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TITANOSAUR (DINOSAURIA: SAUROPODA) VERTEBRAE FROM THE UPPER CRETACEOUS LAMETA FORMATION OF WESTERN AND CENTRAL INDIA

BY

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Abstract — Cretaceous dinosaurs were first reported from the Indian subcontinent in the late 1800s, and titanosaur sauropod and abelisauroid theropod remains are now known from central, western, and southern parts of India and from central western Pakistan. Although dinosaur remains are abundant, associated or articulated specimens are extremely rare, and so are complex skeletal elements such as cranial bones and presacral vertebrae. The historical pattern of sampling and collecting has limited the inferences about patterns of diversity, phylogenetic affinity, and paleobiogeographic relationships of Indian dinosaurs. Here we report on three titanosaur vertebrae representing regions of the skeleton that are complex and otherwise poorly represented in the Indian record, including two anterior dorsal vertebrae pertaining to a single individual from Rahioli, in Gujarat State (western India), and an anterior caudal neural arch from Bara Simla, in Madhya Pradesh State (central India). Phylogenetic analysis places the two individuals within Titanosauria, but further resolution of their affinities is precluded by their incompleteness and that of titanosaur vertebral columns in general, lack of coding of character data for titanosaur presacral and anterior caudal vertebrae, and relatively coarse understanding of the evolutionary relationships of titanosaurs. Comparisons with contemporaneous and spatially proximal titanosaurs from Indo-Pakistan, Madagascar, and South America provide insights into their affinities. The dorsal vertebrae share close affinity with *Isisaurus* from India and *Mendozasaurus* from Argentina. Few local comparisons are available for the anterior caudal vertebra, which shares characteristics with *Tengrisaurus* from the Early Cretaceous of Russia.

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INTRODUCTION

Remains of India's first dinosaur were discovered by (then) Captain W. H. Sleeman in 1828 in exposures of the Late Cretaceous-aged Lameta Formation in the hills near Jabalpur, in what is now Madhya Pradesh State (Sleeman, 1844; Fig. 1). These remains, which consisted of two caudal vertebrae, were passed among naturalists in India and later combined with a partial femur that was found later at or near the same site by H. B. Medlicott (1872). These elements were presented to the Geological Survey of India and eventually described in 1877 by Richard Lydekker as *Titanosaurus indicus* (for additional detail see Carrano et al., 2010). The femur was later removed from the type series by Huene and Matley (1933) because it was thought to pertain to a different species. This and the remaining type elements of *T. indicus* were lost until quite recently, during which time the better-preserved of the two caudal vertebrae served as the *de facto* type of the species because a cast was available at the Natural History Museum (London) and excellent figures had been prepared by Falconer (1868: pl. 34, figs. 3–5) and Lydekker (1879: pl. 4, figs. 1–2). This latter caudal vertebra was very recently re-discovered in the collections of the Geological Survey of India (Mohabey et al., 2013).

A re-evaluation of the validity of *Titanosaurus indicus* concluded that the remains upon which it was based were not sufficient to defend its uniqueness at the generic or specific level (Wilson and Upchurch, 2003). The one then-valid feature identified by Lydekker (1877) as diagnostic of the species, procoely of the distal caudal vertebrae, obsolesced to characterize a much broader range of taxa than *T. indicus*, *Titanosaurus*, and even Titanosauridae, which had long served as a wastebasket family for Late Cretaceous sauropods. For this reason, Wilson and Upchurch (2003: pp. 152–154) recommended sinking "*Titanosaurus*" and associated rank taxa such as "Titanosauridae" (for a dissenting opinion see Salgado, 2003). The higher-level taxa Titanosauriformes (Salgado et al., 1997), Titanosauria (Bonaparte and Coria, 1993), and Eutitanosauria (Sanz et al., 1999) remain available and are in current use.

Continued collection at the "*Titanosaurus indicus*" type locality Bara Simla and nearby Chhota Simla by Charles Matley and Durgasankar Bhattacharji produced numerous dinosaur bones, many of which have been published. These pertain to both small- and large-bodied abelisauroid theropod species and at least two titanosaurian sauropod genera (Matley, 1921, 1924; Huene and Matley, 1933; Swinton, 1947). Despite the large number of bones collected from these localities, we

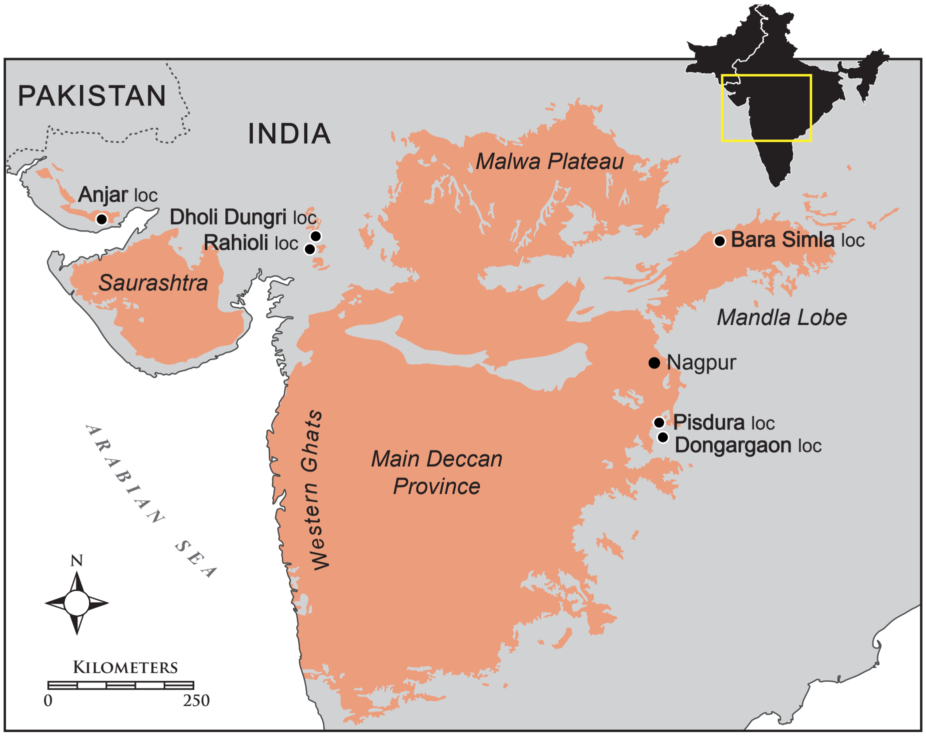

FIGURE 1 — Map of India showing dinosaur-bearing fossil localities (*loc*) associated with the Deccan Volcanic Province (orange). The Deccan Volcanic Province is composed of lobes and subregions that have distinct spatial and temporal signatures (outline based on Dasgupta et al., 1993). The Pisdura and Dongargaon localities are associated with the Main Deccan Province, Bara Simla is associated with the Mandla Lobe, Rahioli and Dholi Dungri are associated with unclassified units between the Malwa Plateau and Saurashtra, and the Anjar locality is associated with Saurashtra. Anjar, located in Kachchh, is one of the few intertrappean localities that has yielded dinosaur bones thus far (Ghevariya, 1988); nearly all other dinosaur-bearing localities are infratrappean. Note that each white-bordered, filled circle marks the position of a locality (*loc*), not the corresponding city. The border between India and Pakistan on both inset and enlarged maps is approximate.

are aware of no sauropod presacral, sacral, or anterior caudal vertebrae collected or described from there. Until now, the only such elements recorded from the Cretaceous of India are the presacral vertebrae and sacrum of *Isisaurus colberti* (Jain and Bandyopadhyay, 1997), collected at Dongargaon, south-central India, and an axis vertebra from nearby exposures of the Lameta Formation in Shivapur (Wilson and Mohabey, 2006). No anteriormost caudal vertebrae are known.

Sauropod presacral vertebrae—and to some extent sacral and anterior caudal vertebrae—are complex, character-rich anatomical units, owing to the variation in the shape and position of their various projections (e.g., diapophyses, neural spine), patterns of internal and external pneumaticity, and vertebral laminae. This variation has heterogeneous sources, including taxonomic, serial, and ontogenetic factors (see Wilson, 2012; Woodruff and Fowler, 2012; Wedel and Taylor, 2013). For this reason, presacral, sacral, and anterior caudal vertebrae, especially those whose serial position and ontogenetic status can be constrained, can offer critical information on lower-level taxonomic identity that is not provided by other, more commonly preserved elements such as limb bones or mid- to posterior caudal vertebrae.

Here we describe from Late Cretaceous horizons two sauropod dorsal vertebrae from western India and an anterior caudal neural arch from central India (Fig. 1). One of the elements was described preliminarily as a braincase of possible ornithischian affinity by Mohabey (1989), who later correctly identified it as a dorsal vertebra (see Wilson et al., 2005: p. 106). The other dorsal vertebra, which is more complete and better preserved, was never formally described. These two vertebrae are of similar serial position in the dorsal column and were collected from the same locality, suggesting that they pertain to a single individual (see below). The caudal neural arch, in contrast, was collected from Bara Simla. Although it is incomplete, it bears a complex external pneumatic pattern and is from a serial position that is not yet represented in titanosaur remains collected from Indo-Pakistan or Madagascar. Together, these three vertebrae preserve important information that contributes to our understanding of the Indian dinosaur fauna during the end of the Cretaceous.

INSTITUTIONAL ABBREVIATIONS

GSI	— Geological Survey of India, Kolkata (Calcutta), India.
GSP	— Geological Survey of Pakistan, Quetta, Pakistan.
IANIGLA	— Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, colección Paleovertebrados, Mendoza, Argentina.
ISI	— Indian Statistical Institute, Kolkata (Calcutta), India.
MLP	— Museo de La Plata, La Plata, Argentina.
PVL	— Laboratorio de Paleovertebrados, Instituto Miguel Lillo, Tucumán, Argentina.
UM	— University of Michigan Museum of Paleontology, Ann Arbor, U.S.A.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
SAUROPODA Marsh, 1878
TITANOSAURIA Bonaparte and Coria, 1993

Referred Specimens.— The new material described here includes two anterior dorsal vertebrae (GSI/GC/2905, GSI/GC/OGF107) and an anterior caudal neural arch (338/GSI/PAL/CR/2017). The former pertain to the second and third dorsal vertebrae, respectively, and they probably belong to the same individual (see below). The latter pertains to one of the first five caudal vertebrae, but a more specific serial assignment is difficult without preservation of its transverse processes. The dorsal vertebrae are referred to Titanosauria on the basis of their camellate pneumaticity, which is present in both the centrum and neural arch. The caudal neural arch is referred to Titanosauria on the basis of a distinctive process on the spinoprezygapophyseal lamina and distolaterally expanded prezygapophyseal processes. Original specimens are housed in the paleontological collections of the Geological Survey of India (Central Region) headquarters in Nagpur (GSI/GC/2905, GSI/GC/OGF107, 338/GSI/PAL/CR/2017); casts of each are housed at the University of Michigan Museum of Paleontology (UM 118188, 118187, 118189).

Locality and Horizon.— All three specimens come from exposures of the Late Cretaceous-aged Lameta Formation in India, which are associated with Deccan Trap basalts. Lameta Formation sediments have been traditionally called "infratrappean" (e.g., Blanford, 1867), based on their position beneath flows of the Deccan Trap basalts. This field-based terminology has led to the misconception that infratrappean horizons represent a single lithostratigraphic unit that is universally the same age and always older than the so-called "intertrappean" horizons that are positioned between basaltic flows of the Deccan Traps. However, infratrappean deposits are not uniformly older than intertrappean deposits, which are themselves not all equivalent in age, and infratrappean sediments from different inland basins may be time transgressive (Hansen et al., 2005). To date, nearly all of the localities preserving dinosaur bones in the Late Cretaceous of India are infratrappean in position. Exceptions include an associated partial titanosaur skeleton, now lost, that was found in an intertrappean deposit near Anjar, Gujarat (Ghevariya, 1988; Fig. 1), isolated bones from Ranipur, near Jabalpur (Mathur et al., 1990; Sahni and Tripathi, 1990; DMM and JAW, unpublished data), and sauropod bones from a well section in Ukala, near Dhar (Mohabey and Samant, 2013; Mohabey et al., 2018).

The three vertebrae described herein were collected from distinct depositional basins geographically separated by more than 850 km. Available magnetic polarity data suggest that Lameta Formation sediments exposed at Bara Simla are overlain by basalts deposited during magnetochron C29r, whereas those at Rahioli are overlain by basalts deposited during magnetochron C30n (Hansen et al., 2005; Mohabey and Samant, 2013). Radiometric age estimates are not yet available for these horizons.

The two dorsal vertebrae (GSI/GC/OGF107, GSI/GC/2905) were found at the Rahioli locality, in Kheda District, Gujarat State, western India (23° 3' 25.7" N, 73° 20' 31.8" E). They were collected in December 1984 by DMM at a spot <5 m from the pits left behind by the 1982–1984 Geological Survey of India excavation, which recovered remains that would later be described as the titanosaur *Jainosaurus* (e.g., Mathur and Pant, 1986) and the abelisaur *Rajasaurus* (Wilson et al., 2003). The two dorsal vertebrae were found in close association, with the more anterior element (GSI/GC/OGF107) positioned on top of the more posterior element (GSI/GC/2905). These two vertebrae were given field numbers OGF 107 and OGF 106, respectively ("OGF" refers to "Operation Gujarat fossil"). The specimen originally given field number OGF 106 was later accessioned as GSI/GC/2905 when it was initially described (Mohabey, 1989); the other retains its OGF number. The bones from the GSI pit excavations were preserved in a gray to greenish ossiferous conglomeratic layer that underlies medium- to coarse-grained indurated to friable sandstone that preserves dinosaur teeth (Mathur and Srivastava, 1987) and a fine-grained arenaceous limestone (calcrete) that preserves dinosaur eggs (Mohabey, 1984; Srivastava et al., 1986).

We recently inventoried the dinosaur bones collected from Rahioli in 1982–1984 by the GSI, which are housed at the GSI Western Region headquarters in Jaipur. This collection contains more than 350 titanosaur and abelisaur limb and girdle elements, but only one cranial element (*Rajasaurus* braincase) and very few (ca. 15) presacral elements. Although the high-energy environment suggested by the lithology of the deposit could be interpreted as having disrupted associations and damaged fragile cranial and pneumatic presacral elements, two facts about the quarry argue against this as the sole explanation for the observed pattern. First, close associations are recorded in the quarry, including the associated partial skeleton of *Rajasaurus* (Wilson et al., 2003: fig. 2) and the two dorsal vertebrae described here. Second, in addition to the two well-preserved sauropod presacral vertebrae described here, presacral vertebrae preserved elsewhere in the same exposure (JAW pers. obs.) and abelisaur cranial fragments left behind in pits (DMM pers. obs.) point towards a collection bias rather than a depositional or taphonomic bias.

Approximately 200 m north-northwest of the GSI pits is a second set of pits that was excavated by the Indian Statistical Institute (ISI) in the 1990s. The ISI pits produced the abelisaur *Rahiolisaurus* (Chatterjee and Rudra, 1996; Novas et al., 2010) and a braincase of the titanosaur *Isisaurus* (ISIR 467; Chatterjee and Rudra, 1996; Wilson et al., 2005). Lithological sections measured by DMM and JAW at Rahioli suggest that the GSI and ISI quarries represent lateral facies variants of one another. The layer that yielded *Rahiolisaurus* and *Isisaurus* in the ISI pits (23° 3' 25" N, 73° 20' 32" E) is a white to gray, medium- to very coarse-grained sandstone, occasionally cherty and with small pockets of conglomeratic sandstones, that unconformably overlies the granitic basement rock. The layer in the GSI pits that yielded titanosaur bones and *Rajasaurus* (23° 3' 25" N, 73° 20' 31" E), in contrast, is a 2.5 m to >3 m thick, hard, cherty gray to green oligomictic matrix-supported conglomerate with angular to subangular clasts of quartz, feldspar, chert, granite, and pegmatites (up to 20 cm). This layer unconformably overlies pegmatites and granites and grades vertically in to medium- to coarse-grained, patchily pebbly sandstone that contains fragmentary dinosaur bones.

The anterior caudal neural arch (338/GSI/PAL/CR/2017) is from the type locality of the sauropods "*Titanosaurus indicus*" and *Jainosaurus septentrionalis* at Bara Simla in Jabalpur, Madhya Pradesh State, central India. It was surface-collected by the authors in 2012 from a gulley on the north side of the track road leading up to the block house atop Bara Simla (23° 10' 13.7" N, 79° 58' 19.4" E). A large sauropod chevron measuring 47 cm proximodistally was found in situ nearby in the "Sauropod Bed" near the contact between the "Main Limestone" and the "Greensand" (see Matley, 1921; Huene and Matley, 1933: fig. 1).

Comments.— Remains of the titanosaurs *Isisaurus* and *Jainosaurus* have been collected from the Rahioli locality, and remains of *Jainosaurus* and the non-diagnostic "*Titanosaurus indicus*" have been recorded from the Bara Simla and Chhota Simla localities. Currently, only *Isisaurus* is known from presacral remains that can be compared directly to the two complete vertebrae described below. Anteriormost caudal vertebrae are not known for *Isisaurus* nor for any other Cretaceous Indian sauropod, and so there are no direct comparisons that can be made with the element described below.

DESCRIPTION

In the description of vertebral elements that follows, we use non-standardized orientational descriptors (e.g., "anterior," "posterior") rather than the corresponding terms specified by the Nomina Anatomica Avium or Nomina Anatomica Veterinaria (i.e., "cranial," "caudal"). Similarly, we use non-standard anatomical terms typically applied to sauropod axial elements rather than those specified by the NAA/NAV. That is, we use "centrum" instead of "corpus," and "prezygapophysis" rather than "cranial zygapophysis" (see Harris, 2004; Wilson, 2006). We apply current terminology for internal pneumaticity (Britt, 1993), vertebral laminae (Wilson, 1999, 2012), and vertebral fossae (Wilson et al., 2011b). Measurements are provided in Tables 1–4. The floor of the neural canal was used to establish horizontal in the description, measurements, and anatomical figures.

Dorsal Vertebra 2 (GSI/GC/OGF107)
Figs. 2–5; Tables 1–2

GSI/GC/OGF107 is a vertebra from the anterior part of the dorsal series. It most probably pertains to dorsal vertebra 2, but we cannot rule out the possibility that it is the first dorsal vertebra. Its estimated serial position is based on the position of the parapophysis on the anteroventral margin of

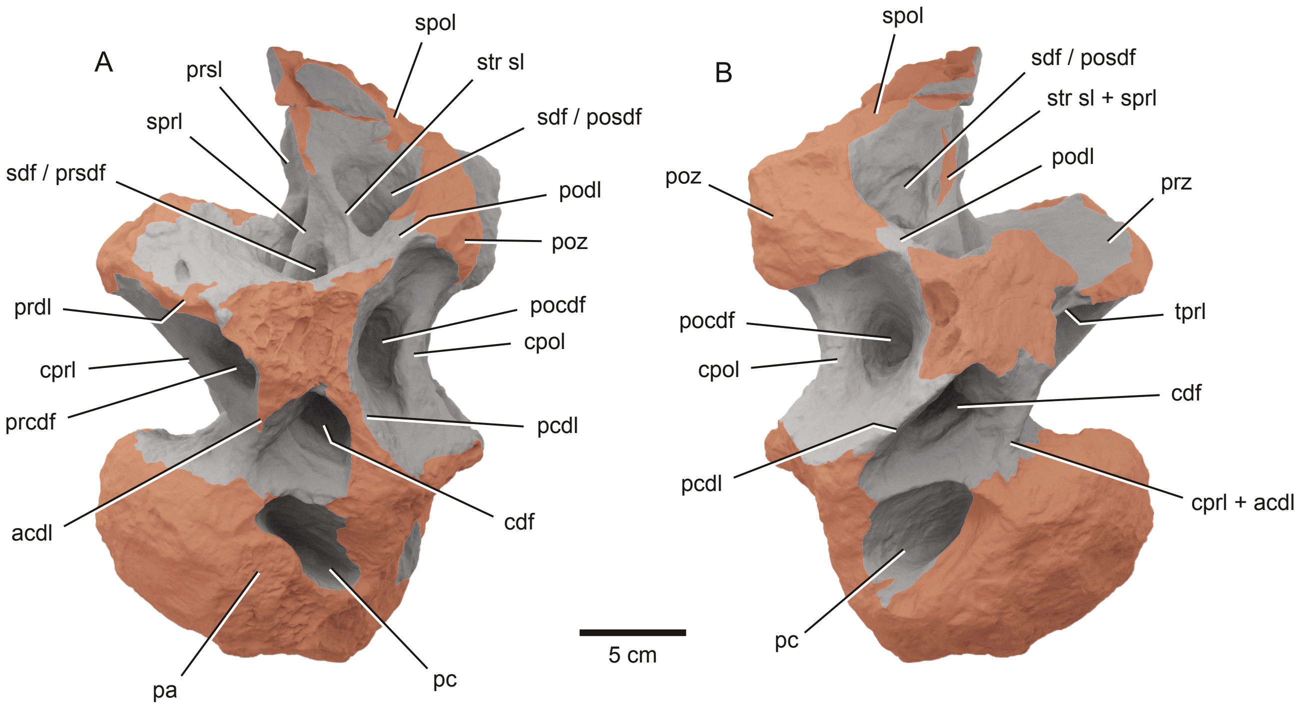

FIGURE 2 —Titanosaur dorsal vertebra 2 (GSI/GC/OGF107). Three-dimensional model based on photogrammetry of the original specimen in left lateral (A) and right lateral (B) views. Orange tone indicates broken areas. A plus sign ("+") between abbreviations for vertebral laminae means that the laminae are conjoined. A forward slash ("/") indicates that the identified structure is serially transitional between two structures but does not unambiguously represent either of them. Abbreviations: *acdl*, anterior centrodiapophyseal lamina; *cdf*, centrodiapophyseal fossa; *cpol*, centropostzygapophyseal lamina; *cprl*, centroprezygapophyseal lamina; *pa*, parapophysis; *pc*, pleurocoel; *pcdl*, posterior centrodiapophyseal lamina; *pocdf*, postzygapophyseal centrodiapophyseal fossa; *podl*, postzygodiapophyseal lamina; *posdf*, postzygapophyseal spinodiapophyseal fossa; *poz*, postzygapophysis; *prcdf*, prezygapophyseal centrodiapophyseal fossa; *prdl*, prezygodiapophyseal lamina; *prsdf*, prezygapophyseal spinodiapophyseal fossa; *prsl*, prespinal lamina; *prz*, prezygapophysis; *sdf*, spinodiapophyseal fossa; *spol*, spinopostzygapophyseal lamina; *sprl*, spinoprezygapophyseal lamina; *str sl*, stranded spinal lamina; *tprl*, intraprezygapophyseal lamina.

the pleurocoel, as best seen on the left side of the vertebra. In the cervical vertebrae of skeletally mature sauropods, the rib articulations are fused to the cervical rib, and the parapophysis extends from a position on the ventrolateral margin of the centrum (Wilson and Sereno, 1998). In contrast, mid-dorsal and posterior dorsal ribs are unfused to their corresponding vertebrae, which have the parapophysis positioned on the neural arch near the diapophysis and prezygapophysis. There is a gradual transition in the anterior dorsal region between these two parapophyseal positions—on the ventrolateral edge of the centrum in the cervical region and on the neural arch in mid-dorsal to posterior dorsal region. The general pattern for this transition in sauropods is that the parapophysis migrates dorsally in the first four dorsal vertebrae, taking positions on the ventral, anterior, and dorsal margins of the pleurocoel in dorsal vertebrae 1–3, respectively, eventually attaining a more vertically elongated shape and spanning the neurocentral junction in dorsal vertebra 4 (e.g., *Euhelopus zdanskyi*; Wilson and Upchurch, 2009).

GSI/GC/OGF107 is fairly well preserved but lacks the right prezygapophysis, most of the postzygapophyses, both diapophyses, and the distal portion of the neural spine. The condyle of the centrum is eroded ventrally, and the cotylar rim is not well preserved. Small-to-medium sized hematitic stains (<2 cm) mottle the surface of the bone.

Centrum.— The dimensions of the centrum are unknown because of the damage to its ventral surface, but it is clear that it is opisthocoelous with a marked anterior convexity that makes up at least one-third of the preserved length of the centrum (ca. 6 of 18 cm). The centrum is not quite as broad as it is long (transverse width = 15.2 cm; Table 2). Minimum estimates are possible for lateral convexity (0.39) and dorsoventral convexity (0.59) of the centrum, which are the ratios of condyle anteroposterior length to condyle transverse width and height, respectively (Fronimos and Wilson, 2017: fig. 6). These values suggest that dorsal centrum 2 was more resistant to forces translating the intervertebral joint dorsoventrally than transversely. The pleurocentral foramen is elliptical in outline, as best preserved in the right side where the long axis of the ellipse is more than twice as long as the short axis (7.1 cm x 2.7 cm; Table 1). The pleurocoel is oriented anterodorsally with respect to the vertebral axis; its

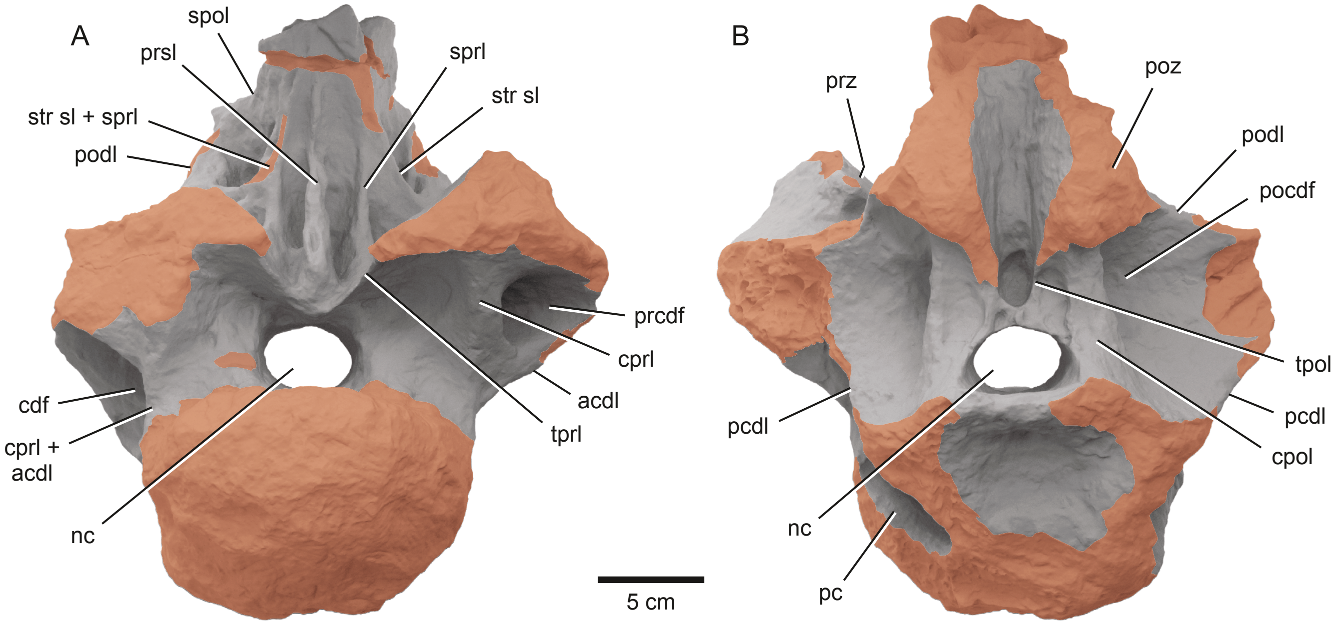

FIGURE 3 — Titanosaur dorsal vertebra 2 (GSI/GC/OGF107). Three-dimensional model based on photogrammetry of the original specimen in anterior (A) and posterior (B) views. Orange tone indicates broken areas. A plus sign ("+") between abbreviations for vertebral laminae means that both are present (i.e., laminae are conjoined). Abbreviations: *acdl*, anterior centrodiapophyseal lamina; *cdf*, centrodiapophyseal fossa; *cpol*, centropostzygapophyseal lamina; *cprl*, centroprezygapophyseal lamina; *nc*, neural canal; *pc*, pleurocoel; *pcdl*, posterior centrodiapophyseal lamina; *pocdf*, postzygapophyseal centrodiapophyseal fossa; *podl*, postzygodiapophyseal lamina; *poz*, postzygapophysis; *prcdf*, prezygapophyseal centrodiapophyseal fossa; *prsl*, prespinal lamina; *prz*, prezygapophysis; *spol*, spinopostzygapophyseal lamina; *sprl*, spinoprezygapophyseal lamina; *str sl*, stranded spinal lamina; *tpol*, intrapostzygapophyseal lamina; *tprl*, intraprezygapophyseal lamina.

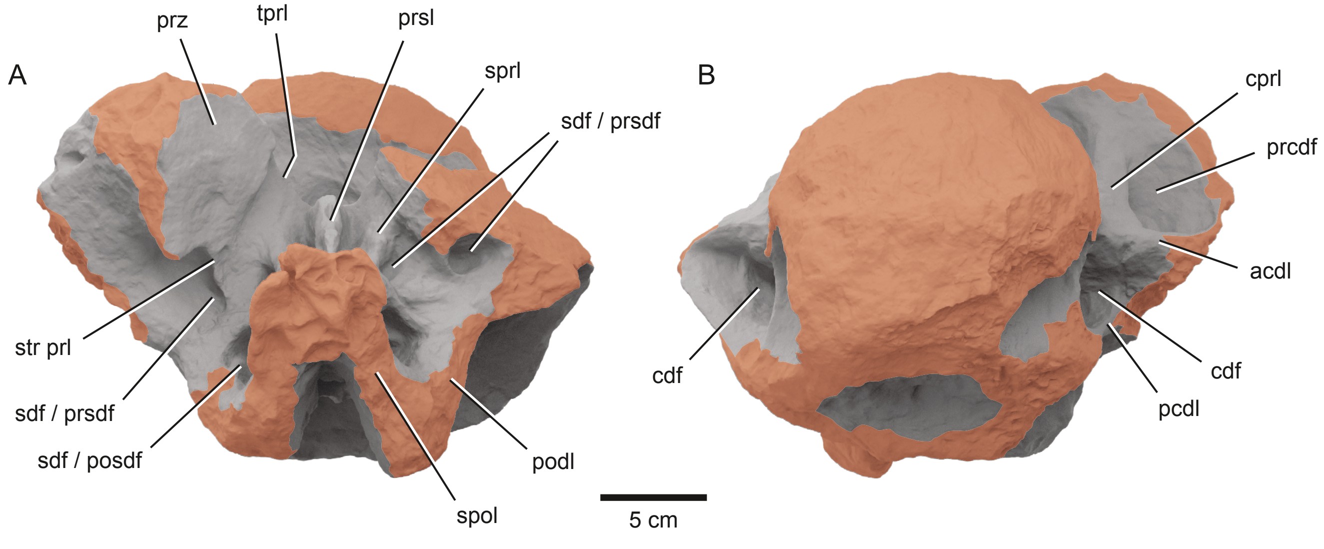

FIGURE 4 — Titanosaur dorsal vertebra 2 (GSI/GC/OGF107). Three-dimensional model based on photogrammetry of the original specimen in dorsal (A) and ventral (B) views. Orange tone indicates broken areas. A forward slash ("/") indicates that the identified structure is serially transitional between two structures but does not unambiguously represent either of them. Abbreviations: *acdl*, anterior centrodiapophyseal lamina; *cdf*, centrodiapophyseal fossa; *cprl*, centroprezygapophyseal lamina; *pcdl*, posterior centrodiapophyseal lamina; *podl*, postzygodiapophyseal lamina; *posdf*, postzygapophyseal spinodiapophyseal fossa; *prcdf*, prezygapophyseal centrodiapophyseal fossa; *prsdf*, prezygapophyseal spinodiapophyseal fossa; *prsl*, prespinal lamina; *prz*, prezygapophysis; *sdf*, spinodiapophyseal fossa; *spol*, spinopostzygapophyseal lamina; *sprl*, spinoprezygapophyseal lamina; *str prl*, stranded prezygapophyseal lamina; *tprl*, intraprezygapophyseal lamina.

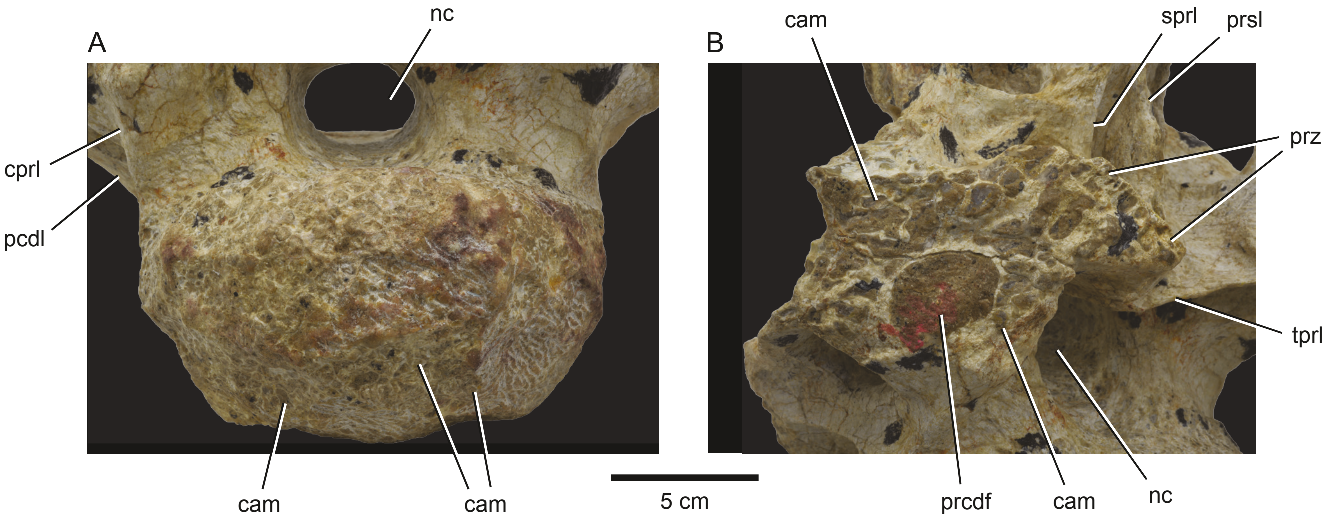

FIGURE 5 — Titanosaur dorsal vertebra 2 (GSI/GC/OGF107). Photographs showing pneumaticity in the centrum (A) and neural arch (B). Centrum is shown in anterior view; neural arch is in right lateral view. Abbreviations: *cam*, camellae; *cprl*, centroprezygapophyseal lamina; *nc*, neural canal; *pcdl*, posterior centrodiapophyseal lamina; *prcdf*, prezygapophyseal centrodiapophyseal fossa; *prsl*, prespinal lamina; *prz*, prezygapophysis; *sprl*, spinoprezygapophyseal lamina; *tprl*, intraprezygapophyseal lamina.

TABLE 1 — Measurements (cm) of vertebral fossae on the left and right sides of dorsal vertebra 2 (GSI/GC/OGF107). Depth measurement is the shortest distance between the deepest point of the fossa and the plane of the opening to that fossa. Long and short axes were taken at the interpreted margin of the fossa, which was based on bone texture and change in slope. An "i" indicates an incomplete measurement. Abbreviations: *CDF*, centrodiapophyseal fossa; *CPOF*, centropostzygapophyseal fossa; *POCDF*, postzygapophyseal centrodiapophyseal fossa; *POSDF*, postzygapophyseal spinodiapophyseal fossa; *PRCDF*, prezygapophyseal centrodiapophyseal fossa; *PRSDF*, prezygapophyseal spinodiapophyseal fossa; *SPRF*, spinoprezygapophyseal fossa.

Vertebral Fossa	Left			Right		
	Depth	Long Axis	Short Axis	Depth	Long Axis	Short Axis
SPRF	1.9	10.5i	1.4	2.5	10.5i	1.6
PRSDF	1.2	3.3	1.9	3.0	4.1	1.9
POSDF	3.9	4.3i	4.1	9.7	4.2	3.7
PRCDF	—	—	—	5.1	5.1	5.1
POCDF	5.3	8.3	8.0i	6.9	8.8	5.0i
CPOF	0.5	5.3	2.0	1.0	3.1	1.8
CDF	7.5	6.2	4.4	11.0	4.3	2.9
Pleurocoel	4.4	6.2	4.0i	3.8	7.1	2.7

long axis intersects the floor of the neural canal at an angle of approximately 41 degrees.

Costal Articulations.— The parapophysis is not well preserved on either side of the centrum, but its position can be inferred based on the rounded, dorsally directed deflection of the anteroventral margin of the pleurocoel on the left side (Fig. 2A). The surface of the parapophysis is sheared away, and so its exact shape cannot be determined.

The diapophysis is not preserved on either side of the neural arch, but the laminae that tie into it circumscribe its position. These laminae are oriented in a cruciate fashion, with two pairs of nearly collinear laminae oriented at nearly right angles to one another. The posterior centrodiapophyseal lamina (PCDL) and prezygodiapophyseal lamina (PRDL) are oriented anteroventrally-posterodorsally and 'crossed' by the anterodorsally-posteroventrally oriented anterior centrodiapophyseal lamina (ACDL) and postzygodiapophyseal lamina (PODL). A stranded lamina ties into the PODL, as discussed below.

Zygapophyses.— The prezygapophysis on the left side is nearly completely preserved, lacking only its anterior and lateral margins. As preserved it is level with the anterior margin of the centrum in lateral view, but it would have extended slightly beyond it when complete. The prezygapophyseal articular surface is fairly flat and oriented dorsomedially. Its posterior edge bears a rounded corner that overhangs a pneumatic fossa (see below).

The base of the postzygapophyses are preserved, but no part of their articular surface is present.

Neural Spine.— The neural spine is oriented nearly vertically when the neural canal is aligned horizontally. It is incompletely preserved, and so the details of its shape and

TABLE 2 — Measurements (cm) of dorsal vertebrae 2 (GSI/GC/OGF107) and 3 (GSI/GC/2905). Dorsoventral and lateral convexity measurements are the ratios of condyle length to either condyle height or width, respectively (see Fronimos and Wilson, 2017). An "i" indicates an incomplete measurement. "L" and "R" indicate left and right, respectively.

Measurement	GSI/GC/ OGF107	GSI/GC/ 2905
neural canal		
width, anterior	5.0	5.1
width, posterior	5.1	4.9
height, anterior	4.1	4.2
height, posterior	3.7	4.3
centrum		
length	18.0	14.3
height, posterior	10.1i	9.3
condyle		
length	6.0	4.6
width	15.2	14.2
height	—	9.4
dorsoventral convexity	—	0.49
lateral convexity	0.39	0.33
parapophysis		
L, dorsoventral height	3.3i	6.1i
L, anteroposterior length	3.7	2.6i
R, dorsoventral height	—	7.0
R, anteroposterior length	—	3.5

length cannot be determined. Its vertebral laminae are well preserved, as discussed below.

Vertebral Laminae & Pneumaticity.— Anterior dorsal vertebra GSI/GC/OGF107 forms part of the transition between the arrangement of vertebral laminae in the cervical series and that in the mid-dorsal and posterior dorsal series. In the cervical series of most neosauropods, vertebrae are anteroposteriorly elongate and dorsoventrally low. In contrast, mid-dorsal to posterior dorsal vertebrae are anteroposteriorly abbreviate and dorsoventrally tall. The shape of the neural arch is strongly affected by these proportional differences. For example, consider the four projections of the presacral neural arch (viz., neural spine, diapophyses, zygapophyses) and the laminae that interconnect them, which define a quadrilateral space in lateral view (Fig. 6) that is comparable to the "zona lateral dorsal" of Bonaparte (1999: p. 118; fig. 1). In the cervical series, the long axis of that quadrilateral is anteroposteriorly directed and braced by the epipophyseal-prezygapophyseal lamina (EPRL), which horizontally separates vertically stacked spinodiapophyseal fossae (SDF1, SDF2). In the mid-dorsal to posterior dorsal series, in contrast, the long axis of the neural arch quadrilateral is dorsoventrally elongate and braced by the spinodiapophyseal lamina (SPDL), which vertically separates the prezygapophyseal spinodiapophyseal fossa (PRSDF) and the postzygapophyseal spinodiapophyseal fossa (POSDF). The SPDL and associated fossae are not present in cervical vertebrae, and the EPRL and associated fossae are not present in mid-dorsal to posterior dorsal vertebrae. In transitional vertebrae such as GSI/GC/OGF107, though, elements of both may be present.

Disappearance of the EPRL and appearance of the SPDL took place in piecemeal fashion in GSI/GC/OGF107, based on the presence of 'stranded' prezygapophyseal and spinal laminae, respectively. 'Stranded' laminae contact only one of two landmarks but represent serial variants of true laminae that join two landmarks in preceding and/or subsequent vertebrae (see Wilson, 2012: p. 97). Left and right prezygapophyses each bear a short stranded lamina that separates two small fossae. The stranded prezygapophyseal lamina ends abruptly, as do the associated fossae. This lamina is asymmetrically developed on either side of the vertebra, with the left slightly longer than the right (3 cm vs. 2 cm long). It is likely that this stranded prezygapophyseal lamina is a remnant of the EPRL present in the cervical vertebrae. Likewise, the two small fossae on either side of the stranded prezygapophyseal lamina are serial variants of the spinodiapophyseal fossae present in the cervical series. Interestingly, these fossae also represent serial variants of the PRSDF (present in more posterior vertebrae) because an incipient SPDL is also present in this vertebra. This incipient SPDL, which is technically a stranded spinal lamina, is conjoined with the spinoprezygapophyseal lamina (SPRL) in a thick compound lamina on the distal portion of the neural spine. The incipient SPDL diverges laterally toward the diapophysis, eventually contacting the postzygodiapophyseal lamina (PODL) to partly define the triangular fossa that represents a serial variant of the SDFs and the POSDF. The pneumatic fossae associated with these 'stranded' laminae (i.e., relictual EPRL and incipient SPDL) are referred to as "SDF/PRSDF" and "SDF/POSDF" in Figures 2 and 4.

The relative development of the EPRL and SPDL in GSI/GC/OGF107—the EPRL being much further reduced and the SPDL much more developed—is consistent with the estimated anterior dorsal serial position of GSI/GC/OGF107. It is likely that the balance between these two laminae would be tipped more towards the EPRL in the preceding vertebra (dorsal vertebra 1) and more towards the SPDL in the succeeding vertebra (dorsal vertebra 3), which is described below.

Other vertebral laminae in GSI/GC/OGF107 have an arrangement similar to that found in other titanosaurs. The diapophysis has two laminae extending towards the centrum, the anterior centrodiapophyseal lamina (ACDL) and the posterior centrodiapophyseal lamina (PCDL). These laminae diverge ventrally at an angle of 50–55°, framing all but the ventral margin of the centrodiapophyseal fossa (CDF). The ACDL merges with the centroprezygapophyseal lamina (CPRL) just before reaching the anterior centrum. Together,

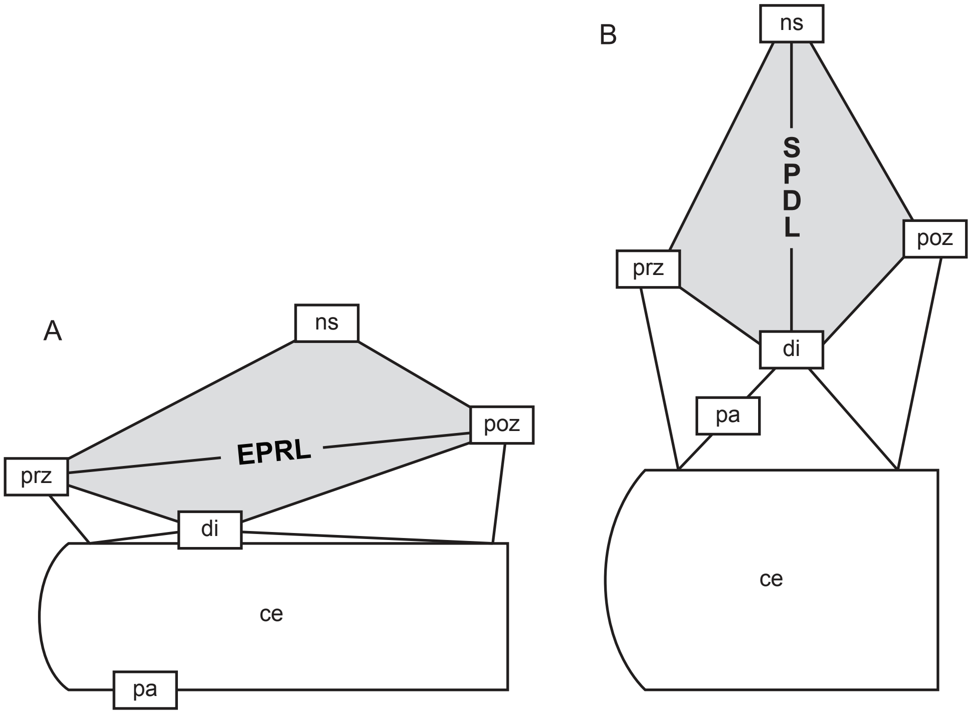

FIGURE 6 — Schematic depictions of the neural arch laminae of cervical (A) and dorsal (B) vertebrae of sauropod dinosaurs. The four main projections of the neural arch (neural spine, prezygapophysis, postzygapophysis, diapophysis) approximate an elongate quadrilateral (gray tone). In cervical vertebrae, the long axis of the quadrilateral is braced by the EPRL; in dorsal vertebrae, it is braced by the SPDL. Abbreviations: *ce*, centrum; *di*, diapophysis; *eprl*, epipophyseal prezygapophyseal lamina; *ns*, neural spine; *pa*, parapophysis; *poz*, postzygapophysis; *prz*, prezygapophysis; *spdl*, spinodiapophyseal lamina.

the ACDL, CPRL, and PRDL form the margin of the PRCDF, which is well preserved on the left side and can be seen in oblique section on the right side (Fig. 5B). The diapophysis also has laminae extending towards the zygapophyses, the PRDL and PODL. The PODL merges with the stranded spinal lamina (i.e., the incipient SPDL) midway along the distance to the diapophysis.

Spinoprezygapophyseal laminae (SPRLs) flank a median prespinal lamina (PRSL) and define vertically elongate SPRFs. Near the base of the neural arch, each SPRF is subdivided by transverse ridges resembling those preserved in the anterior caudal neural arch (338/GSI/PAL/CR/2017) described below. Intraprezygapophyseal laminae (TPRLs) tie in to the ventral PRSL at the midline. The TPRLs are the most delicate of all preserved laminae, with a minimum thickness of only 2 mm. The TPRLs, CPRLs, neural canal, and centrum bound paramedian CPRFs that are subtly subdivided by a low oblique ridge. Small, well defined fossae (ca. 0.5 cm) are present within the upper subdivision of each CPRF.

The spinopostzygapophyseal laminae (SPOLs) are quite broad as preserved, averaging about 2.5 cm along their length. Together they define a fairly narrow (4.5 cm) postspinal fossa that bears a low postspinal lamina (POSL). Two sets of laminae emerge from the ventral portion of each postzygapophysis, the centropostzygapophyseal lamina (CPOL) and the intrapostzygapophyseal lamina (TPOL). Whereas the corresponding laminae on the prezygapophyses define a fairly large, subdivided fossa, there is very little development of the centropostzygapophyseal fossae (CPOFs). There is a small CPOF present on the right side (3.1 cm tall x 1.8 cm wide x 1.0 cm deep) and a broader, shallower fossa on the left (5.3 cm tall x 2.0 cm wide x 0.5 cm deep; Table 1). Like the SPOLs, the CPOLs are fairly robust laminae. They form the posterior margin of the largest fossa on the neural arch, the posterior centrodiapophyseal fossa (POCDF). The POCDF is bordered dorsally by the PODL and anteriorly by the PCDL.

Computed tomography imaging was not capable of resolving differences in density between bone and matrix in GSI/GC/OGF107, and so detailed reconstruction and interpretation of internal pneumaticity is not possible. However, the presence of numerous breaks on the centrum and neural arch allows for coarse evaluation of regional differences in pneumaticity. Camellate pneumaticity is present throughout the centrum as well as in the zygapophyses, diapophysis, and neural spine. Size of the camellae differs between centrum and neural arch. Camellae in the centrum tend to be smaller, and interstitial bone is thinner. In contrast, the camellae of the neural arch are larger and subdivided by thicker bony septa (Fig. 5).

Dorsal Vertebra 3 or 4 (GSI/GC/2905)
Figs. 7–9; Tables 2–3

We estimate that GSI/GC/2905 is an anterior dorsal vertebra, possibly dorsal vertebra 3 or 4, based on the position of the parapophysis on the anterodorsal margin of the pleurocoel, extending dorsally towards the neural arch. This vertebra was preserved in association with GSI/GC/OGF107; based on its similar serial position, it is likely that they pertain to the same individual.

GSI/GC/2905 is moderately well preserved and includes much of the centrum and the anterior portion of the neural arch. The centrum lacks most of the ventral portion of the anterior articular surface (condyle) and much of the perimeter of the posterior articular surface (cotyle). The neural arch includes the prezygapophyses and the left diapophysis, but the right diapophysis, postzygapophyses, and neural spine were not preserved. The anterior margin of the left prezygapophysis and the posterior and distal portions of the left diapophysis have been broken away.

Centrum.— The centrum is opisthocoelous, as evidenced by the convex condyle, but due to preservation the depth of the cotyle cannot be measured in this specimen. Minimum estimates are possible for lateral condylar convexity (>0.33) and dorsoventral convexity (>0.49), which are consistent with values for the preceding vertebra (GSI/GC/OGF107). The pleurocoel is relatively small and elliptical, with its long axis nearly two times the length of its short axis (left = 6.0 x 3.2 cm; right = 5.9 x 3.2 cm). Like GSI/GC/OGF107, the long axis of the pleurocoel in GSI/GC/2905 is angled anterodorsally approximately 23 degrees with respect to the vertebral axis, which is established by the floor of the neural canal.

Costal Articulations.— The parapophysis is recognizable on both sides of the centrum. It is a dorsoventrally elongate structure that is slightly emarginated on its ventral half by the pleurocoel. It appears to traverse the neurocentral junction, but most of it is positioned on the centrum. There is some uncertainty about the extent of the left parapophysis, owing to damage near the neurocentral junction, and it is possible that it extends to the other side of the epoxy-filled crack (height = 9.4 cm).

The left diapophysis is more completely preserved than the right but lacks its posterior end and its distal surface. Nevertheless, all the vertebral laminae supporting the diapophysis are preserved, as is a well-marked, transversely oriented fossa on its dorsal surface (see below). The diapophysis is horizontally oriented and extends directly laterally with respect to the sagittal plane. It is broader anteroposteriorly than it is tall dorsoventrally.

Zygapophyses.— The left prezygapophysis is the better

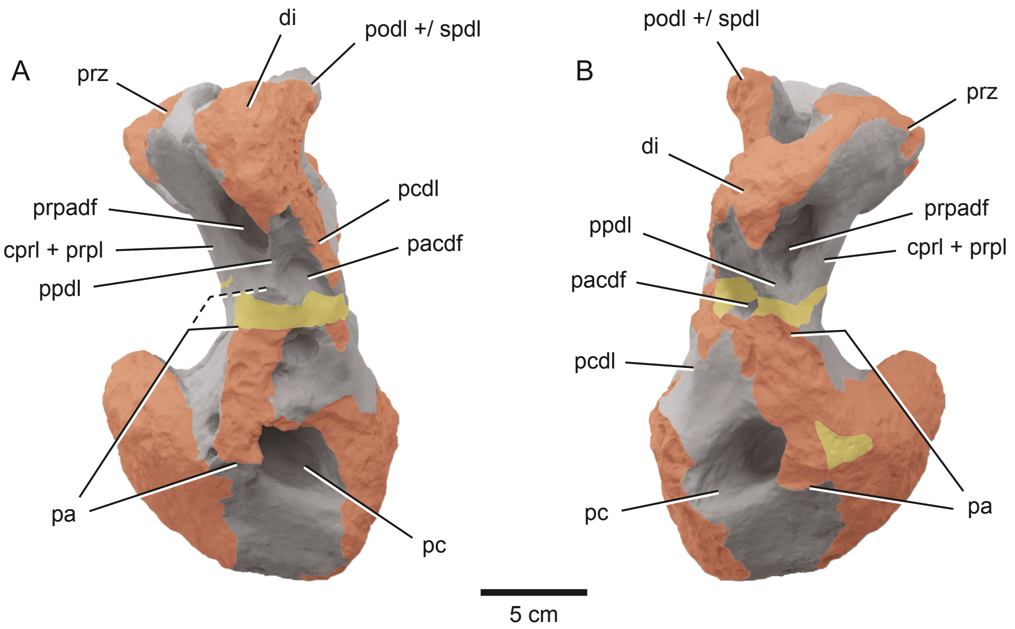

FIGURE 7 — Titanosaur dorsal vertebra 3 (GSI/GC/2905). Three-dimensional model based on photogrammetry of a cast specimen in left lateral (A) and right lateral (B) views. Orange tone indicates broken areas; yellow tone indicates matrix (in this case, epoxy filling a deep crack). A plus sign (“+”) between abbreviations for vertebral laminae means that the laminae are conjoined. A plus and forward slash (“+/”) indicates that the identified structure is ambiguous and either or both are present. The dashed leader line indicates uncertainty in the dorsal extent of the parapophysis. Abbreviations: *cprl*, centroprezygapophyseal lamina; *di*, diapophysis; *pa*, parapophysis; *pacdf*, parapophyseal centrodiapophyseal fossa; *pc*, pleurocoel; *pcdl*, posterior centrodiapophyseal lamina; *podl*, postzygodiapophyseal lamina; *ppdl*, parapodiapophyseal lamina; *prpadf*, prezygapophyseal paradiapophyseal fossa; *prpl*, prezygoparapophyseal lamina; *prz*, prezygapophysis; *spdl*, spinodiapophyseal lamina.

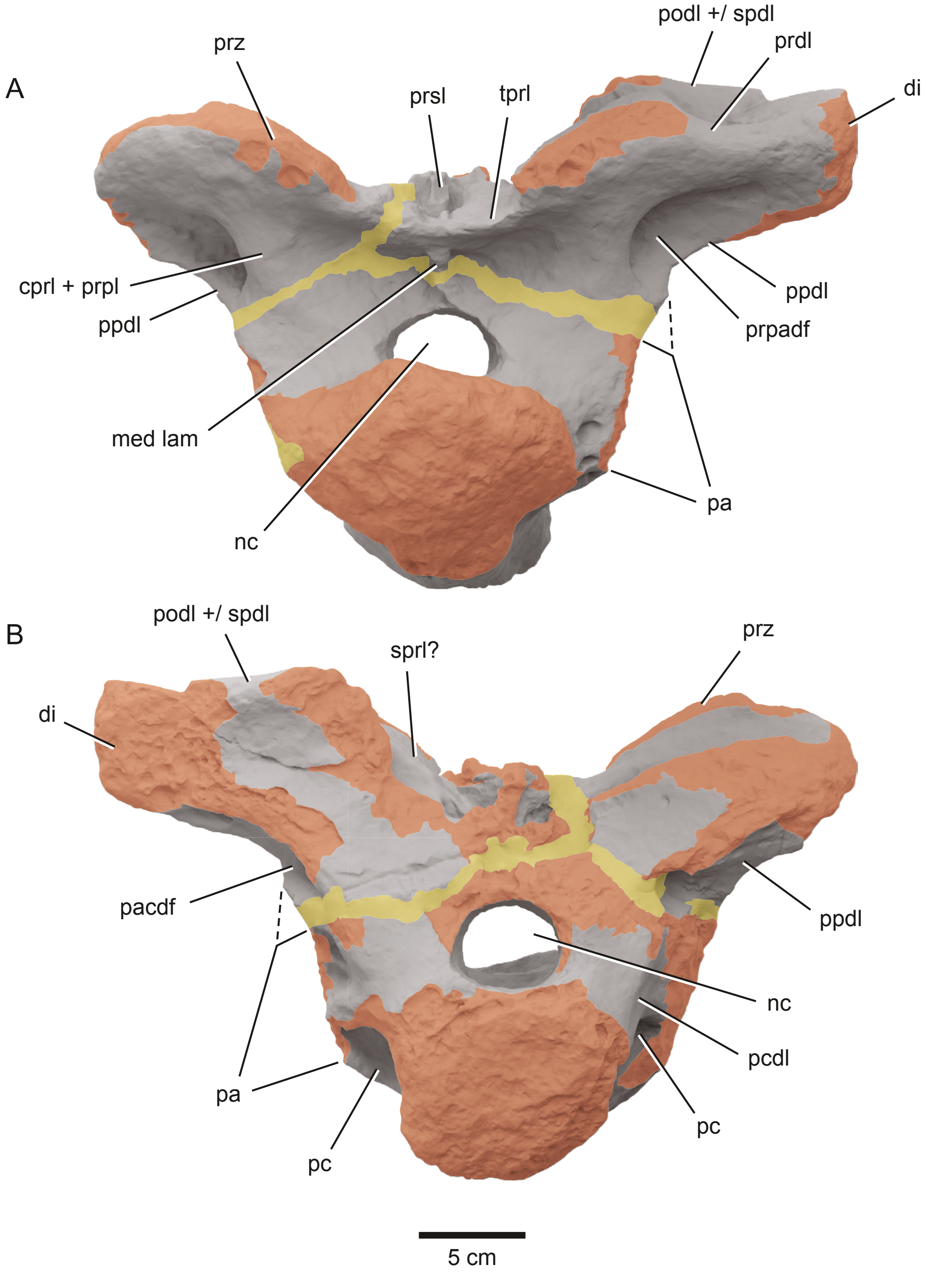

FIGURE 8 — Titanosaur dorsal vertebra 3 (GSI/GC/2905). Three-dimensional model based on photogrammetry of a cast specimen in anterior (A) and posterior (B) views. Orange tone indicates broken areas; yellow tone indicates matrix (in this case, epoxy filling a deep crack). A plus sign ("+") between abbreviations for vertebral laminae means that the laminae are conjoined. A plus and forward slash ("+/") indicates that the identified structure is ambiguous and either or both are present. A question mark ("?") indicates an uncertain identification. The dashed leader line indicates uncertainty in the dorsal extent of the parapophysis. Abbreviations: *cprl*, centroprezygapophyseal lamina; *di*, diapophysis; *med lam*; median lamina; *nc*, neural canal; *pa*, parapophysis; *pacdf*, parapophyseal centrodiapophyseal fossa; *pc*, pleurocoel; *pcdl*, posterior centrodiapophyseal lamina; *podl*, postzygodiapophyseal lamina; *ppdl*, parapodiapophyseal lamina; *prdl*, prezygodiapophyseal lamina; *prpadf*, prezygapophyseal paradiapophyseal fossa; *prpl*, prezygoparapophyseal lamina; *prsl*; prespinal lamina; *prz*, prezygapophysis; *spdl*, spinodiapophyseal lamina; *sprl*, spinoprezygapophyseal lamina; *tprl*, intraprezygapophyseal lamina.

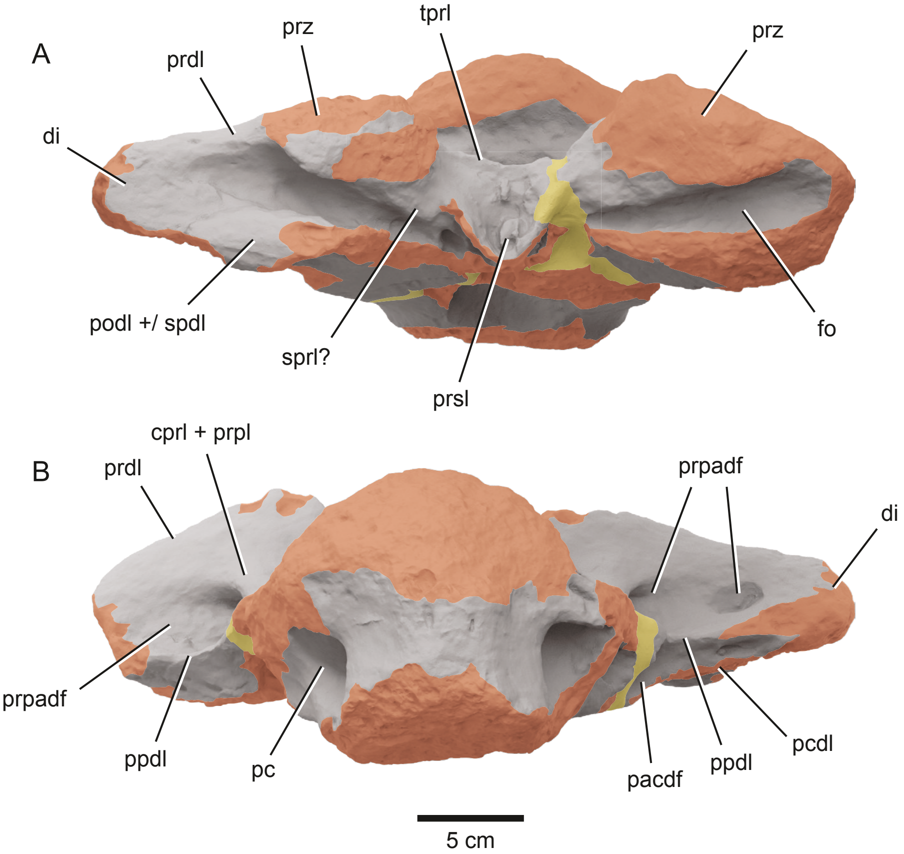

FIGURE 9 — Titanosaur dorsal vertebra 3 (GSI/GC/2905). Three-dimensional model based on photogrammetry of a cast specimen in dorsal (A) and ventral (B) views. Orange tone indicates broken areas; yellow tone indicates matrix (in this case, epoxy filling a deep crack). A plus sign ("+") between abbreviations for vertebral laminae means that both are present (i.e., laminae are conjoined). A plus and forward slash ("+/") between abbreviations for vertebral laminae means that identity of the structure is ambiguous and either or both could be present. A question mark ("?") indicates an uncertain identification. Abbreviations: *cprl*, centroprezygapophyseal lamina; *di*, diapophysis; *fo*, fossa; *pacdf*, parapophyseal centrodiapophyseal fossa; *pc*, pleurocoel; *pcdl*, posterior centrodiapophyseal lamina; *podl*, postzygodiapophyseal lamina; *ppdl*, parapodiapophyseal lamina; *prdl*, prezygodiapophyseal lamina; *prpadf*, prezygapophyseal paradiapophyseal fossa; *prpl*, prezygoparapophyseal lamina; *prsl*; prespinal lamina; *prz*, prezygapophysis; *spdl*, spinodiapophyseal lamina; *sprl*, spinoprezygapophyseal lamina; *tprl*, intraprezygapophyseal lamina.

preserved of the two, but it lacks the anterior and lateral margins of its articular surface. Like GSI/GC/OGF107, the prezygapophyses bear sharply defined TPRLs that form a roof over entrance to the neural canal. They fuse at the midline and are supported below by a median lamina, which is incipiently developed in GSI/GC/OGF107. A lamina emerges from the posteromedial edge of the prezygapophysis, as in GSI/GC/OGF107, but its terminus is unclear. It may have continued as the SPRL, as in the preceding vertebra. As in GSI/GC/OGF107, the posterior corner of the prezygapophyseal articular surface extends posteriorly over a fossa, but in this case that fossa can unambiguously be identified as an elongate PRSDF.

Postzygapophyses were not preserved.

Neural Spine.— Most of the neural spine is missing, but the base of the prespinal lamina (PRSL) is preserved.

Vertebral Laminae and Pneumaticity.— Four diapophyseal laminae are preserved. The identity of three of them is clear because both landmarks are preserved. Below the diapophysis are two laminae that form an acute angle defining a small fossa. The more anterior of the two, the paradiapophyseal lamina (PPDL), extends to the parapophysis. The more posterior of the two is the vertically oriented PCDL. The parapophyseal centrodiapophyseal fossa (PACDF) they bound is relatively small and shallow, but there are indications that it is subdivided into dorsal and ventral fossae. The measurements in Table 4 reflect this interpretation. Dorsally, there are two diapophyseal laminae preserved, which are transversely oriented. The more anterior of the two is the robust PRDL, which extends medially towards the prezygapophysis. On the posterior edge of the diapophysis, running nearly parallel to the PRDL, is a partially preserved lamina that could represent the PODL, the

TABLE 3 — Measurements (cm) of vertebral fossae on the left and right sides of dorsal vertebra 3 (GSI/GC/2905). Depth measurement is the shortest distance between the deepest point of the fossa and the plane of the opening to that fossa. Long and short axes were taken at the interpreted margin of the fossa, which was based on bone texture and change in slope. An "i" indicates an incomplete measurement; an "e" indicates an estimate. Abbreviations: *PACDF*, parapophyseal centrodiapophyseal fossa; *PRPADF*, prezygapophyseal parapodiapophyseal fossa.

Vertebral Fossa	Left			Right		
	Depth	Long Axis	Short Axis	Depth	Long Axis	Short Axis
PRPADF	2.3	7.5	3.2	1.8	6.3i	—
PACDF	1.1	6.0e	2.6	2.0	5.1i	1.8i
Pleurocoel	3.9	6.0	3.2	3.6	5.9	3.2

SPDL, or both if they were conjoined near the neural spine as they are in GSI/GC/OGF107 and some lognkosaurians. Together with the PRDL, the PODL+/SPDL defines a narrow (ca. 2 cm), transversely oriented fossa similar to that present in anterior dorsal vertebrae of the lognkosaurines *Mendozasaurus* (González Riga, 2005: fig. 5C; González Riga et al., 2018: fig. 8F) and *Futalognkosaurus* (Calvo et al., 2007b: fig. 13).

Three prezygapophyseal laminae are also present. As mentioned above, the TPRLs extend to the neural canal. Lateral to each TRPL is a broad lamina (ca. 4 cm) that is poorly defined medially but sharply defined laterally by a fossa bounded by the prezygapophysis, parapophysis, and diapophysis (i.e., the PRPADF). The lamina extends ventrally from the prezygapophysis towards the centrum and parapophysis and represents a composite of the CPRL and PRPL. The PRPADF is completely preserved on the left side, where it is subdivided into two smaller fossae; one is large and tucked behind the CPRL + PRPL, and the other is smaller and located near the diapophysis. A partially preserved lamina emerging from the medial surface of the prezygapophysis may represent a SPRL.

Anterior Caudal Vertebra (338/GSI/PAL/CR/2017)
Figs. 10–12; Table 4

Specimen 338/GSI/PAL/CR/2017 is an anterior caudal neural arch that was broken away from its centrum. It was surface collected, and the break is clean, but no additional remains were found in the area. It is possible that the centrum was collected prior to our exploration of the site, which is located alongside the track road leading up Bara Simla. The neural arch is nearly complete, lacking only the distal portion of the left side of its neural spine, and it preserves fine structural details such as delicate vertebral laminae (ca. 1 mm thick) and striations on the prezygapophyses. The neural arch has experienced slight anteroposterior shearing, with its right side translated nearly 2 cm forward of its left side. In addition to this preservational asymmetry, there is also natural asymmetry in the development of the pneumatic spaces on either side of the neural arch (see below).

The neural arch is fairly large, with an interzygapophyseal distance of 28.5 cm. The neural spine was not complete distally on the left side, and the base of the neural arch is not complete, but the preserved portion of the specimen allows us to estimate that the height of the neural arch was more than 16 cm, or at least 56% the interzygapophyseal distance.

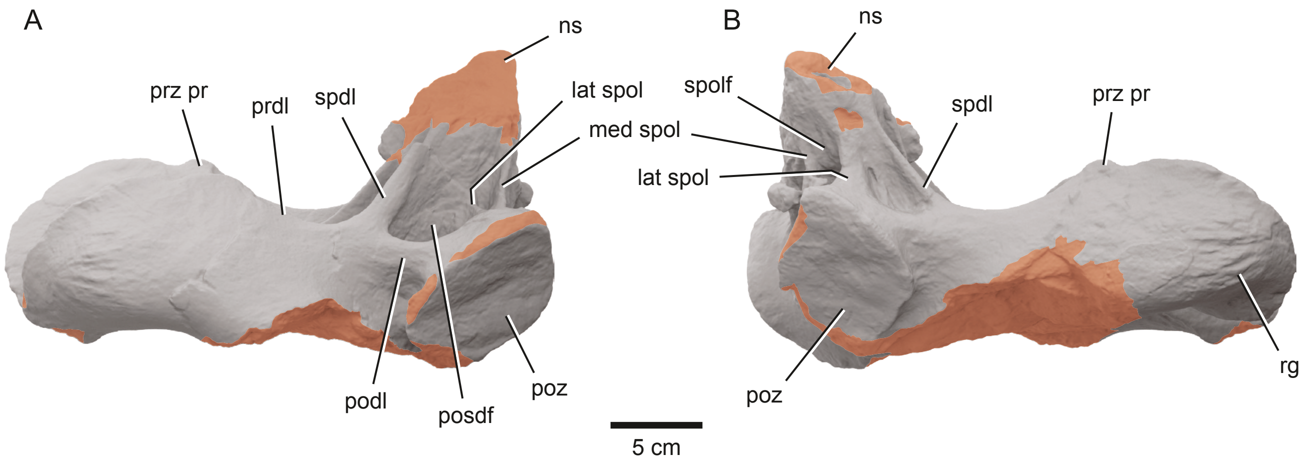

FIGURE 10 — Titanosaur anterior caudal vertebra (338/GSI/PAL/CR/2017). Three-dimensional model based on photogrammetry of the original specimen in left lateral (A) and right lateral (B) views. Orange tone indicates broken areas. Abbreviations: *lat spol*, lateral spinopostzygapophyseal lamina; *med spol*, medial spinopostzygapophyseal lamina; *ns*, neural spine; *podl*, postzygodiapophyseal lamina; *posdf*, postzygapophyseal spinodiapophyseal fossa; *poz*; postzygapophysis; *prdl*, prezygodiapophyseal lamina; *prz pr*, prezygapophyseal process; *rg*, rugosity; *spdl*, spinodiapophyseal lamina; *spolf*, spinopostzygapophyseal lamina fossa.

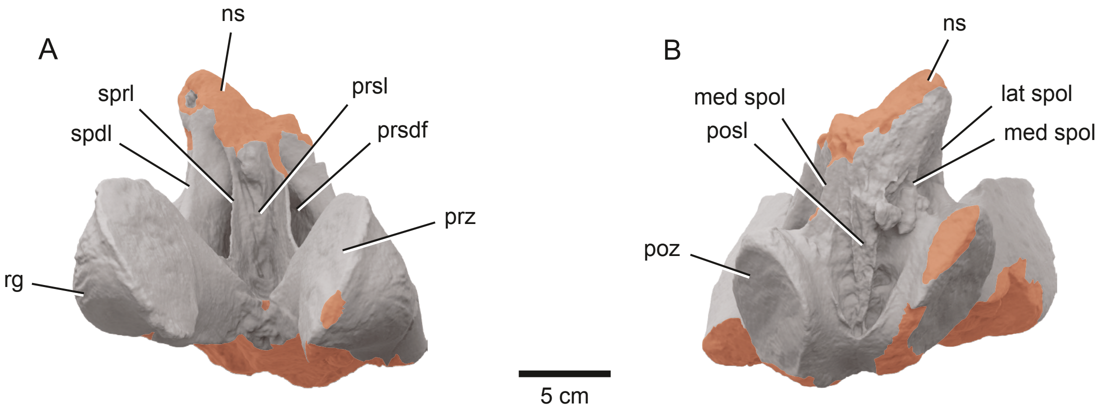

FIGURE 11 — Titanosaur anterior caudal vertebra (338/GSI/PAL/CR/2017). Three-dimensional model based on photogrammetry of the original specimen in anterior (A) and posterior (B) views. Orange tone indicates broken areas. Abbreviations: *lat spol*, lateral spinopostzygapophyseal lamina; *med spol*, medial spinopostzygapophyseal lamina; *ns*, neural spine; *posl*, postspinal lamina; *poz*; postzygapophysis; *prsdf*, prezygapophyseal spinodiapophyseal fossa; *prsl*, prespinal lamina; *prz*; prezygapophysis; *rg*, rugosity; *spdl*, spinodiapophyseal lamina; *sprl*, spinoprezygapophyseal lamina.

The degree of lamination, external pneumaticity, and relative size of the prezygapophyses indicate that this is an anterior caudal vertebra, but further refinement of this serial determination is not possible without transverse processes and centrum.

Zygapophyses.— The prezygapophyses are the most prominent processes preserved on the neural arch. They extend away from the vertebra approximately 16 cm from the preserved base of the neural arch. The prezygapophyseal processes are quite robust (8.5 cm dorsoventrally x 6.5 cm transversely), and they expand laterally and bear a roughened distolateral surface. Similarly expanded prezygapophyseal processes are present in caudal vertebrae of the lognkosaurian *Mendozasaurus* (IANIGLA-Pv-065/5–6; González-Riga, 2003). The prezygapophyseal articular facets are large and elliptical (10.5 x 8.9 cm), and their long axis is tipped anteroventrally approximately 38 degrees with respect to the prezygapophyseal process. The prezygapophyseal facets are flat and outwardly canted approximately 30 degrees laterally with respect to the mid-sagittal plane.

The pre- and postzygapophyseal articular facets bear distinctive surface groovings, which are developed to varying degrees on each of the four. The left prezygapophysis bears conspicuous coarse-scale undulations and fine-scale striae. Although similar structures are present on the right prezygapophysis, they are not mirror images of one another. The postzygapophyses bear only faint structures and finer scale undulations. Although we are not aware of similar striations on the zygapophyseal articulations of other sauropods, these features appear to be natural. Post-mortem alteration of the bone by scavengers, for example gnawing or scraping, typically would leave behind sharp traces that expose the internal cortex of the bone. In addition, scavenging might be expected to extend beyond the zygapophyses to other regions of the vertebra.

Neural Spine.— The neural spine is incomplete on the left side, but enough of the right side is preserved to infer its overall shape. The neural spine is fairly short, rising only 6 cm above the level of the postzygapophyses. It expands slightly towards its distal end, reaching a maximum transverse breadth of approximately 8 cm (estimate made by doubling distance from midline to right lateral edge of spine). Interspinous ligament attachments are developed as prespinal and postspinal laminae (PRSL, POSL), which increase in breadth towards the spine summit. The distal neural spine appears to have a roughened surface texture, as in many titanosaur caudal neural spines (e.g., *Futalognkosaurus*; Calvo et al., 2007b). A small fossa that may be pneumatic in origin is present within this roughened region on the right side of the neural spine summit.

Vertebral Laminae & Pneumaticity.— The most conspicuous feature of this caudal neural arch is the architecture of its vertebral laminae and pneumatic fossae, which is somewhat asymmetrically developed. Vertebral laminae are more prominent and pneumatic fossae are deeper and more sharply defined on the left side than on the right. Pneumaticity in this caudal neural arch is restricted to external pneumatic fossae bounded by vertebral laminae; the broken ventral surface of the neural arch reveals that there is no internal camellate pneumaticity, unlike the condition in saltasaurine titanosaurs (Powell, 1987, 2003; Zurriaguz et al., 2017).

Two pairs of vertebral laminae and three vertebral fossae extend anteriorly from the neural spine. Closest to the midline, the paired spinoprezygapophyseal laminae (SPRLs) extend towards the prezygapophyses and are separated from one another by a median spinoprezygapophyseal fossa (SPRF), which is partially divided by the prespinal lamina (PRSL). The SPRF is subdivided by short, transversely oriented struts at the midline, where it reaches its deepest point (3.2 cm; Table 4). Similarly subdivided pneumatic fossae are present in the

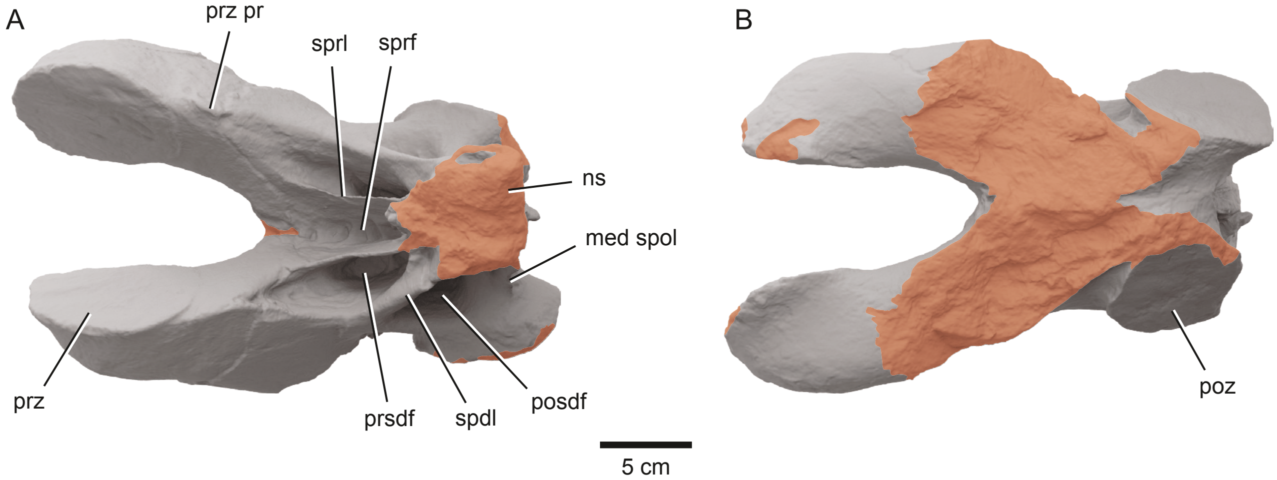

FIGURE 12 — Titanosaur anterior caudal vertebra (338/GSI/PAL/CR/2017). Three-dimensional model based on photogrammetry of the original specimen in dorsal (A) and ventral (B) views. Orange tone indicates broken areas. Abbreviations: *med spol*, medial spinopostzygapophyseal lamina; *ns*, neural spine; *posdf*, postzygapophyseal spinodiapophyseal fossa; *poz*; postzygapophysis; *prsdf*, prezygapophyseal spinodiapophyseal fossa; *prz*; prezygapophysis; *prz pr*, prezygapophyseal process; *spdl*, spinodiapophyseal lamina; *sprf*, spinoprezygapophyseal fossa; *sprl*, spinoprezygapophyseal lamina.

caudal vertebrae of *Bonatitan* (Martinelli and Forasiepi, 2004: fig. 13). The right SPRL is extremely delicate, narrowing to a transverse width of only 2 mm. A second set of vertebral laminae laterally flank the SPRLs as they emerge from the neural spine. On the left side, this lamina extends anterolaterally to intersect laminae emerging from the prezygapophysis and postzygapophysis. On the right side, a similar configuration is present, but the lamina extending from the postzygapophysis is less well developed. We interpret this as the spinodiapophyseal lamina (SPDL) intersecting the prezygodiapophyseal lamina (PRDL) and postzygodiapophyseal lamina (PODL) near the preservational margin of the neural arch. One shortcoming of this interpretation is that there are no preserved transverse processes nor any roughening or other signs of a ‘diapophyseal’ region. The alternative interpretation, that the second set of laminae emerging from the neural spine are duplicated SPRLs and the zygapophyseal laminae are EPRLs, is less likely because no such pattern has been recorded thus far in sauropod dinosaurs.

TABLE 4 — Measurements (cm) of vertebral fossae on the left and right sides of the anterior caudal vertebra (338/GSI/PAL/CR/2017). Depth measurement is the shortest distance between the deepest point of the fossa and the plane of the opening to that fossa. Long and short axes were taken at the interpreted margin of the fossa, which was based on bone texture and change in slope. An “i” indicates an incomplete measurement; an “e” indicates an estimate. Measurements for the median fossa (SPRF) were listed in the “Left” column, and “Right” was left blank. Abbreviations: *POSDF*, postzygapophyseal spinodiapophyseal fossa; *PRSDF*, prezygapophyseal spinodiapophyseal fossa; *SPOLF*, spinopostzygapophyseal lamina fossa; *SPRF*, spinoprezygapophyseal fossa.

Vertebral Fossa	Left			Right		
	Depth	Long Axis	Short Axis	Depth	Long Axis	Short Axis
SPRF	3.2	9.7	3.5	—	—	—
PRSDF	4.0	8.3	2.8	4.0	7.5e	2.5
POSDF	6.4	8.0i	3.9	1.6	5.1	2.6
SPOLF	1.0	3.7	1.5	1.5	4.4	2.1

The SPRL and conjoined PRDL-SPDL converge before reaching the prezygapophysis and form a dorsal expansion that likely served as a muscular attachment site. Similar semilunar expansions are present in other titanosaurs, such as *Alamosaurus* (see D’Emic, 2012: character 57).

On either side of the median SPRF, between the SPRL, SPDL, and PRDL, are elongate, elliptical prezygapophyseal spinodiapophyseal fossae (PRSDFs) whose long axis is 8.3 cm (measured on left side; Table 4). Just posterior to the PRSDF, on the posterior side of the SPDL is the smaller, subtriangular postzygapophyseal spinodiapophyseal fossa (POSDF; long axis, left side ca. 8 cm), which is bounded ventrally by the horizontally oriented PODL and posteriorly by a vertically oriented component of the spinopostzygapophyseal lamina (SPOL). The SPOL is divided on both sides, but unequally so. In this instance, pneumaticity is better developed on the right side, where the medial and lateral SPOL both extend from postzygapophysis to neural spine and are separated by a SPOLF. On the left side, in contrast, the lateral SPOL does not reach the neural spine, and as a consequence the SPOLF is much smaller. The interspinous ligament attachment on the postspinal lamina broadens towards the spine summit. It is quite prominent, extending posteriorly beyond the SPOL, and as a consequence there is no development of a postspinal fossa (SPOF).

PHYLOGENETIC AFFINITIES

Interpreting the phylogenetic affinities of fragmentary specimens is challenging because they preserve less information than complete specimens, and so only a subset of available character data can be scored (see Whitlock et al., 2011). Although there are exceptions where individual elements make up a small portion of the skeleton but a large percentage of character data in a given matrix (e.g., mammalian cheek teeth), the most commonly preserved isolated elements tend to be anatomically simple, robust, often serially replicated elements that have a high preservation potential. For sauropod dinosaurs, commonly preserved isolated elements include vertebral centra and shafts of large limb bones. These elements, in isolation, are likely to provide poor estimations of phylogenetic affinities because they constitute a small percentage of character data. Less commonly preserved elements include more anatomically complex structures such as the extremities of the axial column (skull, tail tip) and limbs (manus, pes) and highly pneumatized bones such as presacral vertebrae.

Cladistic Analysis

The titanosaur presacral and anterior caudal vertebrae described in this contribution present an interesting case because they are morphologically complex structures, but relatively little of this information has been coded into phylogenetic characters for titanosaurs. This unfortunate situation may be the result of several interrelated factors, including the lack of complete, articulated vertebral columns for any of the 70+ titanosaur species, a high degree of serial variation evidenced in the few partially complete, articulated vertebral remains that are known (e.g., *Opisthocoelicaudia*, Borsuk-Bialynicka, 1977; *Trigonosaurus*, Campos et al., 2005; *Overosaurus*, Coria et al., 2013), and relatively coarse understanding of titanosaur phylogeny. Character lists from two recent phylogenetic analyses investigating the interrelationships of new titanosaur taxa (Gorscak et al., 2014; Carballido et al., 2017) help to illustrate this point. Both matrices borrow heavily from previously published analyses (e.g., Wilson, 2002; Upchurch et al., 2004) that have a broad taxonomic scope. Although both these source analyses include titanosaur terminal taxa, neither of them was designed to evaluate relationships within that clade specifically. In the Gorscak et al. (2014) matrix, characters coding variation in presacral and caudal vertebrae comprise approximately 29% of the dataset (127/440 characters). Characters associated with anterior dorsal vertebrae (26/440 characters) and anterior caudal vertebrae (30/440 characters) represent approximately 6% and 7% of the dataset, respectively. A similar distribution is seen in the Carballido et al. (2017) matrix, with approximately 32% of the dataset coding variation in presacral and caudal vertebrae (128/405 characters), and approximately 5% associated with anterior dorsal vertebrae (21/405 characters) and 8% associated with anterior caudal vertebrae (33/405 characters). Note that only a subset of this small number of characters can be expected to effectively resolve relationships among titanosaurs, because several of these characters are diagnostic for non-titanosaurian clades (e.g., Diplodocidae) but invariant within titanosaurs. On one hand, these low percentages make sense. The dorsal and caudal regions contribute 15% and 20% to overall skeletal completeness in sauropods, of which the anterior dorsal and anterior caudal regions make up approximately one-third (Mannion and Upchurch, 2010). On the other hand, though, these skeletal elements are among the most complex of the postcranial skeleton and should be expected to make a greater contribution to character data.

Scorings for characters compiled by Gorscak et al. (2014) and Carballido et al. (2017) for the two individuals described here are listed in Table 5. The individual represented by two dorsal vertebrae (GSI/GC/OGF107, GSI/GC/2905) could be scored for 2.8% of the Gorscak et al. (2014) data and 4.4% of the Carballido et al. (2017) data. The individual represented by the anterior caudal neural arch (338/GSI/PAL/CR/2017) could be scored for only 2.8% of the Gorscak et al. (2014) data and 3.0% of the Carballido et al. (2017) data.

We conducted phylogenetic analyses of the new specimens (arranged as two taxa) in PAUP* v. 4.0a (Swofford, 2003). The coding assumptions employed by each set of authors were accepted here; the only additions were the scorings for the two new specimens. Starting trees for branch swapping were generated by stepwise addition, with taxa added randomly and replicated 1,000 times. Branch swapping was by tree-bisection and reconnection. Only the first 246 characters of the Gorscak et al. (2014) were used; the remainder were autapomorphies used in the Bayesian analyses conducted by those authors. The Gorscak et al. (2014) matrix returns 1,476 most parsimonious trees, in which the two Indian taxa are unresolved with respect to other titanosaur taxa. The Carballido et al. (2017) matrix, in contrast, returns many more most parsimonious trees (100,000+) and cannot resolve the two Indian taxa within Neosauropoda, but the individual represented by the dorsal vertebrae (GSI/GC/OGF107) is resolved as sister-taxon to *Mendozasaurus*.

Comparisons

The new Indian vertebrae described here are definitively members of Titanosauria, but their affinities within that group could not be robustly resolved using two of the data matrices currently available. Below we make comparisons to titanosaurs in spatial and temporal proximity to our specimens from the Late Cretaceous of India, beginning with India and Pakistan—for which only limited comparisons can be made to presacral and caudal vertebrae—and then extending to more complete titanosaur skeletons from similar-aged deposits in Madagascar and South America. We make these comparisons

TABLE 5 — Character state scorings for the two titanosaur individuals described here for two recently published matrices exploring the interrelationships of titanosaurs. The numbers in parentheses at the end of the sequence indicate the number of characters that could be scored relative to the total number of characters. Abbreviation: *OTU*, operational taxonomic unit.

OTU	Gorscak et al. (2014)	Carballido et al. (2017)
GSI/GC/OGF107 + GSI/GC/2905	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	??11? ????? ???00	????? ????? ????? ????? ?????
	?101? ????? ?????	????? 1000? 31?1? 2?11? 10001
	????? ????? ?????	????? ????? ?1??? ????? ???00
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ? (7/246)	????? (18/405)
338/GSI/PAL/CR/2017	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ??0?? ?????	????? ????? ????? ????? ?????
	10111 1???? ?????	????? ????? ????? ????? 01???
	????? ????? ?????	????? ????0 ?1??? ??110 1001?
	????? ????? ?????	????? ????1 ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ????? ?????	????? ????? ????? ????? ?????
	????? ?(7/246)	????? (12/405)

with the understanding that the two individuals described here could pertain to the same species or to different species. We defer the question of whether they represent previously described titanosaur species or new species until a time when sufficient morphological information is available to make a convincing case either way.

India.— Hundreds of titanosaur bones have been collected from the Lameta Formation of central and western India, largely thanks to efforts by the Geological Survey of India and the Indian Statistical Institute. The vast majority of these elements are isolated, but there are rare examples of multiple bones found in association, such as the specimen of *Jainosaurus* cf. *septentrionalis* from Chhota Simla (Swinton, 1947; Wilson et al., 2011a). Revision of collections of Indian titanosaur material in repositories in India (Geological Survey of India, Indian Statistical Institute), the United Kingdom (The Natural History Museum), and the United States (American Museum of Natural History) has provided evidence for only two valid species, *Jainosaurus septentrionalis* (Huene and Matley, 1933; Hunt et al., 1994) and *Isisaurus colberti* (Jain and Bandyopadhyay, 1997; Wilson and Upchurch, 2003). To our knowledge, of all the reported bones from the Late Cretaceous of India held in official repositories, complete presacral vertebrae are known only for *Isisaurus*. There are no anterior caudal vertebrae from India that are positionally comparable to 338/GSI/PAL/CR/2017.

The holotype of *Isisaurus colberti* is a partial skeleton that includes numerous presacral vertebrae. Of these, Jain and Bandyopadhyay (1997: pp. 117–118) reported that 3 anterior dorsal vertebrae (ISIR 335/10–12) "were found articulated with the last cervical (ISIR335/9)." The published quarry map (Jain and Bandyopadhyay, 1997: fig. 2A) confirms that four vertebrae were found in close association, and the middle two (ISIR 335/10–11) were found in articulation. The other two vertebrae, however, were not mapped in articulation with this pair. The element considered to be the last cervical vertebra (ISIR 335/9) was mapped just to the east of the pair and was strongly dorsoventrally compressed during preservation. The articulated pair, in contrast, show signs of slight oblique deformation in the anteroposterior and transverse directions, indicating they were preserved in a different orientation than ISIR 335/9. Dorsal vertebra ISIR 335/12 was found to the west of the articulated pair, but it is plausible that it follows them closely in sequence, based on a photograph of the three vertebrae posed in articulation (Jain and Bandyopadhyay, 1997: fig. 7A). Of these four closely associated vertebrae, the third in the sequence (ISIR 335/11) is the best preserved and received the most thorough description and illustrations in Jain and Bandyopadhyay (1997), who identified it as the second dorsal vertebra. However, in contrast to the condition in most anterior dorsal vertebrae, the parapophysis of ISIR 335/11 is completely on the neural arch, indicating that it is from a position posterior to that of the two anterior dorsal vertebrae from Gujarat, which we determined to be dorsal vertebrae 2 and 3. The vertebra immediately preceding ISIR 335/11 in sequence, ISIR 335/10, has the parapophysis positioned on the anterodorsal margin of the pleurocoel and corresponds in position to the second of the two GSI vertebrae (GSI/GC/2905), suggesting it is dorsal vertebra 3. *Isisaurus* vertebra ISIR 335/9 is not a positional match for GSI dorsal vertebra 2 (GSI/GC/OGF107), which we interpret to indicate that ISIR 335/9 is at least one position anterior to GSI/GC/OGF107 and possibly pertains to dorsal vertebra 1. Thus, we have two comparisons available between *Isisaurus* and the GSI specimen: a direct comparison between dorsal vertebra 3 (ISIR 335/11, GSI/GC/2905) and a comparison between dorsal vertebra 1 of *Isisaurus* (ISIR 335/9) and dorsal vertebra 2 of the GSI specimen (GSI/GC/OGF107).

Dorsal vertebra 1 of *Isisaurus* (ISIR 335/9) and dorsal vertebra 2 of the GSI specimen (GSI/GC/OGF107) share several similarities despite differences in their serial position. Both specimens have broad centrum proportions and an inflated, transversely expanded neural spine that in dorsal view resembles a backwardly pointing V with a flattened base. The SPRLs and PRSL are prominent, but the POSL is reduced and scar-like. Both the SPOL and PRDL are thickened, and between them is an elongate, transverse fossa that extends from diapophysis towards the lateral expansion near the summit of the neural spine.

Dorsal vertebra 3 of *Isisaurus* (ISIR 335/10) and the GSI specimen (GSI/GC/2905) match well. Although GSI/GC/2905 is approximately half the size of ISIR 335/10 (centrum length ca. 14 cm vs. 30 cm), both are anteroposteriorly abbreviate, with posterior centrum height approximately two-thirds centrum length. Like GSI/GC/2905, ISIR 335/10 bears a sharply demarcated fossa between the prezygapophysis and diapophysis on the anterior face of the neural arch. This PRPADF is not present in more posterior dorsal vertebrae of *Isisaurus*, indicating serial variation in this pneumatic feature. A photograph of ISIR 335/10 in lateral view (Jain and Bandyopadhyay, 1997: fig. 7A) indicates the presence of a narrow PACDF occupying the space between laminae bracing the diapophysis ventrally (PPDL, PCDL), which is another feature shared by the GSI specimen. The configuration of the TPRLs, however, differs between the two specimens. Whereas in *Isisaurus* they angle ventromedially to contact one another near the roof of the neural canal, in GSI/GC/2905 they are nearly transversely oriented and contact one another dorsal to the roof of the neural canal, reaching it via a vertical median strut (Fig. 8A).

In summary, dorsal vertebrae GSI/GC/OGF107 and GSI/GC/2905 match well with vertebrae of *Isisaurus*, and differences are minor to negligible. In the absence of comparisons with *Jainosaurus*, however, we refrain from formalizing the relationship between the GSI specimens and *Isisaurus*.

Pakistan.— Although dinosaurs were first reported from Pakistan only very recently compared to India (Malkani and Anwar, 2000), numerous bones have been collected by the Geological Survey of Pakistan from exposures of the Pab Formation spread across approximately 25 localities and covering an area of approximately 25 x 80 km in northeastern Balochistan. In general terms, the collection resembles that of India in the lack of documented associations and predominance of limb bone shafts and vertebral centra, but there are important remains that have no parallel in India, such as the partial snout of a titanosaur (e.g., Malkani, 2006: fig. 20B). The bulk of the Late Cretaceous vertebrate fossils from Pakistan have been described in a labyrinthine series of partially overlapping papers by M. S. Malkani that have brought forth a profligacy of new taxa, including 9 monospecific titanosaur genera.

Basic data on these species is difficult to pin down, but the first four named titanosaur species and the fifth named genus are generally considered to have first appeared in a paper presented by Malkani (2004) at the Fifth Pakistan Geological Congress. These taxa include *Pakisaurus balochistani*, *Sulaimanisaurus gingerichi*, *Khetranisaurus barkhani*, *Marisaurus jeffi*, and *Balochisaurus*. Curiously, *Balochisaurus* was the only one of the new taxa not to receive a species name when it first appeared in 2004. Two years later, though, Malkani (2006: p. 114) referred to "*Balochisaurus malkani*," which may be the first appearance of that species epithet. There was also reference to "*Malkanisaurus*" (Malkani, 2006: p. 114), but to our knowledge that taxon name has not reappeared since. There is some uncertainty in the publication date of this paper, because it is not clear whether 2004 refers to the timing of the conference, publication of the abstract volume, or both; some of the accessible copies of that paper confusingly list a 2007 date. This is slightly complicated by the fact that at least one of the new taxon names first appeared a year earlier in the brief description of a possible partial skull, which Malkani (2003) referred to *Marisaurus jeffi*. Even if we provisionally accept the 2004 publication date, ignore the absence of a species name for *Balochisaurus*, and set aside the early appearance of *Marisaurus jeffi*, there are several issues with the publication naming the first Pakistani titanosaurs. Malkani (2004) did not designate a holotype for any of the five named species, all of which are based on caudal vertebrae, and there is insufficient locality data and no documentation of associations, the diagnosis is extremely brief, and there are no photographs or illustrations of the bones. Malkani (2004: p. 71) also spelled the species epithet for *Sulaimanisaurus* as "*S. gingrechi*" in that original paper, rather than "*S. gingerichi*," which appears in subsequent papers. More recently, Malkani (2017a,b) reviewed *Balochisaurus malkani*, *Marisaurus jeffi*, and *Pakisaurus balochistani*, proposing holotypic elements for each and providing additional morphological description and photographs. Malkani (2017a,b), though, appears to have used informal specimen numbers to refer to holotypes of *Balochisaurus malkani* and *Pakisaurus balochistani* (his initials, "MSM," followed by numbers) and did not list numbers at all for *Marisaurus jeffi*.

Three other species were named a decade later by Malkani (2014), which did a better job detailing specimen numbers and providing photographs for *Gspsaurus pakistani*, *Saraikimasoom vitakri*, and *Nicksaurus razashahi*. Two of these three new species were named on the basis of specimens that had been briefly described previously and attributed to other taxa. *Gspsaurus pakistani* was based on possible cranial remains previously referred to *Marisaurus jeffi* (Malkani, 2003), and *Saraikimasoom vitakri* was based on a partial titanosaur snout that was referred previously to *Balochisaurus malkani* (Malkani, 2006). The third taxon, *Nicksaurus razashahi*, is based on a collection of cranial, vertebral, and limb fragments. The three species named by Malkani (2014) were also given informal "MSM" specimen numbers. The ninth Pakistani titanosaur taxon, *Maojandino alami*, first appears in Malkani (2015a) without mention of holotype or specimen numbers. Slightly more information appeared in Malkani (2015b: p. 6), which listed the holotype as "6 cervical, 4 dorsal, and 10 caudal vertebrae along with partial left femur, partial left and right tibiae, and partial radius, a pair of partial distal scapulae, partial sternal plate or ilia, some neural arch and laminae" and provided informal specimen numbers for the vertebral elements.

In sum, Malkani (2004, 2014, 2015a,b, 2017a,b) created nine new titanosaur species, for which there remain serious issues surrounding designation of holotype, diagnosis, lack of overlap amongst holotypic remains of different species, and claims of associations among holotypic elements. The issue of undocumented associations is especially problematic if we take at face value the claimed richness (9 titanosaur species) of the Pab Formation. In addition to these concerns, however, is the more pressing issue of comparison to remains that have been collected from contemporaneous localities in India. This issue is exacerbated by difficulties inherent in individual researchers from India or Pakistan gaining permission to travel to the opposite country to examine collections, but it is clear that when collections from both countries have been examined there are complex elements that are generically or specifically indistinguishable, such as the braincases of *Isisaurus colberti* Wilson et al. (2005) reported from Dongargaon (central India), Rahioli (western India), and Vitakri (central Pakistan). Given the distance separating Vitakri from Dongargaon (ca. 1,450 km) and Rahioli (ca. 850 km), it is possible that materials ascribed to one or more of the 9 named Pakistani species are also generically or specifically identical to Indian taxa.

Regardless of the taxonomic validity of the named Pakistani species, a considerable amount of titanosaur material has been collected from the Pab Formation by the Geological Survey of Pakistan. Of the elements that have been published and the unpublished elements that we have studied first-hand, there are no anterior caudal vertebrae and only one anterior dorsal vertebra that is directly comparable to the Indian elements described here. The GSP specimen is a centrum and base of the neural arch of an anterior dorsal vertebra. It is approximately the same size as GSI/GC/OGF107 and pertains to a similar position in the dorsal series (Fig. 13). Like the GSI specimen, the centrum is fairly short anteroposteriorly and broad transversely. The centrum is strongly opisthocoelous and bears a well-marked pleurocoel that tapers posteriorly and is partially occluded by the parapophysis. The centrum and what is preserved of the neural arch are composed of camellate bone throughout. The main difference between the GSI and the GSP specimens is the degree of development of the PRCADF and the CPRL, which appear to be reduced or absent in the GSP specimen (Fig. 13).

Madagascar.— Three titanosaur species have been named from Madagascar. Two of these are valid, *Rapetosaurus krausei* (Curry Rogers and Forster, 2001) and *Vahiny depereti* (Curry Rogers and Wilson, 2014), but the earliest-named of these, *Titanosaurus madagascariensis* (Depéret, 1896), is probably not.

Titanosaurus madagascariensis (Depéret, 1896) was based on two caudal vertebrae and a humeral midshaft that later were referred to the South American genus *Laplatasaurus* by Huene (1929: p. 91). Direct comparisons are precluded by lack of anatomical overlap between *T. madagascariensis* and *Laplatasaurus araukanicus*, the lectotype of which was more recently designated a tibia and fibula by Bonaparte & Gasparini (1979). Validity of *T. madagascariensis* will remain contentious until restudy of the original materials that form the basis of the species (Wilson and Upchurch, 2003: pp.

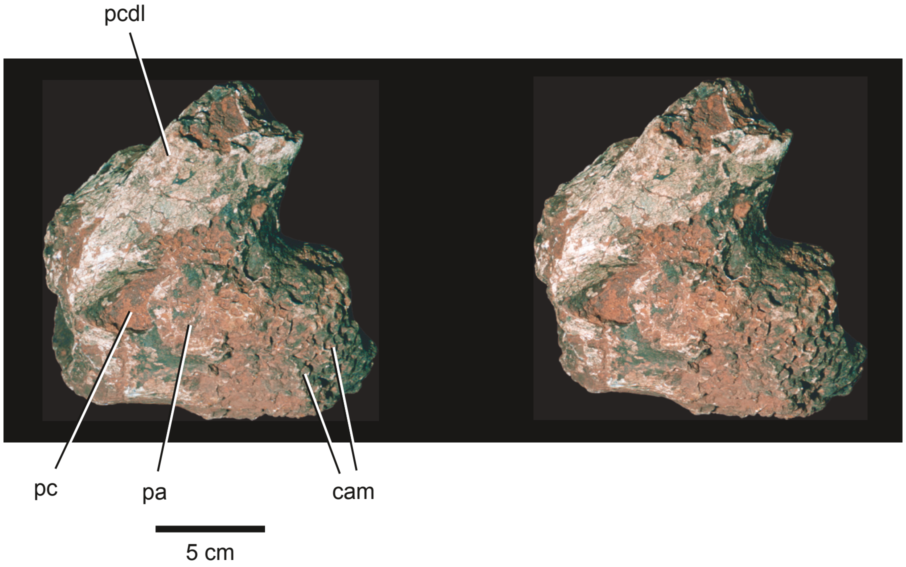

FIGURE 13 — Titanosaur anterior dorsal vertebra (GSP unnumbered) from the Pab Formation in Vitakri, Balochistan, Pakistan. Stereophotographs in right lateral view. Abbreviations: *cam*, camellae; *pa*, parapophysis; *pc*, pleurocoel; *pcdl*, posterior centrodiapophyseal lamina.

144–146). Thevenin (1907) described additional sauropod materials from Madagascar, including three caudal vertebrae he referred to *T. madagascariensis* and an indeterminate dorsal vertebra from the Maroakato plateau (now known to be Late Cretaceous in age; Paleobiology Database Collection number 51253 accessed 03 August 2018). This latter vertebra is from the anterior part of the dorsal series and probably corresponds to the third or fourth dorsal vertebra, based on the position of the parapophysis near the dorsal margin of the pleurocoel (Thevenin, 1907: pl. 1, fig. 20). It resembles the anterior dorsal vertebrae of the GSI specimen in the degree of convexity of the condyle, the anteroposteriorly abbreviate nature of the neural arch, the shape of the pleurocoel, and the pattern of pneumatization in the centrum, which Thevenin (1907: pp. 15) remarked "was constructed of an extremely lacuneous bony tissue" (translated from the French by Matthew Carrano). Although none of these features are individually diagnostic, the Maroakato dorsal vertebra differs from *Rapetosaurus* in most of these respects.

Rapetosaurus krausei is perhaps the best known titanosaur species, represented by cranial remains (Curry Rogers and Forster, 2004) associated with a postcranial skeleton (Curry Rogers, 2009) that includes osteoderms (Curry Rogers et al., 2011). Elements of *Rapetosaurus* are known from several ontogenetic stages, including vertebral, girdle, and limb bones of perinates (Curry Rogers et al., 2016). Hundreds of bones have been collected, some of which are associated as partial skeletons. Perhaps the best is a juvenile individual collected from a fine-grained debris flow (Rogers, 2005) that was described by Curry Rogers (2009). This specimen includes 25 presacral vertebrae that were interpreted to represent 15 postaxial cervical vertebrae and 10 dorsal vertebrae (Curry Rogers, 2009: pp. 1050, 1062). It can be difficult to determine the point of the cervicodorsal transition in articulated specimens, and the task is even more challenging in disarticulated specimens—especially in this case, where the centrum is not preserved for the first two dorsal vertebrae. We provisionally accept the serial designations of Curry Rogers (2009) with the understanding that the true position of the cervicodorsal transition could be one vertebra anterior to its current designation. The most striking differences between dorsal vertebrae of *Rapetosaurus* and the Gujarat specimen are that in the former the centra are more low and elongate (dorsal 3 centrum length/posterior height ca. 1.9 vs. 1.5, respectively) and the neural spines are much more angled posteriorly with respect to the vertebral axis (ca. 20˚ vs. 90˚, respectively). Additionally, in *Rapetosaurus* the neural spines taper towards their summit, the PRSL and SPRLs are less well developed, and the pleurocoel is elongate. Similarities between the two specimens include the anteroposteriorly abbreviate neural arch, the presence of a small PACDF near the base of the neural arch on dorsal vertebra 2, and a well-marked PRPADF on the anterior face of the diapophysis.

Rapetosaurus does not preserve any of the anteriormost caudal vertebrae. The most anterior caudal vertebrae reported by Curry Rogers (2009: p. 1069; fig. 27) were considered to be from the "mid-proximal" part of the series. We estimate these vertebrae correspond to a position posterior to caudal vertebra 10. Few meaningful comparisons can be made between these and the anterior caudal vertebra from Bara Simla (338/GSI/PAL/CR/2017), which likely corresponds to one of the first five in the series.

The presence of a second taxon in the Late Cretaceous of Madagascar has long been recognized, based on differences in proportions of the caudal vertebrae (e.g., Curry Rogers and Forster, 2001). These elements, which came to be known as 'Malagasy Taxon B,' were never incorporated into a formal taxon because of the lack of associations between these non-*Rapetosaurus* remains and concerns about defining a taxon based on caudal centrum proportions alone. Rather, the Malagasy titanosaur species *Vahiny depereti* was described on the basis of a braincase, which provided a broad range of comparisons with that of *Rapetosaurus krausei* (Curry Rogers and Wilson, 2014). To date, however, no postcranial remains have been referred to *Vahiny*, and no anterior dorsal vertebrae or anterior caudal vertebrae have been attributed to 'Malagasy Taxon B.'

South America.— Approximately half the recorded global diversity of titanosaurs comes from South America, where 30–38 valid species have been described (J. A. Wilson and M. D. D'Emic, unpublished data). Many of these taxa are based on fragmentary remains that have little to no overlap with the vertebrae described here (e.g., *Laplatasaurus*, *Malarguesaurus*, *Petrobrasaurus*), but several excellent partial skeletons are known that provide ample comparisons (e.g., *Mendozasaurus*, *Bonitasaura*). Among the many South American titanosaur species are at least two well-defined clades that have been consistently recovered in phylogenetic considerations of the group: Saltasauridae (Bonaparte and Powell, 1980) and Lognkosauria (Calvo et al., 2007a). Saltasauridae includes small-bodied genera such as *Saltasaurus*, *Neuquensaurus*, and *Rocasaurus* and is characterized features of the presacral and anterior caudal vertebrae. Neither of the Indian specimens described here presents features that indicate a close affinity with Saltasauridae. The Bara Simla caudal neural arch lacks camellate pneumaticity, which is present in anterior and middle caudal vertebrae of saltasaurids (Powell, 1992; Zurriaguz and Cerda, 2017). Although anterior dorsal vertebrae are rare within saltasaurids, available comparisons turn up few shared derived characters. No anterior dorsal vertebrae are known for *Rocasaurus munozi* (Salgado and Azpilicueta, 2000), but there are fragmentary specimens known for *Neuquensaurus australis* and *Saltasaurus loricatus*. A *Neuquensaurus* dorsal vertebra 1 or 2 (MLP CS 1373; Huene, 1929: pl. 2, fig. 5) is the closest match to the serial position of the Gujarat vertebrae; the closest *Saltasaurus* element is approximately dorsal vertebra 3 or 4 (PVL 4017-10). Both these elements have more proportionately elongate centra with the neural arch set back farther from the anterior extreme of the vertebra. In addition, the *Saltasaurus* anterior dorsal vertebra is notable for the presence of a double CPRL, which is not present in the Gujarat form.

Lognkosauria was coined to characterize the most recent common ancestor and all descendants of *Mendozasaurus neguyelap* and *Futalognkosaurus dukei* (Calvo et al., 2007a), which has been found to include *Notocolossus*, *Argentinosaurus*, and *Patagotitan* (González Riga et al., 2018: fig. 28), as well as *Puertasaurus*, *Drusilasaura*, and *Quetecsaurus* (Carballido et al., 2017). Close relatives of Lognkosauria include *Bonitasaura* (Gallina and Apesteguía, 2011) and *Alamosaurus* (Tykoski and Fiorillo, 2017). The Gujarat dorsal vertebrae share numerous features with lognkosaurian taxa, especially *Mendozasaurus* and an undescribed vertebra from Lago Barreales. GSI/GC/OGF107 has a similar configuration of laminae as an anterior dorsal vertebra of *Mendozasaurus* (IANIGLA 076/4), which has a well-developed PRSL flanked by a closely arranged, dorsally converging SPRL and SPDL (see González Riga, 2005: fig. 5A–B). The SPDL and SPOL are separated by a fossa that is much narrower than the POSDF of the Gujarat vertebra. A beautifully preserved, undescribed anterior dorsal vertebra from the Portezuelo Formation of Argentina housed at the Centro Paleontológico Lago Barreales (MUCPv-319; Calvo and Bellardini, 2011) is an excellent match for GSI/GC/OGF107. The Lago Barreales vertebra may be referable to *Mendozasaurus* and probably corresponds to dorsal vertebra 2, based on the position of the parapophysis. It is similar in size to GSI/GC/OGF107, and both vertebrae are anteroposteriorly abbreviate, with centrum proportions that are broader than tall. As in *Mendozasaurus* (IANIGLA 076/4), in the Lago Barreales dorsal vertebra the PRSL is well developed and joined dorsally by convergent SPRL and SPDL. The fossa between the SPDL and SPOL is narrow. There is a conspicuous fossa dorsal to the diapophysis that is present in the Gujarat dorsal vertebra and other lognkosaurians; the identity of this fossa hangs on interpretation of the laminae that bound it, which are not clear in any of the Lago Barreales or Gujarat specimens. In each case, this serial position represents a transition between more typically cervical morphology and that of the mid- and posterior dorsal region. There are stranded prezygapophyseal and spinal laminae bounding that fossa that are serially homologous with the EPRL of the cervical series and the SPDL of the dorsal series, respectively. The similarity of these two vertebrae in this aspect of the transition is remarkable and probably indicates their close affinity.

Similarities are also present between the Gujarat dorsal vertebra 3 (GSI/GC/2905) and an anterior dorsal vertebra of *Mendozasaurus* (IANIGLA-PV 066). Like the Gujarat form, *Mendozasaurus* has broad transverse processes, a vertical median lamina below the TRPLs, broad poorly defined CPRLs (González Riga, 2003: fig. 4A–C). Gujarat dorsal GSI/GC/2905 is also similar in general form to *Notocolossus* (González Riga et al. 2015: fig. 2; UNCUYO-LD 301), which lacks median vertical lamina below the TPRLs.

The Bara Simla caudal neural arch (338/GSI/PAL/CR/2017) resembles an anterior caudal vertebra of *Futalognkosaurus* in the configuration of laminae on the neural spine, which have a strong PRSL and SPRL (Calvo et al., 2007b: figs. 16–17), and it shares with *Mendozasaurus* laterally expanded prezygapophyseal processes and SPRL processes (see González Riga et al., 2018: fig. 9L–O).

Other.— No comparisons were available between the Bara Simla caudal neural arch (338/GSI/PAL/CR/2017) and material from Indo-Pakistan or Madagascar. Although some general similarities were recognized with species from South America, such as the presence of enlarged processes just proximal to the prezygapophyseal facets and laterally expanded prezygapophyseal processes, none of these pointed towards a close phylogenetic relationship. Somewhat surprisingly, the specimen that most closely matches the Bara Simla caudal vertebra is not from Gondwana or from the Late Cretaceous. *Tengrisaurus starkovi* was described on the basis of three caudal vertebrae from the Early Cretaceous of the Transbaikalia of Russia by Averianov and Skutschas (2017). The best preserved and holotypic specimen bears a resemblance to the Bara Simla specimen, despite its more posterior serial position in the caudal series. *Tengrisaurus* has a tipped back neural spine with well-developed SPRLs and a prominent, rugose interspinous ligament attachment (Averianov and Skutschas, 2017: fig. 4A). Like the Bara Simla neural arch, the prezygapophyses are large and borne on fattened prezygapophyseal processes (Averianov and Skutchas, 2017: fig. 4B). *Tengrisaurus* bears two small fossae in the space between the SPRLs and prespinal lamina that may represent serial variants of the well-developed PRSDF in the Bara Simla neural arch. *Tengrisaurus* also differs from the Bara Simla neural arch in the lack of well-developed fossae between the neural spine and postzygapophysis, as well as the corresponding laminae.

CONCLUSIONS

Three vertebrae pertaining to two different individuals from the Late Cretaceous of central and western India add to the growing knowledge of titanosaur morphology in the Indian Subcontinent. The two anterior dorsal vertebrae bear strong similarities to both those of *Isisaurus* from India and *Mendozasaurus* from Argentina. This result obliquely points to lognkosaurian affinities for *Isisaurus*, as has been suggested earlier on the basis of evidence from the vertebral column (González-Riga, 2005; Wilson et al., 2011). The anterior caudal neural arch is the first such known from the Late Cretaceous of India and Madagascar. It is highly pneumatic and its affinities remain somewhat enigmatic among Gondwanan forms, though it displays similarities to *Futalognkosaurus* and *Mendozasaurus*. Aspects of the neural spine and neural arch laminae strongly resemble *Tengrisaurus*, from the Early Cretaceous of Russia.

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LITERATURE CITED

AVERIANOV, A., and P. SKUTSCHAS. 2017. A new lithostrotian titanosaur (Dinosauria, Sauropoda) from the Early Cretaceous of Transbaikalia, Russia. Biological Communications, 62: 6–18.

BLANFORD, W. T. 1867. Traps and intertrappean beds of western and central India. Memoirs of the Geological Society of India, 1: 295–330.

BONAPARTE, J. F. 1999. Evolución de las vértebras presacras en Sauropodomorpha. Ameghiniana, 36: 115–187.

_____, and R. A. CORIA. 1993. Un nuevo y gigantesco saurópodo titanosaurio de la Formación Río Limay (Albiano−Cenomaniano) de la Provincia del Neuquén, Argentina. Ameghiniana, 30: 271–282.

_____, and Z. GASPARINI. 1979. Los saurópodos de los grupos Neuquén y Chubut, y sus relaciones cronológicas. Actas del VII Congreso Geológico Argentino, Neuquén, 2: 393–406.

_____, and J. E. POWELL. 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina Sauropoda-Coelurosauria-Carnosauria-Aves). Mémoires de la Société Géologique de France, Nouvelle Série, 139: 19–28.

BORSUK-BIALYNICKA, M. 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii* gen. n., sp. n. from the Upper Cretaceous of Mongolia. Palaeontologia Polonica, 77: 5–64.

BRITT, B. B. 1993. Pneumatic postcranial bones in dinosaurs and other archosaurs. Ph.D. Thesis, University of Calgary, 383 pp.

CALVO, J. O., and F. BELLARDINI. 2011. Nuevo hallazgo de restos de un titanosaurio en la costa sur del Lago

Barreales (Neuquén, Argentina). In R. N. Martínez (ed.), IV Congreso Latinoamericano de Paleontología de Vertebrados, San Juan, Argentina, 21–24 Septiembre 2011, Resúmenes. Ameghiniana, 48: R97–98.

_____, J. D. PORFIRI, B. J. GONZÁLEZ RIGA, and A. W. A. KELLNER. 2007a. A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. Anais da Academia Brasileira de Ciências, 79: 529–541.

_____, _____, _____, and _____. 2007b. Anatomy of *Futalognkosaurus dukei* Calvo, Porfiri, González Riga, and Kellner, 2007 (Dinosauria, Titanosauridae) from the Neuquén Group (Late Cretaceous, Patagonia, Argentina). Arquivos do Museu Nacional, Rio de Janeiro, 65: 511–526.

CAMPOS, D. A., A. W. A. KELLNER, R. J. BERTINI, and R. M. SANTUCCI. 2005. On a titanosaurid (Dinosauria, Sauropoda) vertebral column from the Bauru Group, Late Cretaceous of Brazil. Arquivos do Museu Nacional, Rio de Janeiro, 63: 565–593.

CARBALLIDO, J. L., D. POL, A. OTERO, I. A. CERDA, L. SALGADO, A. C. GARRIDO, J. RAMEZANI, N. R. CÚNEO, and J. M. KRAUSE. 2017. A new giant titanosaur sheds light on body mass evolution among sauropod dinosaurs. Proceedings of the Royal Society B, 284: 20171219.

CARRANO, M. T., J. A. WILSON, and P. M. BARRETT. 2010. The history of dinosaur collecting in central India, 1828–1947. In Moody, R. T. J., E. Buffetaut, D. Naish, and D. M. Martill (eds.), Dinosaurs and Other Extinct Saurians: A Historical Perspective. Geological Society, London, Special Publications, 343: 161–173.

CHATTERJEE, S., and D. K. RUDRA. 1996. KT events in India: impact, rifting, volcanism and dinosaur extinction. Memoirs of the Queensland Museum, 39: 489–532.

CORIA, R. A., L. S. FILIPPI, L. M. CHIAPPE, R. GARCÍA, and A. B. ARCUCCI. 2013. *Overosaurus paradasorum* gen. et sp. nov., a new sauropod dinosaur (Titanosauria: Lithostrotia) from the Late Cretaceous of Neuquén, Patagonia, Argentina. Zootaxa, 3683: 357–376.

CURRY ROGERS, K. 2009. The postcranial osteology of *Rapetosaurus krausei* (Sauropoda: Titanosauria) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology, 29: 1046–1086.

_____, and C. A. FORSTER. 2001. The last of the dinosaur titans: a new sauropod from Madagascar. Nature, 412: 530–534.

_____, and _____. 2004. The skull of *Rapetosaurus krausei* (Sauropoda, Titanosauria) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology, 24: 121–144.

_____, and J. A. WILSON. 2014. *Vahiny depereti*, gen. et sp. nov., a new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous Maevarano Formation, Madagascar. Journal of Vertebrate Paleontology, 34: 606–617.

_____, M. WHITNEY, M. D. D'EMIC, and B. BAGLEY. 2016. Precocity in a tiny titanosaur from the Cretaceous of Madagascar. Science, 352: 450–453.

_____, M. D. D'EMIC, R. R. ROGERS, M. VICKARYOUS, and A. CAGAN. 2011. Sauropod dinosaur osteoderms from the Late Cretaceous of Madagascar. Nature Communications, 2: 564–569.

DASGUPTA, A. K., A. GHOSE, and K. K. CHAKRABORTY. 1993. Geological map of India 1:5,000,000. Geological Survey of India, Hyderabad, India.

D'EMIC, M. D. 2012. The early evolution of titanosauriform sauropod dinosaurs. Zoological Journal of the Linnean Society, 166: 624–671.

DEPÉRET, C. 1896. Note sur les dinosauriens sauropodes & théropodes du Crétacé Supérieur de Madagascar. Bulletin de la Société Géologique de France, 24: 176–194.

FALCONER, H. 1868. Notes on fossil remains found in the Valley of the Indus below Attock, and at Jubbulpoor. In C. Murchison (ed.), Palaeontological Memoirs and Notes of the Late Hugh Falconer, vol. I. Fauna Antiqua Sivalensis, Robert Hardwicke, London, 414–419.

FRONIMOS, J. A., and J. A. WILSON. 2017. Concavo-convex intervertebral joints stabilize the vertebral column in sauropod dinosaurs and crocodylians. Ameghiniana, 54: 151–176.

GALLINA, P. A., and S. APESTEGUÍA. 2011. Cranial anatomy and phylogenetic position of the titanosaurian sauropod *Bonitasaura salgadoi*. Acta Palaeontologica Polonica, 56: 45–60.

GHEVARIYA, Z. G. 1988. Intertrappean dinosaurian fossils from Anjar area, Kachchh District, Gujarat. Current Science, 57: 248–251.

GONZÁLEZ RIGA, B. J. 2003. A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza, Argentina. Ameghiniana, 40: 155–172.

_____. 2005. Nuevos restos fósiles de *Mendozasaurus neguyelap* (Sauropoda, Titanosauria) del Cretácico Tardío de Mendoza, Argentina. Ameghiniana, 42: 535–548.

_____, M. C. LAMANNA, L. D. ORTIZ DAVID, J. O. CALVO, and J. P. CORIA. 2015. A gigantic new dinosaur from Argentina and the evolution of the sauropod hind foot. Scientific Reports, 6: 19165.

_____, P. D. MANNION, S. F. POROPAT, L. D. ORTIZ DAVID, and J. P. CORIA. 2018. Osteology of the Late Cretaceous Argentinean sauropod dinosaur *Mendozasaurus neguyelap*: implications for basal titanosaur relationships. Zoological Journal of the Linnean Society, 184: 136–181.

GORSCAK, E., P. M. O'CONNOR, N. J. STEVENS, and E. M. ROBERTS. 2014. The basal titanosaurian *Rukwatitan bisepultus* (Dinosauria, Sauropoda) from the middle Cretaceous Gulala Formation, Rukwa Rift Basin, southwestern Tanzania. Journal of Vertebrate Paleontology, 34: 1133–1154.

HANSEN, H. J., D. M. MOHABEY, S. LOJEN, P. TOFT, and A. SARKAR. 2005. Orbital cycles and stable carbon isotopes of sediments associated with Deccan volcanic suite, India: implications for the stratigraphic correlation and Cretaceous/Tertiary boundary. Gondwana Geological Magazine, 8: 5–28.

HARRIS, J. D. 2004. Confusing dinosaurs with mammals: tetrapod phylogenetics and anatomical terminology in the world of homology. The Anatomical Record, 281A: 1240–1246.

HUENE, F. v. 1929. Los saurisquios y ornitisquios del Cretáceo Argentino. Anales del Museo de La Plata (series 3), 3: 1–196.

_____, and C. A. MATLEY. 1933. Cretaceous Saurischia and Ornithischia of the Central Provinces of India. Palaeontologia Indica, 21: 1–74.

HUNT, A. G., M. G. LOCKLEY, S. G. LUCAS, and C. A. MEYER. 1994. The global sauropod fossil record. GAIA, 10: 261–279.

JAIN, S. L., AND S. BANDYOPADHYAY. 1997. New titanosaurid (Dinosauria: Sauropoda) from the Late Cretaceous of central India. Journal of Vertebrate Paleontology, 17: 114–136.

LYDEKKER, R. 1877. Notices of new and other Vertebrata from Indian Tertiary and Secondary rocks. Records of the Geological Survey of India, 10: 30–43.

_____. 1879. *Titanosaurus* from the Lameta Group of Jabalpur and Pisdura. Palaeontologia Indica, 1: 20–26.

MALKANI, M. S. 2003. Discovery of partial skull and dentary of Titanosauria (sauropod dinosaur) from the Late Cretaceous Pab Formation of Vitakri area, Barkhan district, Balochistan, Pakistan Geological Bulletin University of Peshawar, 36: 65–71.

_____. 2004. Saurischian dinosaurs from the Late Cretaceous of Pakistan. In S. S. Hussain, and H. D. Akbar (eds.), Abstract volume of 5th Pakistan Geological Congress. National Geological Society of Pakistan, Pakistan Museum of Natural History (Pakistan Science Foundation), Islamabad, Pakistan, 71–73.

_____. 2006. Biodiversity of saurischian dinosaurs from the latest Cretaceous Park of Pakistan. Journal of Applied and Emerging Sciences, 1: 108–140.

_____. 2014. Titanosaurian sauropod dinosaurs from the latest Cretaceous of Pakistan. In D. Cheong, Y. I. Lee, and D. Kim (eds.), Procedings of 2nd Symposium of International Geoscience Program 608 (IGCP 608) "Cretaceous Ecosystem of Asia and Pacific" September 04–06, 2014, Tokyo, Japan, 108–111.

_____. 2015a. Titanosaurian sauropod dinosaurs from Pakistan. In Y. Zhang, S. Z. Wu, and G. Sun (eds.), abstract volume, 12th Symposium on Mesozoic Terrestrial Ecosystems (MTE 12), and 3rd Symposium of International Geoscience Program (IGCP 608) "Cretaceous Ecosystem of Asia and Pacific" August 15–20, 2015, Paleontological Museum of Liaoning/Shenyang Normal University, Shenyang, China, 93–98.

_____. 2015b. Dinosaurs, mesoeucrocodiles, pterosaurs, new fauna and flora from Pakistan. Geological Survey of Pakistan Information Release, 823: 1–32.

_____. 2017a. *Balochisaurus malkani* and *Marisaurus jeffi* balochisaurid titanosaurs of Pakistan: a review. In D. Cheong, Y. I. Lee, and D. Kim (eds.), Proceedings and Fieldguide book for the fifth International Symposium of International Geoscience Programme IGCP Project 608 "Cretaceous Ecosystems and Their Responses to Paleoenvironmental Changes in Asia and the Western Pacific" October 22–28, 2017, Jeju Island, Korea, 40–43.

_____. 2017b. A review of *Pakisaurus* titanosaur: associated skeletons of sauropod and theropod dinosaurs and mesoeucrocodiles from Pakistan: discussion on titanosaurs of Indo-Pak subcontinent. In D. Cheong, Y. I. Lee, and D. Kim (eds.), Proceedings and Fieldguide book for the fifth International Symposium of International Geoscience Programme IGCP Project 608 "Cretaceous Ecosystems and Their Responses to Paleoenvironmental Changes in Asia and the Western Pacific" October 22–28, 2017, Jeju Island, Korea, 116–119.

_____, and C. M. ANWAR. 2000. Discovery of first dinosaur fossil in Pakistan, Barkhan District, Balochistan. Geological Survey of Pakistan Information Release, 732: 1–16.

MANNION, P. D., and P. UPCHURCH. 2010. Completeness metrics and the quality of the sauropodomorph fossil record through geological and historical time. Paleobiology, 36: 283–302.

MARSH, O. C. 1878. Principal characters of American Jurassic dinosaurs. Pt. I. American Journal of Science (series 3), 16: 411–416.

MARTINELLI, A. G., and A. M. FORASIEPI. 2004. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Río Negro Province, Argentina, with the description of a new sauropod dinosaur (Titanosauridae). Revistas del Museo Argentino de Ciencias Naturales, nuevo serie, 6: 257–305.

MATHUR, U. B., and S. C. PANT. 1986. Sauropod dinosaur humeri from Lameta Group (Upper Cretaceous-?Palaeocene) of Kheda Group, Gujarat. Journal of the Palaeontological Society of India, 31: 22–25.

_____, and S. SRIVASTAVA. 1987. Dinosaur teeth from Lameta group (Upper Cretaceous) of Kheda district, Gujarat. Journal of the Geological Society of India, 29: 554–566.

MATHUR, Y. K., S. D. SHARMA, A. SAHNI, and A. JOLLEY. 1990. Palynofossils and age of the Ranipur intertrappean beds Gaur River Jabalpur, MP. Cretaceous Event Stratigraphy and the correlation of Indian Non-marine Strata, Seminar cum workshop IGCP, 216: 58–59.

MATLEY, C. A. 1921. On the stratigraphy, fossils and geological relationships of the Lameta beds of Jubbulpore. Records of the Geological Survey of India, 53: 142–169.

_____. 1924. Note on an armoured dinosaur from the Lameta beds of Jubbulpore. Records of the Geological Survey of India, 55: 105–109.

MEDLICOTT, H. B. 1872. Notes on the Sátpúrá coal-basin. Memoirs of the Geological Survey of India, 10: 133–188.

MOHABEY, D. M. 1984. Study of dinosaurian eggs from infra-trappean limestone in Kheda District, Gujarat. Journal of the Geological Society of India, 25: 329–337.

_____. 1989. The braincase of a dinosaur from the Late Cretaceous Lameta Formation, Kheda District, Gujarat, western India. Indian Journal of Earth Sciences, 16: 132–135.

_____, and B. SAMANT. 2013. Deccan continental flood basalt eruptions terminated Indian dinosaurs before the Cretaceous-Paleogene boundary. Journal of the Geological Society of India, Special Publication, 1: 260–267.

_____, S. SEN, and J. A. WILSON. 2013. India's first dinosaur, rediscovered. Current Science, 104: 34–37.

_____, B. SAMANT, D. A. DEEPESH KUMAR, A. RUDRA, and S. DUTTA. 2018. Record of charcoal from early Maastrichtian intertrappean lake sediments of Bagh Valley, Madhya Pradesh: palaeofire proxy. Current Science, 114: 1540–1544.

NOVAS, F. E., S. CHATTERJEE, D. K. RUDRA, and P. M. DATTA. 2010. *Rahiolisaurus gujaratensis*, n. gen. n. sp., a new abelisaurid theropod from the Late Cretaceous of India. In S. Bandyopadhyay (ed.), New Aspects of Mesozoic Biodiversity. Springer-Verlag, Berlin, 45–62.

OWEN, R. 1842. Report on British fossil reptiles. Pt. II. Report of the British Association for the Advancement of Science, 1841: 60–204.

POWELL, J. E. 1987. Morfología del esqueleto axial de los dinosaurios titanosauridos (Saurischia, Sauropoda) del estado de Minas Gerais, Brasil. Anais do X Congreso Brasileiro de Paleontologia, 1: 155–171.

_____. 1992. Osteología de *Saltasaurus loricatus* (Sauropoda–Titanosauridae) del Cretácico Superior del noroeste Argentino. In J. Sanz and A. Buscalioni (eds.), Los Dinosaurios y Su Entorno Biotico: Actas del Segundo Curso de Paleontología in Cuenca. Instituto "Juan de Valdes," Cuenca, 165–230.

_____. 2003. Revision of South American titanosaurid dinosaurs: palaeobiological, palaeobiogeographical and phylogenetic aspects. Records of the Queen Victoria Museum, 111: 1–94.

ROGERS, R. R. 2005. Fine-grained debris flows and extraordinary vertebrate burials in the Late Cretaceous of Madagascar. Geology, 33: 297–300.

SAHNI, A., and A. TRIPATHI. 1990. Age implications of the Jabalpur Lameta Formation and intertrappean biotas. Cretaceous event stratigraphy and the correlation of the Indian nonmarine strata. Contributions from the Seminar Cum Workshop IGCP, 216: 35–37.

SALGADO, L. 2003. Should we abandon the name Titanosauridae? Some comments on the taxonomy of titanosaurian sauropods (Dinosauria). Revista Española de Paleontología, 18: 15–21.

_____, and C. AZPILICUETA. 2000. Un nuevo saltasaurino (Sauropoda, Titanosauridae) de la provincia de Río Negro (Formacíon Allen, Cretácico Superior), Patagonia, Argentina. Ameghiniana, 37: 259–264.

_____, R. A. CORIA, and J. O. CALVO. 1997. Evolution of titanosaurid sauropods. I: phylogenetic analysis based on the postcranial evidence. Ameghiniana, 34: 3–32.

SANZ, J. L., J. E. POWELL, J. LE LOEUFF, R. MARTÍNEZ, and X. PEREDA-SUBERBIOLA. 1999. Sauropod remains from the Upper Cretaceous of Laño (northcentral Spain), titanosaur phylogenetic relationships. Estudios del Museo de Ciencias Naturales de Alava, 14: 235–255.

SLEEMAN, W. H. 1844. Rambles and Recollections of an Indian Official. Volume I. J. Hatchard and Son, London, 478 pp.

SRIVASTAVA, S., D. M. MOHABEY, A. SAHNI, and S. C. PANT. 1986. Upper Cretaceous dinosaur egg clutches from Kheda District (Gujarat, India). Palaeontographica Abteilung A, 193: 219–233.

SWINTON, W. E. 1947. New discoveries of *Titanosaurus indicus*. Annals and Magazine of Natural History, 14: 112–123.

SWOFFORD, D. L. 2003. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4. Sinauer Associates, Sunderland, Massachusetts.

THEVENIN, A. 1907. Paléontologie de Madagascar. Annales de Paléontologie, 2: 121–136.

TYKOSKI, R. S., and A. R. FIORILLO. 2016. An articulated cervical series of *Alamosaurus sanjuanensis* Gilmore, 1922 (Dinosauria, Sauropoda) from Texas: new perspective on the relationships of North America's last giant sauropod. Journal of Systematic Palaeontology, 15: 339–364.

UPCHURCH, P., P. M. BARRETT, and P. DODSON. 2004. Sauropoda. In D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), The Dinosauria, 2nd Edition. University of California Press, Berkeley, 259–324.

WEDEL, M. J., and M. P. TAYLOR. 2013. Neural spine bifurcation in sauropod dinosaurs of the Morrison Formation: ontogenetic and phylogenetic implications. Palarch's Journal of Vertebrate Palaeontology, 10: 1–34.

WHITLOCK, J. A., M. D. D'EMIC, and J. A. WILSON. 2011. Cretaceous diplodocoids in Asia? Re-evaluating the phylogenetic affinities of a fragmentary specimen. Palaeontology, 54: 351–364.

WILSON, J. A. 1999. A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. Journal of Vertebrate Paleontology, 19: 639–653.

_____. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. Zoological Journal of the Linnean Society, 136: 217–276.

_____. 2006. Anatomical nomenclature of fossil vertebrates: standardized terms or lingua franca? Journal of Vertebrate Paleontology, 26: 511–518.

_____. 2012. New vertebral laminae and patterns of serial variation in vertebral laminae of sauropod dinosaurs. Contributions from the Museum of Paleontology, University of Michigan, 32: 91–110.

_____, and D. M. MOHABEY. 2006. A titanosauriform axis from the Lameta Formation (Upper Cretaceous: Maastrichtian) of central India. Journal of Vertebrate Paleontology, 26: 471–479.

_____, and P. C. SERENO. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. Society of Vertebrate Paleontology Memoir, 5: 1–68 (supplement to Journal of Vertebrate Paleontology 18).

_____, and P. UPCHURCH. 2003. Revision of *Titanosaurus*, the first dinosaur genus with a "Gondwanan" distribution. Journal of Systematic Palaeontology, 1: 125–160.

_____, and _____. 2009. Redescription and reassessment of the phylogenetic affinities of *Euhelopus zdanskyi* (Dinosauria: Sauropoda) from the Early Cretaceous of China. Journal of Systematic Palaeontology, 7: 1–41.

_____, P. M. BARRETT, and M. T. CARRANO. 2011a. An associated partial skeleton of *Jainosaurus* cf. *septentrionalis* (Dinosauria: Sauropoda) from the Late Cretaceous of Chhota Simla, central India. Palaeontology, 54: 981–998.

_____, M. S. MALKANI, and P. D. GINGERICH. 2005. A sauropod braincase from the Pab Formation (Upper Cretaceous, Maastrichtian) of Balochistan, Pakistan. Gondwana Geological Magazine, sp. vol. 8: 101–109.

_____, M. D. D'EMIC, T. IKEJIRI, E. M. MOACDIEH, and J. A. WHITLOCK. 2011b. A nomenclature for vertebral fossae in sauropods and other saurischian dinosaurs. PLoS One, 6: e17114.

_____, P. C. SERENO, S. SRIVASTAVA, D. K. BHATT, A. KHOSLA, and A. SAHNI. 2003. A new abelisaurid (Dinosauria, Theropoda) from the Lameta Formation (Cretaceous, Maastrichtian) of India. Contributions from the Museum of Paleontology, University of Michigan, 31: 1–42.

WOODRUFF, D. C., and D. W. FOWLER. 2012. Ontogenetic influence on neural spine bifurcation in Diplodocoidea (Dinosauria: Sauropoda): a critical phylogenetic character. Journal of Morphology, 273: 754–764.

ZURRIAGUZ, V. L., and I. A. CERDA. 2017. Caudal pneumaticity in derived titanosaurs (Dinosauria: Sauropoda). Cretaceous Research, 73: 14–24.

_____, G. MARTINELLI, G. W. ROUGIER, and M. D. EZCURRA. 2017. A saltasaurine titanosaur (Sauropoda: Titanosauriformes) from the Angostura Colorada Formation (upper Campanian, Cretaceous) of northwestern Patagonia, Argentina. Cretaceous Research, 75: 101–114.

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