dorsoventral height, dorsal edge of centrum-tprl	120
Dorsoventral height, dorsal edge of centrum-tpol	130
Transverse width, midline-lateral end of left transverse process	335*
Transverse width, across transverse processes	790 †
Transverse width, across prezygapophyses	480*, 510 †
Transverse width, across dorsal ends of postzygapophyses	380
Dorsoventral height, dorsal edge of tpri-neural spine apex	360*
Dorsoventral height, dorsal edge of tpol-neural spine apex	325

tioned dorsal to its approximate anteroposterior midline. Though both transverse processes and the neural spine are incompletely preserved, the neural arch was almost certainly considerably wider than tall when complete. The neural canal is subcircular in anterior and posterior views (Fig. 1A-B) and much narrower in transverse dimension than the neural arch pedicels. Dorso-lateral to the neural canal, on the anterior face of the vertebra, are large, deep, well-defined centroprezygapophyseal fossae (*sensu* Wilson *et al.*, 2011b). These fossae are separated by a very thin (<5 mm thick), subvertical median lamina that extends from the dorsal margin of the neural canal to the ventral edge of the intraprezygapophyseal lamina (Fig. 1A). A second, less anteriorly-extensive lamina crosscuts the left centroprezygapophyseal fossa, subdividing it into mediolaterally narrow medial and wider lateral portions. Broadly comparable conditions occur in anterior dorsal vertebrae of several other somphospondylans, including *Chubutisaurus*, *Mendozasaurus*, and *Puertasaurus* (Fig. 3). Nevertheless, the morphologies of these forms differ from that in GMNH-PV 2399. *Chubutisaurus* has a transversely thick, pneumatized, vertical ‘medial pillar’ that does not reach the dorsal margin of the neural canal (Carballido *et al.*, 2011:fig. 2b); similarly, although the median laminae or ‘pillars’ of *Mendozasaurus* (González Riga, 2003:fig. 4a; González Riga, 2005:fig. 5c) and *Puertasaurus* (see Novas *et al.*, 2005b:fig. 2a) do span the distance between the intraprezygapophyseal lamina and the neural canal, they are thick and low in relief. Conversely, in many derived titanosaurs (e.g., *Isisaurus* [Jain and Bandyopadhyay, 1997], *Opisthocoelicaudia* [Borsuk-Bialynicka, 1977], *Pitekunsaurus* [Filippi and Garrido, 2008], the as-yet generically unassigned ‘Peirópolis Series A’ [Powell, 2003]), the intraprezygapophyseal lamina abuts the dorsal margin of the neural canal, leaving no space between these two structures (Fig. 3).

Anteriorly, the mediolaterally broad, well-developed centroprezygapophyseal laminae connect the dorsolateral corners of the centrum with the ventral ends of the prezygapophyses, demarcating the lateral edges of the centroprezygapophyseal fos-

sae. The dorsal margins of these fossae are defined by the robust intraprezygapophyseal lamina, which is so anteroposteriorly extensive that it forms a sort of ‘shelf’ between the prezygapophyses. Although these areas are slightly damaged, it appears that the intraprezygapophyseal lamina bifurcates at its lateral ends, forming shallow fossae immediately medial to the prezygapophyses. This is again comparable to the condition in *Chubutisaurus*, where it appears that the intraprezygapophyseal lamina is laterally bifid, at least on its right side (see Carballido *et al.*, 2011:fig. 2b). Carballido *et al.* (2011: 96) described this morphology as a small, triangular, shallow fossa situated immediately dorsal to their ‘medial centroprezygapophyseal lamina.’ The prezygapophyseal articular facets of the Moroccan vertebra are medio-laterally elongate in dorsal view (with an oval dorsal contour; Fig. 1E) and inclined approximately 30° from the horizontal.

Dorsal to the neural canal, the posterior surface of the neural arch resembles the morphology of the anterior face, with centropostzygapophyseal and intrapostzygapophyseal laminae framing the centropostzygapophyseal fossae (Fig. 1B). Similar to the centroprezygapophyseal laminae, the centropostzygapophyseal laminae are robust. However, the intrapostzygapophyseal lamina is thin, V-shaped, and weakly developed, markedly different from the condition of the intraprezygapophyseal lamina. At the transverse midpoint of the intrapostzygapophyseal lamina (i.e., at the vertex of the ‘V’) is a small (~20 mm tall), triangular structure that may represent a rudimentary hypophyse. The ventral end of this structure tapers to a low ridge that fails to reach the dorsal margin of the neural canal; as such, the ventral portions of the centropostzygapophyseal fossae are confluent. Dorsally, both centropostzygapophyseal laminae are incipiently bifurcated, the left more so than the right.

The lateral sides of the ventral half of the neural arch are each occupied by a pair of very deep, well-defined fossae that are triangular in lateral view (Fig. 1D). Following Wilson *et al.* (2011b), we identify the more posteroventrally-positioned of these as the centrodiaepophyseal fossa. We regard the comparatively anterodorsal fossa as the prezygapophyseal centrodiaepophyseal fossa. The centrodiaepophyseal fossa is bounded ventrally by the centrum, anterodorsally by the thin anterior centrodiaepophyseal lamina, and posterodorsally by the thick, robust posterior centrodiaepophyseal lamina. It is divided (on both the left and right sides of the vertebra) into an anterior trapezoidal portion and a posterior triangular portion by a thin, subvertically-oriented lamina that extends from the dorsal margin of the centrum to the ventral margin of the posterior centrodiaepophyseal lamina. The same or a closely similar lamina present in dorsal vertebrae of the Patagonian saltasaurine titanosaur *Neuquensaurus* was termed the accessory posterior centrodiaepophyseal lamina by Salgado *et al.* (2005:figs. 3a, c; 4a-b). The prezygapophyseal centrodiaepophyseal fossa is delineated by the centroprezygapophyseal lamina anteriorly, the anterior centrodiaepophyseal lamina posteriorly, and the prezygodiaepophyseal lamina dorsally.

The left transverse process is substantially more complete than the right. Although incomplete, it is laterally elongate, ori-

ented approximately horizontally, and triangular in cross section at its broken lateral end (Fig. 1C). The lateral orientation of the transverse process of GMNH-PV 2399 differs from the dorsolaterally-directed processes of anterior dorsal vertebrae of several titanosaurs (Fig. 3), including *Isisaurus* (Jain and Bandyopadhyay, 1997), *Pitekunsaurus* (Filippi and Garrido, 2008), *Saltasaurus* (Powell, 1992, 2003), and especially *Barrosasaurus* (Salgado and Coria, 2009), *Malawisaurus* (Gomani, 2005), and *Muyelensaurus* (Calvo *et al.*, 2008). By contrast, the transverse processes of the basal somphospondylan (euhelopodid *sensu* D'Emic [2012] and Mannion *et al.* [2013]) *Euhelopus* are ventrolaterally directed (Wiman, 1929; Wilson and Upchur-

ch, 2009). However, some of these apparent discrepancies are almost certainly due to positional variation along the dorsal column rather than genuine taxonomic or phylogenetic distinction, as evidenced by selected somphospondylan specimens that preserve complete anterior dorsal sequences, such as 'Peirópolis Series A.' In this unidentified Brazilian titanosaurian, the first dorsal vertebra has laterally-directed transverse processes, as in GMNH-PV 2399; in the second dorsal, however, the transverse processes are dorsolaterally oriented (Powell, 2003; Fig. 3N-O). Similarly, in *Trigonosaurus*, the transverse processes of the first dorsal vertebra are horizontal, but by the fourth dorsal, they become strongly dorsolaterally inclined (Campos *et al.*, 2005: figs. 3, 16).

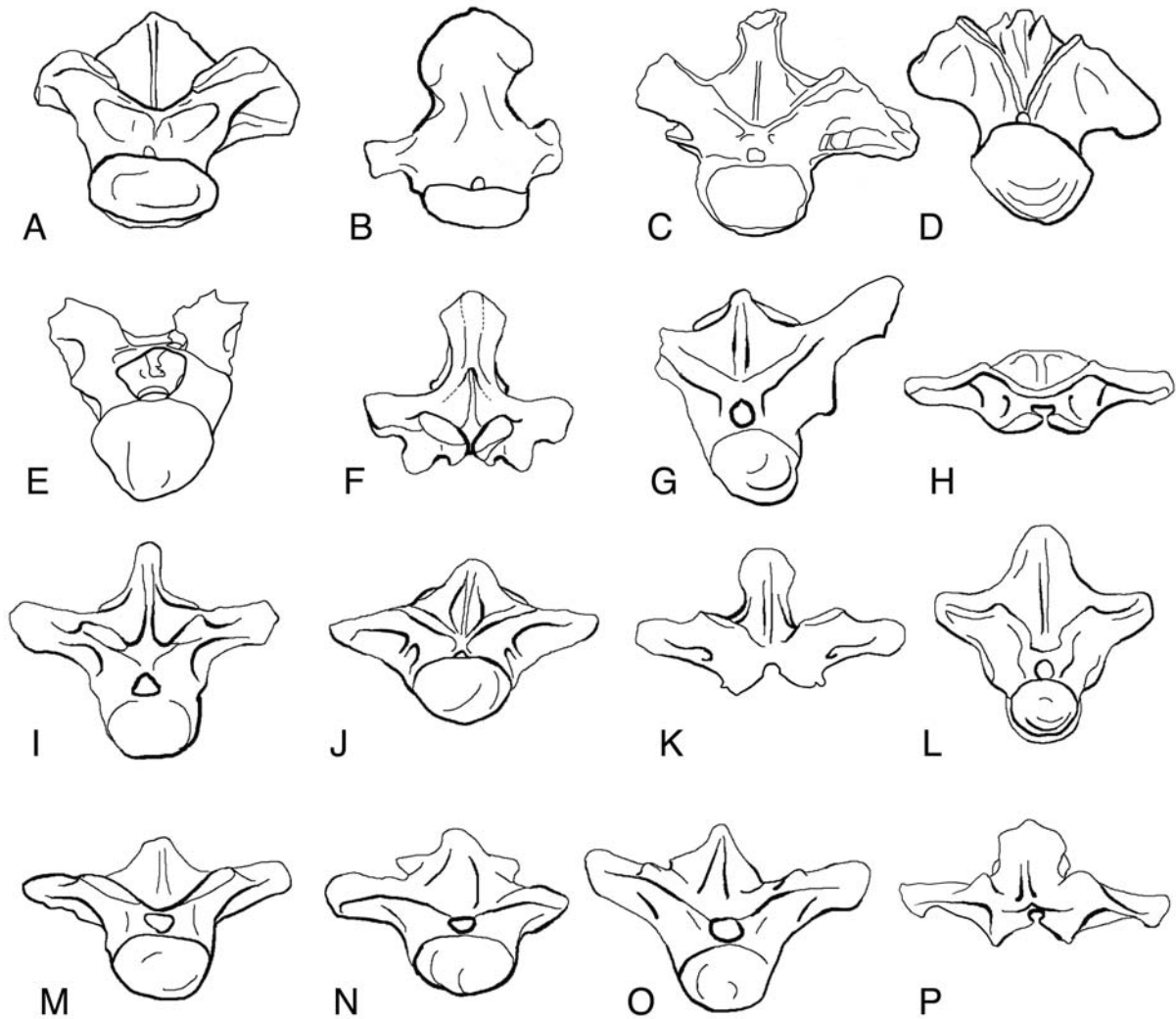


FIGURE 3. Comparative line drawings of somphospondylan anterior dorsal vertebrae in anterior view. (A) GMNH-PV 2399. (B) basal somphospondylan *Ligabuesaurus leanzai* anterior dorsal (after Bonaparte *et al.*, 2006). (C) basal somphospondylan *Sauroposeidon proteles* anterior dorsal (dorsal 2?) (after D'Emic and Foreman, 2012). (D) basal somphospondylan (euhelopodid *sensu* D'Emic, 2012 and Mannion *et al.*, 2013) *Euhelopus zdanskyi* dorsal 2 (redrawn from Wiman, 1929). (E) basal somphospondylan *Chubutisaurus insignis* anterior dorsal (redrawn from Carballido *et al.*, 2011). (F) putative basal titanosaurian *Argentinosaurus huinculensis* anterior dorsal (neural arch only) (modified from Bonaparte and Coria, 1993). (G) basal lithostrotian *Malawisaurus dixeyi* anterior dorsal (after Gomani, 2005). (H) nemegtosaurid *Rapetosaurus krausei* dorsal 1 (neural arch only) (after Curry Rogers, 2009). (I) lognkosaurian *Mendozaesaurus neguyelap* anterior dorsal (redrawn from González Riga, 2003). (J) putative lognkosaurian *Puertasaurus reuili* dorsal 2 (redrawn from Novas *et al.*, 2005b). (K) 'derived titanosaurian' *Bonitasaura salgadoi* dorsal 1 (neural arch only) (after Gallina, 2011). (L) 'derived titanosaurian' *Isisaurus colberti* dorsal 2 (redrawn from Jain and Bandyopadhyay, 1997). (M) 'derived titanosaurian' *Pitekunsaurus macayai* anterior dorsal (redrawn from Filippi and Garrido, 2008). (N) 'derived titanosaurian' 'Peirópolis Series A' dorsal 1 (after Powell, 2003). (O) 'derived titanosaurian' 'Peirópolis Series A' dorsal 2 (after Powell, 2003). (P) saltasaurid *Alamosaurus sanjuanensis* anterior dorsal (neural arch only) (redrawn from Lehman and Coulson, 2002). Not to scale.

The entirety of the posterior surface of the transverse process of the Kem Kem vertebra is occupied by the postzygapophyseal centrodiapophyseal fossa, which is delineated dorsally by the postzygodiapophyseal lamina, medially by the centropostzygapophyseal lamina, and ventrally by the posterior centrodiapophyseal lamina (Fig. 1B). Though generally broad and shallow, this fossa becomes much deeper medially, adjacent to the centropostzygapophyseal lamina and postzygapophysis. At its dorsoventral midline, the postzygapophyseal centrodiapophyseal fossa is ornamented by a distinctive, highly rugose patch of bone that progressively expands in dorsoventral depth laterally, such that, at its lateral extreme, it covers nearly the entire posterior surface of the transverse process (Fig. 1B). The texture of this patch is suggestive of ligamentous attachment in this area. Laterally, the transverse process shows indications of a dorsoventral expansion that was perhaps slightly more pronounced ventrally than dorsally.

Each of the transverse processes forms the ventral margin of a deep excavation that, following Wilson *et al.* (2011b), we interpret as a portion of the spinodiapophyseal fossa, specifically spinodiapophyseal fossa 2. This fossa is defined by the prominent spinoprezygapophyseal lamina anteriorly and the postzygodiapophyseal lamina posteriorly, and dorsally by a well-developed, subhorizontal lamina that connects the former two laminae. Based on its position and orientation, we tentatively interpret this lamina as a serial homologue of the epipophyseal-prezygapophyseal lamina that is more commonly found in sauropod cervical vertebrae (Wilson and Upchurch, 2009; Wilson *et al.*, 2011b; Wilson, 2012). The same or a closely similar lamina, also identified as the epipophyseal-prezygapophyseal lamina, occurs in the anterior dorsals of the somphospondylan *Euhelopus* (Wilson and Upchurch, 2009: fig. 13). In turn, this subhorizontal lamina comprises the ventral margin of another deep cavity that we identify as another part of the spinodiapophyseal fossa, the spinodiapophyseal fossa 1 of Wilson *et al.* (2011b). The other boundaries of this fossa are the spinoprezygapophyseal lamina anteriorly and the spinopostzygapophyseal lamina posteriorly. On the right side of the vertebra, the spinodiapophyseal fossa 1 is partitioned by another thin, anterodorsally-oriented lamina that intersects the putative epipophyseal-prezygapophyseal lamina at its posterior end and is consequently interpreted as a branch of the latter. The postzygapophyses are nearly completely preserved, and their facets have the shape of a mediolaterally elongate oval. They are slightly arched ventrally at their medial extremes.

Dorsal to the intraprezygapophyseal lamina, the entire anterior surface of the neural arch is occupied by the spinoprezygapophyseal fossae and the prespinal lamina that separates them. The latter is prominent, subequal in transverse thickness throughout its length, and extends to the base of the neural spine. The posterior surface of the neural arch dorsal to the intrapostzygapophyseal lamina is dominated by the channel-like spinopostzygapophyseal fossa. Though this area is damaged, the postspinal lamina is clearly present, but does not extend ventral to the dorsal ends of the postzygapophyses. The incomplete neural spine is made up of the spinoprezygapophyseal laminae anterolaterally and the spinopostzygapophyseal laminae posterolaterally. The preserved portion of the spine is anteroposteriorly compressed and subvertically oriented.

Ischium

The right ischium GMNH-PV 2314 is plate-like and preserved in two pieces. The much larger, more complete piece (Fig. 4; Table 2) is broken along most of its margins, with the exception of the posterior edge, which is strongly concave in medial and lateral views (Fig. 4A). The blade is anteroposteriorly broad throughout its length. The broken anterior margin of the ischium reveals that its interior is comprised by large, polygonal, possibly pneumatic chambers. Given that pelvic girdle elements—namely, ilia—with comparable internal chambers occur in certain somphospondylan taxa (e.g., *Euhelopus* [Wilson and Upchurch, 2009], *Epachthosaurus* [Martínez *et al.*, 2004], *Lirainosaurus* [Sanz *et al.*, 1999], *Sonidosaurus* [Xu *et al.*, 2006], saltasaurine titanosaurs [Cerdeña *et al.*, 2012]), including the coeval Egyptian form *Paralititan* (MCL, pers. obs.), the presence of chambers in the Moroccan ischium is not entirely surprising. Furthermore, ischial pneumaticity would not be unprecedented within Neosauropoda, as the recently-described Tunisian rebbachisaurid *Tataouinea* has been shown to possess a large, presumably pneumatic foramen on the proximal end of this bone (Fanti *et al.*, 2013).

The most striking feature of the new Moroccan ischium is the presence of approximately 15 deep, ~8 mm wide, slightly curved, mostly subparallel furrows that extend across almost the entire lateral surface of the proximal end (Fig. 4C). Several of these furrows increase slightly in width and depth toward the anterior edge of the bone. Interspersed among them are roughly 20 ovate pits of about the same width, many of which are clustered or aligned with one another. Although the pits as a whole are restricted to the anterior two-thirds of the ischium, most are individually better defined at the end that is closest to the posterior margin of the bone. Additional furrows occur on the posterior edge (Fig. 4B), on both the proximal end and the shaft (Fig. 4D-E). The smaller ischial fragment is also marked by at least two deep furrows and between two and four pits; one of the pits is situated at the approximate midlength of one of the furrows. Given their close similarity to previously reported Mesozoic reptile tooth marks (e.g., Fiorillo, 1991; Hunt *et al.*, 1994; Chure *et al.*, 2000; Rogers *et al.*, 2003; Hone and Rauhut, 2010; Hone and Watabe, 2010; Longrich *et al.*, 2010; Schwimmer, 2010; Bell *et al.*, 2012), we interpret these structures as feeding traces left by a very large carnivorous archosaur. The pits correspond to the ‘punctures’ of Hone and Watabe (2010), and their arrangement suggests that the carnivore in question bit deeply into this titanosauriform ischium but then released a minimum of three (and probably more) times. We identify the furrows as ‘bite-and-drag’ marks *sensu* Hone and Watabe (2010) that indicate persistent ‘puncture and pull’ feeding of the type that Erickson and Olson (1996) hypothesized for *Tyrannosaurus rex*.

TABLE 2. Measurements (mm) of titanosauriform ischium GMNH-PV 2314. * = specimen incomplete, measurement as preserved.

Proximodistal length	950*
Anteroposterior length, proximal	270*
Anteroposterior length, distal	260*

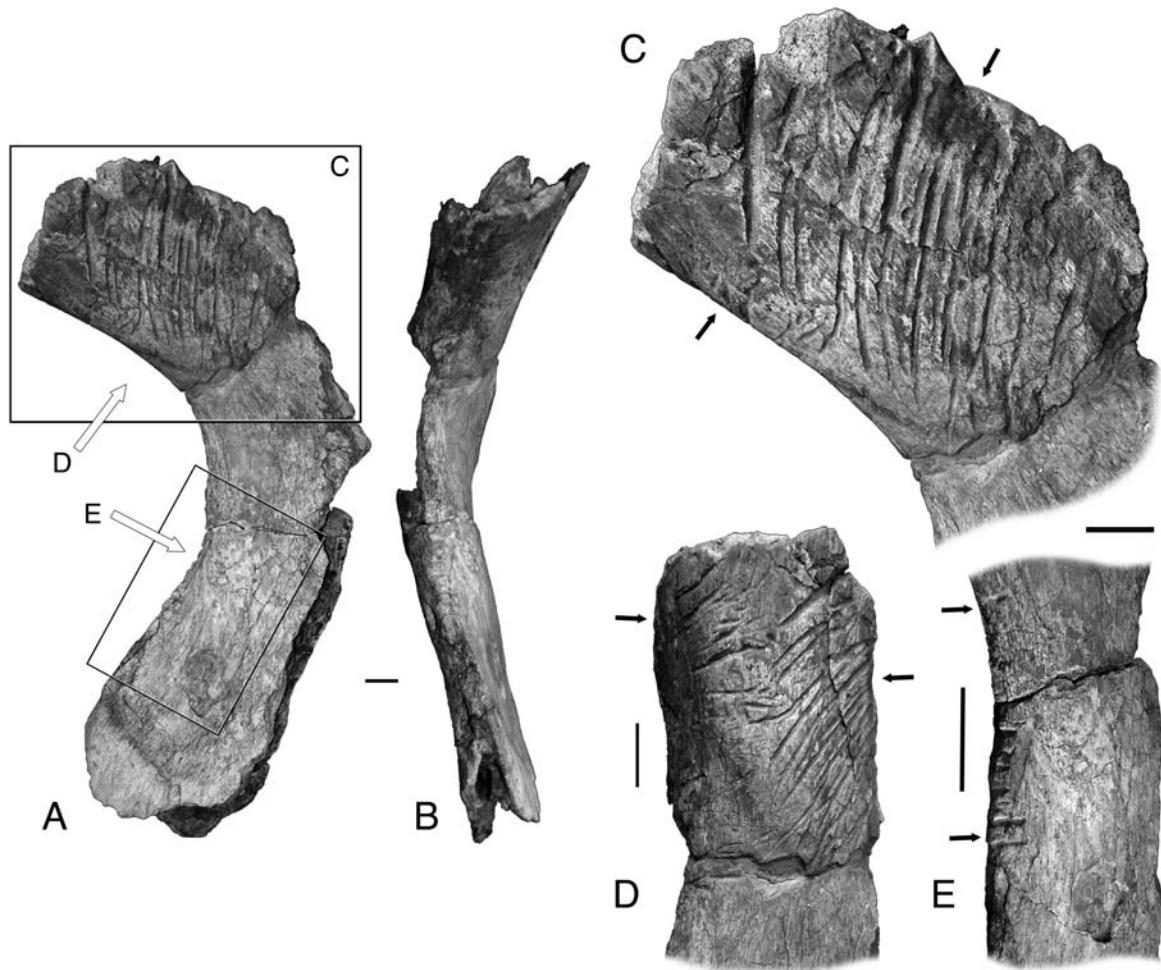


FIGURE 4. Partial titanosauriform right ischium (GMNH-PV 2314) in lateral (A) and posterior (B) views. (C) - (E) details of tooth-marked areas (tooth marks indicated by solid black arrows). Proximal end in lateral (C) and posterior (D) views. (E) shaft in posterior view. Boxes in (A) indicate approximate areas shown in (C) - (E); large, open arrows indicate approximate viewing angle. Scale bars equal 10 cm.

DISCUSSION

Systematic Assessment

The lower-level evolutionary relationships of titanosauriform sauropods are poorly resolved at present, a situation that has been commented on by multiple authors (e.g., Curry Rogers, 2005; Wilson, 2005, 2006; González Riga, 2011; D'Emic, 2012; Mannion *et al.*, 2013). Nevertheless, most recent analyses (e.g., Wilson, 2002; Upchurch *et al.*, 2004; Curry Rogers, 2005; González Riga *et al.*, 2008; Hocknull *et al.*, 2009; Gallina and Apesteguía, 2010; Carballido *et al.*, 2011; Zaher *et al.*, 2011; D'Emic, 2012; Mannion *et al.*, 2013) concur on the monophyly of Titanosauriformes and several of its subclades, most commonly Somphospondyli, Titanosauria, Lithostrotia, Nemegtosauridae, Saltasauridae, Opisthocoelicaudiinae, Saltasaurinae, and (sometimes) Lognkosauria. Although we considered conducting a numerical phylogenetic analysis to attempt to ascertain the affinities of GMNH-PV 2399 and GMNH-PV 2314, the preponderance of missing data for the taxon or taxa represented by these specimens renders the recovery of meaningful results unlikely. Instead, we used the lists of proposed synapomorphies of Titanosauriformes and its subclades published by Curry Rogers (2005), Gallina and Apesteguía (2010), Carballido *et al.* (2011),

D'Emic (2012), and Mannion *et al.* (2013) to assess the phylogenetic positions of the specimens.

Curry Rogers (2005) performed two analyses of titanosauriform interrelationships, the first with all taxa in her phylogenetic data matrix included, and the second including only taxa that preserved 15 percent or more of the available character information. In the first analysis, Titanosauriformes and its most inclusive subclades were supported by very few unambiguous synapomorphies of the anterior dorsal vertebrae (Curry Rogers, 2005:appendix 2.3). Specifically, Titanosauriformes was supported by only two anterior dorsal synapomorphies, whereas Somphospondyli, Titanosauria, Lithostrotia, and Saltasauridae were supported by none. Because of this, we used the list of unambiguous synapomorphies generated by the second, less taxonomically inclusive analysis (Curry Rogers, 2005:appendix 2.4) to investigate the affinities of GMNH-PV 2399. Based on the results of this analysis, the new vertebra pertains to Somphospondyli because it has 1) camellate ('spongy') bone texture (character 110, state 1); 2) deep and simple lateral pneumatic fossae of the centrum ('pleurocoels') (character 147, state 0); 3) prespinal lamina present along entire length of neural spine (character 160, state 3); and 4) absence of hyposphene-hypantrum articulations (character 162, state 0). (Although a rudimen-

tary hyposphene may be present at the vertex of the intrapostzygapophyseal lamina, there is no hypantrum on the anterior surface.) GMNH-PV 2399 lacks the proposed somphospondylan synapomorphy of dorsolaterally-directed transverse processes (character 154, state 0); however, since laterally-directed processes also occur in anterior dorsal vertebrae of many undoubted somphospondylans (e.g., *Bonitasaura* [Gallina, 2011], *Ligabuesaurus* [Bonaparte *et al.*, 2006], *Mendozasaurus* [González Riga, 2003, 2005], *Puertasaurus* [Novas *et al.*, 2005b], *Rapetosaurus* [Curry Rogers, 2009]; Fig. 3) the morphology present in the Kem Kem vertebra does not preclude its referral to that clade. Furthermore, as noted above, the orientation of the transverse processes varies within the anterior dorsal series of some somphospondylan taxa (e.g., 'Peirópolis Series A'; Fig. 3N-O). GMNH-PV 2399 does clearly lack the only applicable unambiguous synapomorphy of Curry Rogers' (2005) titanosaurian node C (identified as *Saltasauridae* but taxonomically more comparable to *Lithostrotia* of most other authors [e.g., Upchurch *et al.*, 2004; D'Emic, 2012]): dorsal boundary of neural canal in anterior dorsals either intraprezygapophyseal lamina or ventral extension of prespinal fossa (character 149, states 0 and 1), indicating that the specimen does not belong to that clade. Similarly, the Moroccan fossil lacks shallow lateral pneumatic fossae (character 111, state 1), suggesting that it is not referable to titanosaurian node D (*Lithostrotia* of Curry Rogers, 2005). As such, according to the titanosauriform synapomorphies hypothesized by Curry Rogers (2005), GMNH-PV 2399 resides within Somphospondyli, perhaps as a non-titanosaurian somphospondylan or a basal titanosaurian.

Following Gallina and Apesteguía (2010), the taxon represented by GMNH-PV 2399 is a member of 'Titanosauroida' (i.e., titanosaurs more derived than *Andesaurus* + *Malawisaurus*) because its prespinal lamina is present throughout the entire length of the neural spine (character 36, state 2). Moreover, the Moroccan vertebra possesses a subvertically-oriented neural spine, and as such, it also exhibits the only scorable synapomorphy of the 'titanosauroid' clade *Bonitasaura* + Lognkosauria: anterior dorsal neural spines not inclined posteriorly more than 20 degrees from the vertical (character 34, state 0).

According to the study of Carballido *et al.* (2011), GMNH-PV 2399 possesses one unambiguous synapomorphy of the clade comprised by somphospondylans more derived than *Chubutisaurus*: a prespinal lamina (character 125, state 1). This position is further supported by the presence of an additional two ambiguous synapomorphies: 1) absence of infradiapophyseal pneumatic foramen (character 102, state 0); and 2) posterior centrodiapophyseal lamina ventrally expanded as product of accessory posterior centrodiapophyseal lamina (character 134, state 1). However, the anterior surface of the neural arch of the Moroccan vertebra possesses a large, deep cavity (subdivided by very thin, nearly vertical laminae) dorsal and dorsolateral to the neural canal (i.e., the centroprezygapophyseal fossae) (character 108, state 1). Carballido *et al.* (2011) hypothesized the absence of this cavity (character 108, state 0) as a third ambiguous synapomorphy of somphospondylans to the exclusion of *Chubutisaurus*.

Based on the unambiguous synapomorphies postulated by D'Emic (2012:appendix 3), the Kem Kem vertebra is referable to Somphospondyli because it possesses a prespinal lamina

(character 33, state 1) and because, as far as can be ascertained (Fig. 2), the entirety of its interior is permeated by subcentimeter-scale pneumatic chambers (character 18, state 2). Due to incomplete preservation, another of D'Emic's (2012) potentially applicable somphospondylan synapomorphies (anterior dorsal neural spines dorsally expanded and 'paddle-shaped' [character 35, state 1]) cannot be reliably scored in GMNH-PV 2399. A fourth proposed synapomorphy, anterior dorsal vertebrae with low (as opposed to sharply defined) spinodiapophyseal laminae on anterior surface of neural spine (character 31, state 1), is problematic, as the spinodiapophyseal lamina appears to be absent in this vertebra. Perhaps unsurprisingly given its geographic provenance, the Moroccan fossil lacks all anterior dorsal synapomorphies of the East Asian basal somphospondylan clade Euhelopodidae and its subclades for which it can be reliably scored. Lastly, although its neural spine is incomplete, GMNH-PV 2399 appears to lack the only applicable synapomorphy of D'Emic's (2012) clade *Chubutisaurus* + Titanosauria (dorsal vertebrae with reclined neural spines; character 46, state 1). Nevertheless, this character varies within the anterior dorsal series of some species within this clade. For example, in the recently described Patagonian titanosaurian *Overosaurus paradorsorum*, the neural spine of the first dorsal vertebra appears anterodorsally inclined, whereas that of the second dorsal is approximately vertical (Coria *et al.*, 2013:fig. 3a). The neural spines of subsequent anterior and middle dorsals are 'reclined' (i.e., posterodorsally oriented). A similar or the same pattern is evident in the Brazilian titanosaurian *Trigonosaurus*: the neural spine of dorsal 1 is anterodorsally oriented (see Campos *et al.*, 2005: fig. 2), whereas those of dorsals 4 and 5 are posterodorsally inclined (Campos *et al.*, 2005:fig. 15). Consequently, in our view, the subvertical orientation of the neural spine of GMNH-PV 2399 does not preclude the referral of this specimen to D'Emic's (2012) *Chubutisaurus* + Titanosauria clade.

Lastly, according to the results of Mannion *et al.*'s (2013) analysis of their 'Lusotitan standard discrete matrix' ('LSDM'; see Mannion *et al.*, 2013:appendix 4), GMNH-PV 2399 is referable to Titanosauriformes because, although incomplete dorsally, its neural spine appears triangular in lateral view (character 159, state 1; an ambiguous synapomorphy). Conversely, the Kem Kem vertebra lacks the two ambiguous synapomorphies of Brachiosauridae for which it can be evaluated: a ventral keel on the centrum (character 142, state 1) and laterally elongate, dorsoventrally narrow diapophyses (character 154, state 1). (Although the transverse processes of the new specimen are incomplete, it seems unlikely that, if intact, they would have approached the elongate condition seen in anterior and middle dorsal vertebrae of brachiosaurids such as *Brachiosaurus* and *Giraffatitan*; see, for example, Taylor, 2009: fig. 1a, d). GMNH-PV 2399 also lacks the applicable (ambiguous) synapomorphies of Euhelopodidae (state 1 of characters 132 and 138) and Titanosauria (state 0 of character 144 and state 1 of character 145). As such, based on the results of Mannion *et al.*'s (2013) 'LSDM' analysis, the Moroccan fossil is assignable only to Titanosauriformes. Within that clade, the specimen does not belong to Brachiosauridae or Euhelopodidae. It would also appear to be excluded from Titanosauria, although this contrasts with the result obtained from our examination of Gallina and Apesteguía's (2010) hypothesized titanosaurian synapomorphies.

To summarize from the discussion above, the anterior dorsal vertebra GMNH-PV 2399 exhibits multiple previously-proposed synapomorphies of Somphospondyli (i.e., the majority of the applicable synapomorphies proposed by Curry Rogers [2005] and D'Emic [2012]), firmly establishing its inclusion within that clade and confirming the presence of these sauropods in the 'Kem Kem beds.' Among somphospondylans, the specimen appears more derived than *Chubutisaurus* (based on, for instance, its possession of a prespinal lamina that extends the length of the neural spine; see Carballido *et al.*, 2011). Conversely, it is clearly not a euhelopodid *sensu* D'Emic (2012) and Mannion *et al.* (2013). Whether or not the Kem Kem vertebra pertains to Titanosauria cannot, at present, be conclusively determined; if it does, however, it is likely a basal representative of this clade, as it lacks conditions postulated by Curry Rogers (2005) as synapomorphies of her derived titanosaurian nodes C and D, respectively.

Unfortunately, the ischium GMNH-PV 2314 is too incomplete to permit a precise assessment of its systematic position. It does, however, strongly resemble the corresponding portions of the ischia of many non-titanosaurian somphospondylans (e.g., *Euhelopus* [Wiman, 1929], *Tastavinsaurus* [Canudo *et al.*, 2008; Royo-Torres *et al.*, 2012]) and titanosaurs (e.g., *Andesaurus* [Calvo and Bonaparte, 1991; Mannion and Calvo, 2011], *Malawisaurus* [Gomani, 2005], *Rapetosaurus* [Curry Rogers, 2009]) in being plate-like and strongly curved in lateral view; accordingly, we refer this bone to Somphospondyli. The ischia of rebbachisaurid diplodocoids — the only non-titanosauriform sauropod clade known to have persisted into the Late Cretaceous — differ markedly from GMNH-PV 2314 and other somphospondylan ischia in being straight-shafted and narrow in lateral view (e.g., Calvo and Salgado, 1995; Pereda Suberbiola *et al.*, 2003; Carballido *et al.*, 2012; Fanti *et al.*, 2013).

Afro-Arabian Late Cretaceous Sauropod Diversity

Only a few relatively complete, phylogenetically informative sauropod fossils have been described from the Late Cretaceous of continental Africa and the Arabian Peninsula. These include the holotypic partial skeleton of the rebbachisaurid *Rebbachisaurus* (Lavocat, 1954; Wilson and Allain, 2013) from the 'Kem Kem beds,' and those of the titanosaurs *Aegyptosaurus* (Stromer, 1932) and *Paralititan* (Smith *et al.*, 2001) from paralic deposits of the at least approximately coeval (Cenomanian) Bahariya Formation of Egypt. Articulated limbs of medium-sized titanosauriforms have been described from shallow marine settings in the Turonian of Angola and the Maastrichtian of Morocco, respectively: the type scapula and forelimb of *Angolatitan* (Mateus *et al.*, 2011) and the femur, tibia, and fibula of an unidentified taxon (OCP DEK/GE 31; Pereda Suberbiola *et al.*, 2004). A sixth associated partial skeleton—undoubtedly that of a titanosauriform, and possibly that of a titanosaurian—comes from the Campanian of Egypt (Brinkmann and Buffetaut, 1990; Wiechmann, 1999a, b; MCL, pers. obs.), but this specimen has not been formally described and as such will not be considered further here. Thus, two major neo-sauropod lineages, Rebbachisauridae and Titanosauriformes, co-existed on the African mainland during the Cenomanian, as was also the case in South America (Calvo and Salgado, 1995; Salgado and Coria, 2005; Salgado and Bonaparte, 2007; Novas,

2009; Ibiricu *et al.*, 2013; Mannion and Barrett, 2013). A literal interpretation of the African sauropod fossil record would suggest that, as in South America, only titanosauriforms survived beyond the early Late Cretaceous (Mannion and Barrett, 2013); nevertheless, in our view, the poor quality of this record renders such conclusions premature. Incidentally, the recent intimation (Taquet, 2010) that *Paralititan* is known only from a humerus that actually pertains to *Rebbachisaurus* is incorrect; instead, the former taxon is based on CGM 81119, an associated partial skeleton (that includes, among other bones, both humeri) that bears multiple titanosaurian synapomorphies (e.g., strongly procoelous anterior caudal vertebrae, proximolateral process on humerus; Smith *et al.*, 2001).

Of the four associated titanosauriform skeletons that have been described from the Afro-Arabian Late Cretaceous (those of *Aegyptosaurus*, *Paralititan*, *Angolatitan*, and the unidentified Maastrichtian taxon from Morocco), only the former two include dorsal vertebrae and are thus directly comparable to the new Kem Kem vertebra (GMNH-PV 2399). The only published phylogenetic analysis that includes both *Paralititan* and *Aegyptosaurus* (Curry Rogers, 2005) recovered these taxa as basal and derived members of Titanosauria, respectively. Below, we compare dorsal vertebrae assigned to these genera to GMNH-PV 2399.

The *Aegyptosaurus* holotype (BSP 1912 VIII 61, now destroyed) included a centrum that Stromer (1932) tentatively identified as pertaining to the dorsal sequence (his 'centrum a'). Regrettably, 'centrum a' was one of the few *Aegyptosaurus* elements that Stromer (1932) did not illustrate; as such, comparisons with GMNH-PV 2399 must be based exclusively on his brief description and measurements (Stromer, 1932:3-4, table 1). Stromer (1932) noted that the anterior surface of 'centrum a' was dorsoventrally taller than it was transversely wide. The centrum was strongly opisthocoelous, slightly curved ventrally, and about as tall anteriorly as it was anteroposteriorly long. Its interior was composed of coarsely cancellous (presumably camellate) bone, and a deep pneumatic fossa invaded each lateral surface. The neural arch spanned the length of the centrum. Most of these features are also present in GMNH-PV 2399, but are of little systematic utility as they are widespread within Eusauropoda (e.g., opisthocoely, pneumatic fossae) or Titanosauriformes (camellate tissue) (Wilson, 2002; Upchurch *et al.*, 2004).

The proportions of *Aegyptosaurus* 'centrum a' did differ substantially from those of GMNH-PV 2399. For instance, the ratio of anterior centrum width to height was approximately 0.8 in the former (calculated from Stromer, 1932: table 1) but is roughly 2.0 in the latter (Table 1); in the associated dorsal series of *Rapetosaurus* (FMNH PR 2209) this ratio ranges from 1.07 in dorsal 10 to 1.78 in dorsal 4 (calculated from Curry Rogers, 2009: table 1). Hence, the proportional differences between 'centrum a' and the Kem Kem vertebra are greater than those seen within the dorsal column of *Rapetosaurus*, suggesting that the two North African fossils may represent different titanosauriform taxa. Given that, as above, GMNH-PV 2399 likely pertains to a non-titanosaurian somphospondylan or a basal titanosaurian, this is consistent with the derived position of *Aegyptosaurus* within Titanosauria recovered by Curry Rogers (2005). Nevertheless, in the absence of more information on 'centrum a,' and *Aegyptosaurus* in general, we cannot completely rule out the

possibility that GMNH-PV 2399 might belong to this taxon.

Paralititan is a large titanosaurian from the Cenomanian of Egypt, and as such, it is similar in geographic and stratigraphic occurrence and inferred body size to the taxon represented by GMNH-PV 2399. Furthermore, if, as proposed by Curry Rogers (2005), *Paralititan* is a basal member of Titanosauria, it is comparable in presumed phylogenetic position to the new Moroccan vertebra as well. The *Paralititan* holotype (CGM 81119) includes two fragmentary dorsal vertebrae, but these pertain to the posterior part of the series and as such do not directly overlap with GMNH-PV 2399. CGM 81119 also includes a partial ischium, but because both this bone and the Kem Kem ischium GMNH-PV 2314 are incomplete, comparisons between them yield few meaningful insights (MCL, pers. obs.).

In addition to the *Aegyptosaurus* holotype and a few other sauropod elements, Stromer (1932) described an isolated, incomplete anterior dorsal vertebra from the Bahariya Formation that was also destroyed in World War II (BSP 1912 VIII 64). Based on its large size and its resemblance to the dorsals of selected titanosaurs, Smith *et al.* (2001) tentatively referred this bone to *Paralititan*. From what can be ascertained from Stromer's (1932) description and illustration, the specimen compares favorably to the Kem Kem vertebra in several regards (Fig. 5). Most notably, the Egyptian vertebra was close in size to GMNH-PV 2399 (e.g., posterior transverse centrum widths of 350 mm in the former versus 345 mm in the latter), and the posterior articular cotyle of its centrum was substantially transversely wider than dorsoventrally tall. Nevertheless, the centrum of the Moroccan specimen is much longer than its Egyptian counterpart (~380 mm versus 250 mm) and proportionally even wider (Table 1). Indeed, the ratio of posterior centrum width to height is 1.68 in GMNH-PV 2399 versus only 1.25 in BSP 1912 VIII 64 (Stromer, 1932); by comparison, this same ratio ranges from 0.92 to 0.67 in dorsal vertebrae 1-6 of *Euhelopus* (PMU 233 [Wiman, 1929; Wilson and Upchurch, 2009]) and 1.65-1.42 in dorsals 3-6 of *Rapetosaurus* (Curry Rogers, 2009). The range of proportions between the Moroccan and Egyptian vertebrae may therefore be slightly greater than what would be expected for anterior dorsals of a single titanosauriform taxon. The ventral end of the transverse process (i.e., the base of the posterior centrodiapophyseal lamina) also appears to have projected dorsolaterally in the Bahariya form (Fig. 5B), rather than more directly dorsally as in the Kem Kem vertebra (Fig. 5A). As noted above, however, the orientation of the transverse processes can change considerably within the anterior dorsal sequences of single titanosauriform specimens (e.g., 'Peirópolis Series A'; Powell, 2003). Consequently, as is the case for *Aegyptosaurus*, we cannot entirely discount the possibility that GMNH-PV 2399 might pertain to the taxon represented by BSP 1912 VIII 64. Still, the distinctions between these two vertebrae are noteworthy in light of the hypothesis that the 'middle' Cretaceous sauropod fauna of Morocco and other areas of northwestern Africa may have differed from that of the remainder of the continent (Mannion and Barrett, 2013).

Additional, isolated and fragmentary titanosauriform material from the 'Kem Kem beds' was described, or at least mentioned, by Russell (1996), Sereno *et al.* (1996), Kellner and Mader (1997), and Cavin *et al.* (2010). These fossils correspond to teeth, caudal vertebrae, and an astragalus, and as such cannot

be compared with the dorsal vertebra and ischium described herein. Recently, Mannion and Barrett (2013) described a fragmentary middle-posterior dorsal neural arch from the 'Kem Kem beds' that these authors tentatively attributed to a somphospondylan. Although this bone does display similarities with the vertebra described here (e.g., a complex, extensive system of internal camellae), its incomplete nature and lack of positional overlap with GMNH-PV 2399 precludes a detailed assessment of the relationships of the two specimens.

Apart from the new Kem Kem fossils, comparisons between other African Late Cretaceous titanosauriform specimens do offer insights into the diversity of these sauropods on this landmass during this interval (Fig. 6). First, the resemblance between overlapping elements of *Paralititan* and *Angolatitan* is remarkable. The scapulae of both of these early Late Cretaceous sauropods possess a well-developed posteroventral process, aspects of which were originally proposed as autapomorphic for both taxa but also occur in other titanosauriforms (e.g., *Chubutisaurus* [Carballido *et al.*, 2011], *Ligabuesaurus* [Bonaparte *et al.*, 2006], *Wintonotitan* [Hocknull *et al.*, 2009]). Furthermore, both of the proposed humeral autapomorphies of *Angolatitan* — an acute

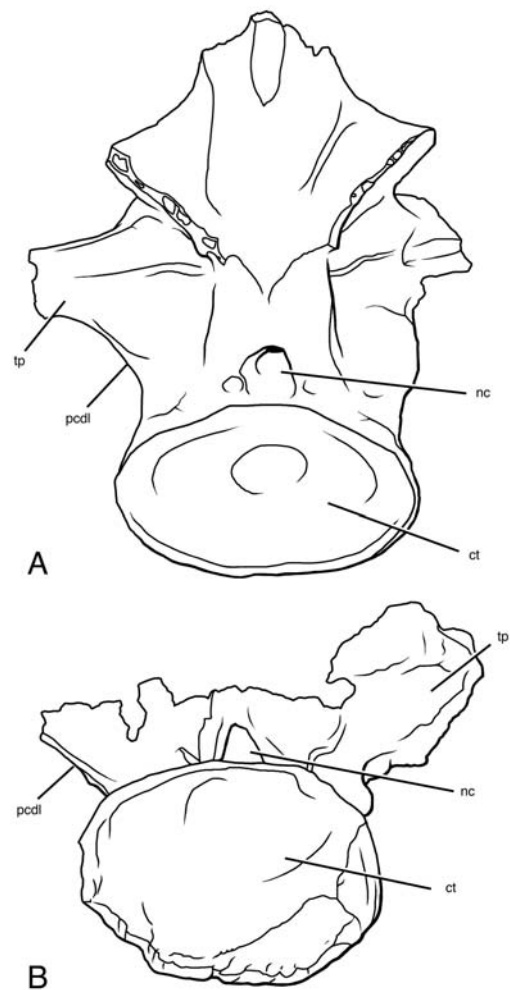


FIGURE 5. Comparative line drawings of North African Cenomanian titanosauriform anterior dorsal vertebrae in posterior view, scaled to same centrum height. (A) GMNH-PV 2399. (B) BSP 1912 VIII 64, cf. *Paralititan stromeri* (Smith *et al.*, 2001) from the Bahariya Formation of Egypt (redrawn from Stromer, 1932). Abbreviations see text.

proximomedial margin and a rectangular proximolateral corner—are also present in *Paralititan* (Smith *et al.*, 2001; Mateus *et al.*, 2011; Fig. 6B-C). The systematic position of *Angolatitan* within Somphospondyli is unresolved: whereas Mateus *et al.* (2011) considered this genus a non-titanosaurian somphospondylan, D’Emic (2012:table 9) suggested lithostrotian relationships. Mannion *et al.* (2013) included *Angolatitan* in both of their phylogenetic analyses, recovering the taxon as a non-titanosaurian somphospondylan in one analysis and as a basal titanosaurian in the other. *Paralititan*, conversely, is widely regarded as a titanosaurian on the basis of features such as strongly procoelous anterior caudal vertebrae (Smith *et al.*, 2001; Wilson, 2002; Upchurch *et al.*, 2004). Although a detailed reassessment of the affinities of these taxa is beyond the scope of the present work, their strong similarities suggest that they may be close relatives. If so, *Paralititan* and *Angolatitan* may represent a single titanosauriform lineage that occurred in coastal paleoecosystems on the African mainland during the Cenomanian-Turonian.

By contrast, an examination of Maastrichtian titanosauriform material from North Africa suggests the presence of two highly distinct taxa. Rauhut and Werner (1997) described TUB Vb-646, an isolated but well-preserved left femur from the Ammonite Hill Member of the Dakhla Formation of the Dakhla Oasis, Egypt. This bone exhibits clear differences with the femur of a coeval titanosauriform hindlimb from Morocco, OCP DEK/GE 31 (Pereda Suberbiola *et al.*, 2004; Fig. 6E-F). In the Egyptian specimen, the proximal margin is straighter, the femoral head projects much more strongly medially, and the apex of the proximolateral ‘bulge’ is more distally positioned and angular rather than smoothly rounded. Most notably, the distal end of the Dakhla femur is markedly expanded mediolaterally, such that it is nearly as wide as the proximal end, and has a bulbous, posteromedially-projecting medial condyle. Since we have not personally examined OCP DEK/GE 31, some of these distinctions could conceivably be due to taphonomic distortion and/or

the angle at which this specimen has been depicted in its published description (Pereda Suberbiola *et al.*, 2004:figs. 2a, 3a). Nevertheless, other differences (e.g., the morphology of the distal end) are almost certainly genuine, and moreover, seem outside the range of morphological variation expected for a single taxon. As such, it appears that at least two titanosauriform species were present in the latest Cretaceous of North Africa. Interestingly, the known occurrences of these forms (one in Egypt, the other in Morocco) are consistent with Mannion and Barrett’s (2013) suggestion that the emplacement of the Trans-Saharan Seaway during the ‘middle’ Cretaceous may have impeded sauropod dispersal between northwestern Africa and the remainder of the continent, leading to the development of distinct assemblages of these dinosaurs in both regions. Evaluation of this hypothesis must await the discovery of additional phylogenetically informative sauropod fossils from the Late Cretaceous of northwestern Africa and other areas of the continent.

Finally, and intriguingly, of the handful of Maastrichtian sauropod fossils that have been described from Afro-Arabia to date, two of the most informative (OCP DEK/GE 31 and TUB Vb-646) have both been independently regarded as pertaining to non-titanosaurian titanosauriforms (Rauhut and Werner, 1997; Pereda Suberbiola *et al.*, 2004). Although the incompleteness of both specimens renders these identifications tentative, they are nonetheless interesting in that, if accurate, these forms would represent the only non-titanosaurian sauropods known from Maastrichtian sediments worldwide (Wilson, 2005). Furthermore, the Moroccan hindlimb is late Maastrichtian in age (Pereda Suberbiola *et al.*, 2004), suggesting that its lineage may have survived to the very end of the Mesozoic. Multiple works (e.g., Sampson *et al.*, 1998; Sereno *et al.*, 2004; Krause *et al.*, 2007; Ali and Krause, 2011; Fanti, 2012) have proposed that Afro-Arabia separated from the remaining Gondwanan landmasses at approximately 120–100 Ma, existing as an ‘island continent’ for the remainder of the Cretaceous and developing an increasingly endemic terrestrial vertebrate fauna. The persistence of non-ti-

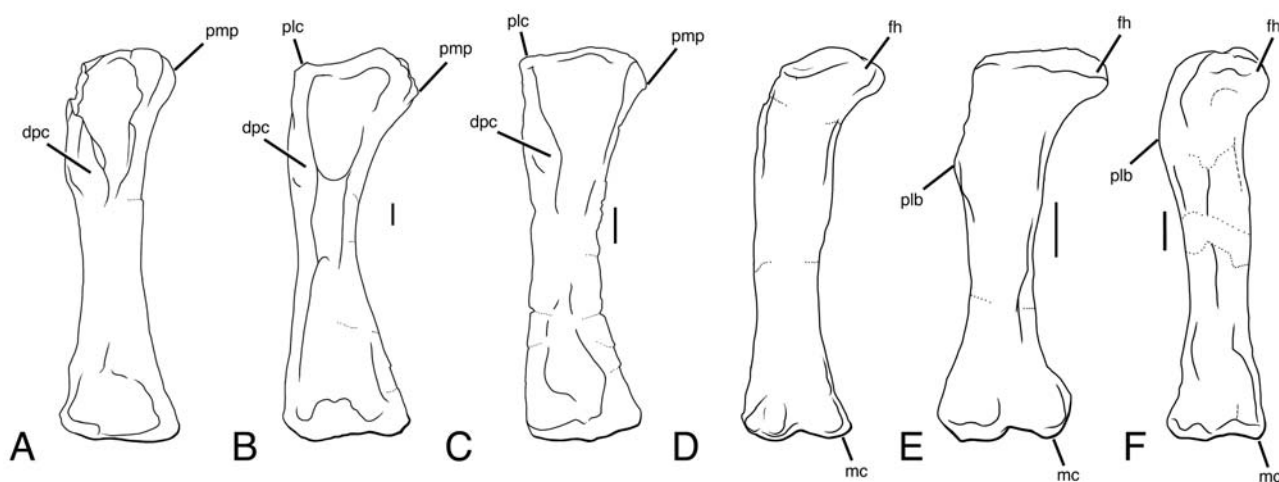


FIGURE 6. Comparative line drawings of proximal limb elements of titanosauriform sauropods from the Late Cretaceous of continental Africa, scaled to same length. (A)–(C), humeri in anterior view. (A) *Aegyptosaurus baharijensis* left humerus (reversed and redrawn from Stromer, 1932). (B) *Paralititan stromeri* right humerus (redrawn from Smith *et al.*, 2001). (C) *Angolatitan adamastor* right humerus (after Mateus *et al.*, 2011). (D)–(F), femora in posterior view. (D) *Aegyptosaurus* left femur (redrawn from Stromer, 1932). (E) left femur of unidentified taxon from Maastrichtian of Egypt (after Rauhut and Werner, 1997). (F) right femur (reversed) of unidentified taxon from Maastrichtian of Morocco (after Pereda Suberbiola *et al.*, 2004). Abbreviations see text.

titanosaurian titanosauriforms into the late Maastrichtian of North Africa after their apparent extinction elsewhere would be congruent with this paleobiogeographic hypothesis.

Paleoecological Implications

The tooth marks on the somphospondylan ischium GMNH-PV 2314 provide important insights into the fossil ecosystem preserved in the ‘Kem Kem beds.’ The only carnivorous taxa described from these strata, and indeed the North African Late Cretaceous in general, that were large and powerful enough to have produced these feeding traces are non-avian theropod dinosaurs, namely the spinosaurid *Spinosaurus* (Stromer, 1915; Dal Sasso *et al.*, 2005), the carcharodontosaurids *Carcharodontosaurus* (Stromer, 1931; Sereno *et al.*, 1996; Brusatte and Sereno, 2007) and *Sauroniops* (Cau *et al.*, 2012, 2013), and perhaps the enigmatic theropods *Bahariasaurus* (Stromer, 1934), *Deltadromeus* (Sereno *et al.*, 1996), and/or *Sigilmassasaurus* (Russell, 1996; McFeeters *et al.*, 2013). Abelisauroids were also part of the Kem Kem paleoecosystem, but known material indicates taxa that were probably too small to have produced these traces (Russell, 1996; Mahler, 2005; Novas *et al.*, 2005a; D’Orazi Porchetti *et al.*, 2011). Gigantic pholidosaurid crocodyliforms such as *Sarcosuchus* are of sufficient size to have made these bite marks (Sereno *et al.*, 2001), but such taxa are, to date, restricted to Early Cretaceous (Aptian-Albian) units that are at least a few million years older than the ‘Kem Kem beds.’ Similarly, although at least some North African early Late Cretaceous stomatosuchid (e.g., *Stomatosuchus*; Stromer, 1925) and aegyptosuchid (*Aegisuchus* [Holliday and Gardner, 2012]; *Aegyptosuchus* [Stromer, 1933]) crocodyliforms were very large, these animals have been reconstructed as weak-jawed, small-toothed piscivores (Stromer 1925, 1936; Sereno and Larsson, 2009; Holliday and Gardner, 2012) and as such it seems unlikely that they could have left the deep punctures and gouges seen on GMNH-PV 2314. Thus, we consider it probable that these traces were made by a very large theropod.

Craniodental remains are as yet unknown for *Bahariasaurus*, *Deltadromeus*, and *Sigilmassasaurus*, precluding conclusive assessments of their dietary preferences. Furthermore, the validity of *Deltadromeus* (Carrano and Sampson, 2008) and *Sigilmassasaurus* (Sereno *et al.*, 1996; Brusatte and Sereno, 2007)—and even the theropodan nature of the latter taxon (Canale *et al.*, 2008)—have been repeatedly questioned in the literature. Consequently, we consider it most parsimonious to assume that the feeding traces on GMNH-PV 2314 were left by *Carcharodontosaurus* (presumably *C. saharicus*, since *C. iguidensis* is not known to occur in the ‘Kem Kem beds’), *Sauroniops*, or *Spinosaurus*, and that at least one of these enormous theropods fed on the titanosauriform individual represented by this ischium.

Although our conclusion that a large-bodied carcharodontosaurid or *Spinosaurus* fed on a coeval titanosauriform taxon may not seem surprising, it is noteworthy in light of the seemingly peculiar nature of North Africa’s early Late Cretaceous continental paleoecosystems. Numerous authors (Stromer, 1936; Russell, 1996; Sereno *et al.*, 1996; Nothdurft *et al.*, 2002; Russell and Paesler, 2003; Mahler, 2005; Cau and Maganuco, 2009; McGowan and Dyke, 2009; Cavin *et al.*, 2010; Dyke, 2010; Ibrahim, 2010; D’Orazi Porchetti *et al.*, 2011; Belvedere *et al.*, 2013; Läng *et al.*, 2013) have called attention to the apparent

abundance and diversity of large theropods in the ‘Kem Kem beds’ and/or the Bahariya Formation versus the relative rarity of herbivorous dinosaurs and other terrestrial prey species in these units (‘Stromer’s Riddle’ of Nothdurft *et al.*, 2002; McGowan and Dyke, 2009, and Belvedere *et al.*, 2013). While some workers (McGowan and Dyke, 2009; Dyke, 2010) have argued that this paradox is an artifact of collecting biases and/or time averaging, others have attempted to explain it by proposing that some or even all large North African Cenomanian theropods may have fed primarily on the fishes that were also common in these paleoecosystems (Bakker *et al.*, 1992; Russell, 1996; Cau and Maganuco, 2009; Cavin *et al.*, 2010; Läng *et al.*, 2013). Although this may well have been true for *Spinosaurus* (e.g., Milner, 2001; Rayfield *et al.*, 2007; Amiot *et al.*, 2010), there is, at present, no evidence that carcharodontosaurids exhibited any piscivorous inclination (*contra* Bakker *et al.*, 1992); indeed, the craniodental anatomy of these latter theropods strongly suggests macropredatory habits (Mazzetta *et al.*, 2004; Therrien *et al.*, 2005). Regardless, along with the discovery of a shed tooth associated with the *Paralititan* type skeleton (Smith *et al.*, 2001), the feeding traces on the titanosauriform ischium GMNH-PV 2314 demonstrate that at least one very large African Late Cretaceous theropod ate sauropods at least some of the time.

CONCLUSIONS

We describe two titanosauriform sauropod dinosaur fossils from the Cenomanian ‘Kem Kem beds’ of Morocco that collectively provide new insight into sauropod diversity and paleoecology in the early Late Cretaceous of North Africa. Although the specimens pertain to the titanosauriform clade Somphospondyli, their precise systematic position(s) within that clade (as non-titanosaurian somphospondylans or basal titanosaurians) cannot be conclusively determined. One of the bones, a nearly complete, beautifully-preserved anterior dorsal vertebra, is among the most anatomically informative titanosauriform elements yet recovered from the Late Cretaceous of continental Africa and the Arabian Peninsula. Comparisons with approximately coeval forms from the Bahariya Formation of Egypt—the titanosaurians *Aegyptosaurus* and *Paralititan*—suggest, but do not definitively demonstrate, that the vertebra does not belong to either of these taxa. Some early Late Cretaceous (Cenomanian-Turonian) somphospondylans from the African mainland appear strongly similar to one another: for example, the scapulae and humeri of *Paralititan* and *Angolatitan* share distinctive morphologies that may indicate a close phylogenetic relationship. By contrast, the femur of the only known titanosauriform partial skeleton from the Maastrichtian of continental Africa shows significant differences with an isolated titanosauriform femur from similarly-aged beds in Egypt, suggesting that at least two distinct lineages of these sauropods inhabited this landmass near the end of the Mesozoic. The second bone, an incomplete ischium, preserves little morphological information; nevertheless, the specimen is noteworthy in exhibiting numerous grooves and pits that we interpret as feeding traces left by a very large non-avian theropod. Previous works have proposed that at least some North African early Late Cretaceous theropods may have fed primarily on fishes; thus, the new traces are important in demonstrating that sauropods were a food source for at least one such theropod as well.

ACKNOWLEDGMENTS

We are indebted to Masatoshi Ichijo, Yosuke Yamashita, and their staff at the natural history exhibition firm HAN Project 21, Co., Ltd. (Tokyo, Japan) for facilitating our collaborative research on Kem Kem dinosaur fossils during 2009 and 2012. We also thank Yuji Takakuwa and Toshiyuki Kimura (Gunma Museum of Natural History) for assistance with the study of GMNH-PV 2399. Lindsay Wright and Mark Klingler (Carnegie Museum of Natural History) skillfully executed Figures 3, 5, and 6, while Klingler and Joanne DiGnazio (Carnegie Museum of Natural History) constructed Figures 1, 2, and 4. We are grateful to Ken Carpenter (Utah State University-Eastern, Price, Utah, USA) and Jeff Wilson (University of Michigan, Ann Arbor, Michigan, USA) for informative discussions, Allen Shaw (Standing Rock Paleontology Department, Fort Yates, North Dakota, USA) for photographing GMNH-PV 2314, and Sam Tamura, Ritsuko Tachikawa, and Azusa Zamami for serving as MCL's interpreters during his 2009 and 2012 visits to Japan. MCL acknowledges the HAN Project 21, Co., Ltd. and the Gunma Museum of Natural History for sponsoring these visits. The manuscript benefited from thorough reviews by Eric Gorscak and Pat O'Connor (Ohio University, Athens, Ohio, USA) and from editorial comments by Yuji Takakuwa.

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モロッコのセノマン階から産出した新たなティタノサウルス形類恐竜(竜脚類)の標本: 北アフリカの後期白亜紀における古生態と竜脚類の多様性

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要旨: 竜脚類恐竜の一つのグループであるティタノサウルス形類は、一般に Gondwana 地塊の白亜紀の古生態系において最も多様化し、かつ普通に見られた大型の植物食動物だったと見なされている。それにも拘わらず、アフリカ大陸や当時接続していたアラビア半島の後期白亜紀の堆積物におけるこのグループの化石記録は少ない。今回筆者らは、モロッコの後期白亜紀前半(セノマン期)の堆積物である‘ケム・ケム層(Kem Kem Beds)’から産出した2点の新しいティタノサウルス形類の化石を記載する。これらの化石は、当時のアフリカ-アラビア地域に生息していたこの仲間の形態と古生態に関する理解を深めるものである。

一番目の標本(GMNH-PV 2399)は、ほぼ完全な前位胴椎で、おそらく基盤ティタノサウルス類に分類されるソノフォスポンディリ類の大型の仲間に属する。二番目の標本(GMNH-PV 2314)は部分的な坐骨で、ソノフォスポンディリ類より下位の分類に関しては不明であるが、おそらくカルカロドントサウルス類かスピノサウルス属だと考えられる非常に大型の肉食恐竜のはっきりした噛み痕が残っている。この捕食痕は、少なくとも竜脚類が後期白亜紀のアフリカにいた獣脚類の飼生物であったことを示す直接証拠である。これらの新しい標本が、既にアフリカの上部白亜系から報告されている三つの属(*Aegyptosaurus*, *Paralititan* and *Angolatitan*)のいずれかに分類されるものなのか、それともこれまで知られていなかった未記載種に分類されるものなのかは確認できない。

キーワード: 恐竜, 竜脚類, ティタノサウルス形類, ソノフォスポンディリ類, 後期白亜紀, セノマニアン, アフリカ, モロッコ, ‘ケム・ケム層’, 古生態