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THEROPOD AND SAUROPOD DINOSAURS FROM THE CAMPANIAN–MAASTRICHTIAN BAGUA BASIN OF PERÚ, INCLUDING THE FIRST POSSIBLE REPORT OF SPINOSAURIDAE IN WESTERN SOUTH AMERICA

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Abstract. We provide the first detailed description of osteo-dental non-avian dinosaur fossils from the Fundo El Triunfo Formation in the Bagua Basin (Campanian–Maastrichtian) in northwestern Perú. The material described in this work includes three isolated teeth, which we refer to Spinosauridae based on the presence of diagnostic dental features, as well as abundant though fragmentary postcranial material that we refer to Titanosauria. A multivariate analysis was performed and provide additional support for referral of the teeth to Spinosauridae. These teeth possibly expand the geographical distribution and temporal range of Spinosauridae, representing their first record in western South America and the youngest remains of the group. The new material also provides key information on the size and distribution of titanosaurs in northern South America during the latest Cretaceous. These findings increase the very scarce record of non-avian dinosaur skeletal material in Perú, emphasizing the country's potential for future paleontological exploration.

Key words. Bagua Basin. Perú. South America. Dinosauria. Gondwana. Late Cretaceous. Theropoda. Titanosauria. Tooth crowns.

Resumen. REGISTRO DEL CRETÁCICO TARDÍO DE DINOSAURIOS DE LA FORMACIÓN FUNDO EL TRIUNFO (CUENCA BAGUA, PERÚ) Y PRIMER POSIBLE REPORTE DE SPINOSAURIDAE EN EL OESTE SUDAMERICANO. Presentamos la primera descripción detallada de material osteodental de dinosaurios no avianos de la Formación Fundo El Triunfo en la Cuenca Bagua (Campaniano–Maastrichtiano) en el noroeste de Perú. El material descrito en este trabajo incluye tres dientes aislados que a los que referimos a Spinosauridae, en base a la presencia de características dentales diagnósticas. Así también, reportamos y describimos abundante material esquelético fragmentario poscraneal que identificamos como pertenecientes a Titanosauria. Se realizó un análisis multivariado que proporcionó apoyo adicional a la asignación de los dientes a Spinosauridae. Los dientes encontrados posiblemente expanden la distribución geográfica y el rango temporal de Spinosauridae y representarían el primer registro de Spinosauridae en el oeste de América del Sur; y los restos más recientes para el grupo. Así también, el material esquelético de titanosaurios proporciona información importante sobre el tamaño y distribución de los titanosaurios en el norte de Sudamérica durante el Cretácico Tardío. Estos hallazgos contribuyen a aumentar el escaso registro de material esquelético de dinosaurios no aviares en Perú., enfatizando el potencial de este país para exploraciones paleontológicas a futuro.

Palabras clave. Cuenca Bagua. Perú. Sudamérica. Dinosauria. Gondwana. Cretácico Tardío. Theropoda. Titanosauria. Coronas de dientes.

The Bagua Basin in northwestern Perú is one of the few localities in northern South America that produces dinosaurian remains. Most non-avian dinosaur fossils from South America come from localities in Argentina and Brazil and, to a lesser extent, Chile. Excluding Brazil, the northern South American records of these animals are rare, with some exceptions from Colombia, Venezuela, and, most recently, Ecuador (Apesteguía *et al.*, 2020; Barrett *et al.*, 2014; Carballido *et al.*, 2015; Langer *et al.*, 2014; Rincón *et al.*, 2022).

Although the majority of named species of dinosaurs from northern South America come from beds of Cretaceous age (as most South American taxa in general), the overall fossil record of terrestrial ecosystems is scarce due to the fact that, for the majority of the Cretaceous, a large region of northern South America was occupied by an epicontinental sea (Moreno *et al.*, 2020; Novas, 2009). As a consequence, most South American fossil sites were deposited in marine environments that do not contain dinosaur remains (*e.g.*, Bastiaans *et al.*, 2021; Bermúdez *et al.*, 2013; Caldwell & Bell, 1995; Colbert & Pardo, 1949; Martill, 2007; Páramo-Fonseca *et al.*, 2018).

One of the few localities of northwestern South America, the Bagua Basin, has been reconstructed as mainly terrestrial in nature (Moreno *et al.*, 2020, 2022) and yields non-avian dinosaur skeletal remains. Skeletal and eggshell fossil material referred to titanosaurian sauropods and unidentified theropods were previously reported for this locality (Kerourio & Sigé, 1984; Mourier *et al.*, 1988, 1986). Here, we report the discovery of spinosaurid and titanosaur dinosaurs from the Late Cretaceous of Perú, based on fossils from the Fundo El Triunfo Formation in the Bagua Basin. Additionally, we review current knowledge of Late Cretaceous dinosaur fossils and sites in Perú.

NON-AVIAN DINOSAURIAN FOSSIL RECORD IN PERÚ

Most non-avian dinosaur fossils in Perú are trace fossils. The Carhuaz Formation (Huanzalá-Antamina Locality, Ancash), assigned to the Lower Cretaceous (Valanginian), contains tridactyl ichnofossils of large theropod dinosaurs. (Moreno *et al.*, 2004; Obata *et al.*, 2006; Salas-Gismondi & Chacaltana, 2010). The Querulpa locality in Arequipa preserves the highest number of trace fossils in Perú, consisting of at least 67 tridactyl and tetradactyl footprints from large and medium-sized theropods (Moreno *et al.*, 2012). The Querulpa tracksite is in the Hualhuani Formation, which is Lower Cretaceous (Berriasian) in age (Alván *et al.*, 2018). The last of the known fossil tracksites in Perú is found in the Upper Cretaceous (Campanian–Maastrichtian) Vilquechico Formation in Puno, southeastern Perú. Jaillard *et al.* (1993) identified distinct tridactyl trackways that were assigned to two ichnotaxa. The first trackway contains four footprints of *Ornithomimipus jaillardi*, which was interpreted as an ornithomimid dinosaur. The second trackway records *Hadrosaurichnus titicaensis*, which is larger in size and interpreted to belong to a hadrosaurid dinosaur.

A fourth site containing possible non-avian dinosaurian footprints was discovered by a French team led by Patrice Baby in 2010. The site, of possible Late Cretaceous age, is found in Inambari, Madre de Dios (southeastern Perú). The prints, which are relatively rounded in shape, are thought to belong to sauropod dinosaurs. However, the material awaits a formal study (Palacios Yábar, 2022; Vásquez, 2010).

In addition to the ichnofossils, Sigé (1968) reported dinosaur eggshell fragments from supposedly Upper Cretaceous beds at Laguna Umayo, a vertebrate-bearing site near the city of Puno. Unfortunately, the main reference eggshell material from this site was lost (Vianey-Liaud *et al.*, 1997), but in any event, this mammalian-bearing locality is no longer allocated a Cretaceous age but a Paleocene–Early Eocene age instead (Chornogubsky & Goin, 2015; Gelfo & Sigé, 2011; Sigé *et al.*, 2004) and the corresponding eggshells were likely either of avian or crocodylian origin. As far as the authors of this work are aware, no attempts to replicate the findings described by Kerourio & Sigé (1984) have been made, and thus, in this work, we do not consider Laguna Umayo to be a titanosaur fossil-bearing site (Fig. 16).

Additional eggshell material thought to be of dinosaurian origin was collected through a survey of fossiliferous sites in the Bagua Basin (Mourier *et al.*, 1986; Vianey-Liaud & Lopez-Martinez, 1997). Vianey-Liaud *et al.* (1997) re-evaluated shell fragments from Bagua based on histological and microstructural data. These authors assigned some of the materials to *Megaloolithus*, an oogenus attributed to Titanosauria based on strong structural and surface ornamentation similarities to previously identified eggshell fragments from France. Additional support for the titanosaur affinities of the Bagua eggshells was found through direct comparison to eggshells from the Upper Cretaceous of Auca Mahuevo in Argentina (Anacleto Formation), which are unequivocally assigned to Titanosauria based on the preservation of embryonic remains (Grellet-Tinner *et al.*, 2004). All the *Megaloolithus* fossils collected from the Bagua Basin are now deposited in the Karl Hirsch Eggshell Collection (HEC) at the University of Colorado Museum of Natural History.

THE FOSSIL RECORD OF SPINOSAURIDAE AND TITANOSAURIA IN SOUTH AMERICA

Spinosauridae is a group of tetanuran theropod dinosaurs characterized by elongated skulls, laterally compressed snouts, and conical, crocodile-like teeth (Bertin, 2010; Hendrickx *et al.*, 2015a). Remains of this family are found mainly in northern Africa, but the clade is also represented in Cameroon (Congleton, 1990), Tanzania (Buffetaut, 2013), Europe (*e.g.*, Canudo *et al.*, 2008; Mateus *et al.*, 2011), Asia (*e.g.* Allain *et al.*, 2012; Buffetaut *et al.*, 2005, 2008; Buffetaut & Ingavat, 1986b; Hasegawa *et al.*, 2003; Hattori & Azuma, 2020; Kubota *et al.*, 2017) and South America (Kellner & Campos, 1996; Sues *et al.*, 2002; Machado *et al.*, 2005; Kellner *et al.*, 2011).

Isolated teeth have been referred to Spinosauridae (Buffetaut & Ingavat, 1986a; Congleton, 1990; Martill *et al.*, 1996; Salgado *et al.*, 2009). Many of these referrals remain contentious because various non-dinosaurian clades have independently acquired tooth morphologies similar to those of spinosaurids, interpreted as adaptations for feeding on live prey in aquatic environments (Bertin, 2010; Hasegawa *et al.*, 2010). For example, long teeth with longitudinal ornamentations can be found in marine reptiles such as ichthyosaurs, elasmosaurs, mosasaurs, and crocodylomorphs (Hasegawa *et al.*, 2010). Among theropods, the only other group that registers conidont, fluted crowns besides spinosaurids are theropods within Unenlagiinae (albeit with some notable differences, in particular, the absence of carinae) (Gianechini *et al.*, 2011). Such dental features have been used to suggest piscivory for the group (Brum *et al.*, 2021).

Confirmed occurrences of Spinosauridae in South America include three species from northeastern Brazil: *Irritator challengeri* Martill *et al.*, 1996 and *Angaturama limai* Kellner & Campos, 1996 from the Romualdo Member of the upper Lower Cretaceous Santana Formation and *Oxalaia quilombensis* Kellner *et al.*, 2011 from the lower Upper Cretaceous Alcantara Formation (Kellner *et al.*, 2011; Kellner & Campos, 1996; Lacerda *et al.*, 2023; Medeiros, 2006; Sues *et al.*, 2002). Because *A. limai* and *I. challengeri* were found in the same formation and the material of both holotypes correspond to different regions of the skull, it has been suggested that the two could belong to the same taxon or to the same individual (Charig & Milner, 1997; Dal Sasso *et al.*, 2005; Sereno *et al.*, 1998). Other authors have suggested that there are important anatomical and preservational differences that indicate that the two specimens correspond to different individuals if not two species (Kellner & Campos, 1996; Sales & Schultz, 2017). A reassessment of the osteology of *I. challengeri* by Schade *et al.* (2023) aided by µCT data led to the interpretation that there was indeed no overlap between the holotypes of *Irritator challengeri* and *Angaturama limai*; however, because other arguments have not been invalidated, the question continues to be unresolved (see Schade *et al.*, 2023). *Oxalaia quilombensis* is less complete than the other two Brazilian species, consisting of fused premaxillae and a referred partial maxilla of a large individual (Kellner *et al.*, 2011).

In addition to these three species, indeterminate spinosaurids have been recovered from the Lower Cretaceous (Valanginian–Berriasian) Feliz Deserto Formation of northeast Brazil, including three fragmentary tooth crowns (Lacerda *et al.*, 2023). These teeth were referred to Baryonychinae among Spinosauridae, based on phylogenetic and multivariate analyses, and they represent the first report of that clade in South America. Lacerda *et al.* (2023) identified two features that are intermediate between Spinosaurinae and Baryonychinae: the presence of denticulated carinae bearing a relatively high number of denticles (6–7 per millimeter) and a comparatively high number of labial and lingual flutes, generally a characteristic of most spinosaurines (though there are exceptions, see Table 1). They concluded that such features could represent a transitional form between both clades, which is consistent with the interpretation by Hendrickx *et al.* (2019) that a high number of small denticles may have led to the emergence of unserrated carinae. Additionally, Hattori & Azuma (2020) pointed out that Japanese teeth from the Lower Cretaceous Sebayashi and Kitadani Formations (Barremian and Aptian in age, respectively) also presented features that can be interpreted as intermediate between Spinosaurinae and Baryonychinae, but with a crucial difference: the Japanese teeth preserve denticles of relatively larger size and more sparsely distributed, with no more than four denticles per millimeter. It is also important to point out that the Japanese teeth also have a relatively high number of flutes on their labial and lingual surfaces, compared to those of baryonichines such as *Baryonyx* and *Suchomimus* (of Barremian and Late Aptian age, respectively) (Table 1).

TABLE 1. Character evaluation of spinosaurid teeth by Mateus *et al.* (2011), later expanded by Kubota *et al.* (2017).

Taxon	***Tarvosaurus***	MUPE HB87	***Ostafrikasaurus***	***Siamosaurus***	IVPPV 4793	GMNH-PV-999	KDC-PV-0003	FPDM-V-9999	FPDM-V-10241	***Baryonyx***	***Suchomimus***	LPUFS 5860	***Irritator***	Spinosaurines from Kem Kem Beds	LAP-01	MUSM 5121	MUSM 4269	MUSM 5122
Age	Late Jurassic	?Bathonian	Late Kimmeridgian	Valangian to Barremian	Early Cretaceous	Barremian	Barremian	Aptian		Barremian	Late Aptian	Barriasian-Valanginian	Albian	Early Cenomanian	Early Cenomanian	Campanian–Maastrichtian		
Literature		Serrano-Martinez *et al.* (2016)	Buffetaut (2012)	Buffetaut & Ingavat (1986)	Buffetaut *et al.* (2008)	Hasegawa *et al.* (2003)	Kubota, Takakuwa & Hasegawa (2017)	Hattori & Azuma (2020)	Hattori & Azuma (2020)	Mateus *et al.* (2011)	Sereno *et al.* (1998)	Lacerda *et al.* (2023)	Sues *et al.* (2002)	Mateus *et al.* (2011)	This work	This work	This work	This work
Enamel surface of the crown	smooth	sculptured	sculptured	sculptured	sculptured	sculptured	sculptured	sculptured	sculptured	sculptured	sculptured	sculptured	sculptured	sculptured	sculptured	sculptured	sculptured	sculptured
Presence of flutes	no	no	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes
Tooth crown suboval to subcircular in cross-section	no	no	no	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	N/A	N/A
Exceptionally long and slender tooth roots	no	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	yes	yes	N/A	yes	yes	yes	N/A	N/A	N/A
Curvature of the crown	yes	no	no	no	no	no	n/a	yes	yes	yes	yes	yes	no	no	no	yes	yes	yes
Base of the crown enamel surface	smooth	N/A	N/A	N/A	N/A	N/A	N/A	smooth	smooth?	sculptured	smooth or poorly sculptured	N/A	smooth	N/A	smooth	smooth	N/A	N/A
45-degree orientation of enamel sculpture near interdenticle sulci	no	no	no	N/A	N/A	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	no	N/A	N/A
Carinae bearing 5 or more denticles per mm	no	no	no	N/A	N/A	N/A	no*	no	no	yes	yes	yes	n/a	N/A	N/A	Maybe	N/A	N/A
Irregular denticle size along carinae	no	no	yes	N/A	N/A	N/A	yes	yes	yes	yes	yes	yes	n/a	N/A	N/A	N/A	Maybe	N/A*
Well-pronounced carinae	no	no	no	N/A	no	N/A	no	yes	yes	no	no	yes	yes	yes	yes	yes	yes	N/A*
Number of flutes on both crown sides	N/A	N/A	14	30	24	24	20–?24	17–17	15–13	6–8	0–10*	11–9	7	10–40	28–19	16–9	>16–>6	16–12

Titanosauria is a lineage of macronarian sauropod dinosaurs defined by Wilson & Sereno (1998: p. 22) as "all titanosauriform sauropods more closely related to *Saltasaurus* than to *Brachiosaurus* or *Euhelopus*." Titanosaurs are the most diverse and geographically widespread sauropod clade, representing approximately one-third of all known sauropod diversity. Their earliest representative from the earliest Cretaceous (Berriasian–Valanginian; *Ninjatitan* Gallina *et al.*, 2021), and they are particularly abundant on the landmasses that made up Gondwana (Powell, 2003) and less predominant on Laurasian landmasses, thus, apart from *Alamosaurus*, there are no other confirmed titanosaurs from North America (Fronimos, 2021; González-Riga *et al.*, 2019 Butler *et al.*, 2009).

Titanosaurs were the only sauropods to survive into the latest Cretaceous in South America and other landmasses (Apesteguía *et al.*, 2020; Novas, 2009). During this timeframe, the clade is known for having among its members the largest terrestrial vertebrates of all time (*e.g.*, *Argentinosaurus* Bonaparte & Coria, 1993; *Patagotitan* Carballido *et al.*, 2017), as well as medium and even small-sized species (Apesteguía *et al.*, 2020). This came as a result of multiple radiation events that led to the emergence of specialized forms, such as the giant lonkgosaurians and the small-sized saltasaurines, and at least one genus that independently acquired traits characteristic of other rebbachisaurid sauropods (*Inawentu*; Filippi *et al.*, 2024).

MATERIAL AND METHODS

Material

Most of the specimens described herein were part of the collection of the Instituto Nacional de Cultura (INC), which is now the Dirección Desconcentrada de Cultura de Amazonas. Specimens were lent to the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM), Lima, for an exhibition in 2000. Even though these fossils include the best preserved non-avian dinosaur remains reported in Peru, precise information regarding their original location and date of collection was limited and sometimes non existent.

The described specimens include a nearly complete humerus (MUSM 4667), originally collected and prepared by José Bonaparte, and four articulated caudal vertebrae (MUSM 4672) reported by Mourier *et al.* (1986). Additional skeletal material from the same study, including phalangeal fragments and isolated teeth, has been lost. The collection also contains three fragmentary theropod teeth (MUSM 5121, MUSM 4269, and MUSM 5122) and a small titanosaur vertebra (MUSM 4671). Of these, specimens MUSM 5121, MUSM 4269, and MUSM 4671 were collected during a 2016 MUSM-University of Montpellier expedition, whereas MUSM 5122 was part of the original INC collection.

Methods

Preparation of fossil specimens. Fossil specimens were cleaned and prepared at the MUSM installations using pneumatic airscribes to separate them from the matrix. The only exceptions are the first of a sequence of four anterior caudal vertebrae (MUSM 4672), which was cleaned and prepared in an unspecified laboratory by Thomas Mourier's team (Mourier *et al.*, 1986), and the humerus referred to Titanosauria (MUSM 4667) that was cleaned and prepared by Ángel Jáuregui and José Bonaparte. Further details regarding the process are not available. An incomplete right fibula (MUSM 4674) and distal left tibia (MUSM 4681) from the former INC collections were partially prepared before their arrival at the MUSM collection; no information regarding the preparation process of these specimens was available.

Identifying and describing isolated theropod teeth. We performed a Linear Discriminant Analysis (LDA) using the software PAST v. 5.0.2 (Hammer *et al.*, 2001) to place the better-preserved tooth, MUSM 5121, within descrete theropod groups. The analysis was performed using 12 linear measurements from the dataset of Smith *et al.* (2005) that was subsequently expanded subsequently expanded by other authors (Smith & Lamanna, 2006; Smith & Dalla Vecchia, 2006; Smith, 2007; Sereno & Brusatte, 2008; Molnar *et al.*, 2009; Hocknull *et al.*, 2009; Hendrickx *et al.*, 2015b; Young *et al.*, 2019; Brum *et al.*, 2021; Lacerda *et al.*, 2023). The dataset includes 1,373 teeth (see Supplementary Online Information). We followed the methodology of Young *et al.* (2019), expanded by Hendrickx *et al.* (2020), in which all linear measurements are log-transformed, and a +1 correction was applied to the log values of the flute count for the labial and lingual sides of the tooth to account for the taxa that did not have them. Additionally, a Principal Component Analysis (PCA) was performed using the same measurements to assess the main contributors to the variance. The results of the PCA can be found in the Supplementary Online Information.

We used the methodology proposed by Hendrickx *et al.* (2015a) to describe and assess isolated theropod teeth. We followed the dental nomenclature used by Kubota *et al.* (2017), in which the apical-oriented large longitudinal ornamentations are termed “flutes,” and the micro-sized enamel ornamentations running in between them are “granules.”

Micrography. Micrographs of the enamel surface of all three teeth were taken using a stereoscopic microscope, Perfex Sciences HG 519408, and a trinocular microscope Optika B-193PL, connected to the cameras Amscope MA 1000 and Optika C-B10+.

μCT. When collected, the most complete tooth (MUSM 5121) was broken into three sections and covered almost entirely with sediment. The pieces were later joined together in the preparation process, and a μCT scan was performed once most of the crown was exposed but before the root was cleaned, as the dentine became thinner basally. The material was scanned with a Nikon XT H 225ST μCT system (Nikon Metrology, Brighton, USA) housed in the Department of Earth and Environmental Sciences at the University of Michigan.

3D modeling. We used 3D Slicer 5.2.1 (Fedorov *et al.*, 2012) to examine the μCT data and obtain three-dimensional segmentations that were later rendered in Blender 3.4 (Blender Online Community, 2018). Additionally, due to the size and weight of the nearly complete humerus (MUSM 4667), we performed a surface scan of the material to get a 3D model. The process was made using an EinScan Pro HD scanner, Shinning 3D® edition. Additional 3D modeling of medium-sized skeletal elements (MUSM 4672, MUSM 4673, MUSM 4674) was performed using the photogrammetry software Polycam® in a Samsung Galaxy S™22. Finally, outlines of the cross-section of the humerus and right fibula were obtained by generating a stack of image files from the 3D models using 3D Slicer®.

Institutional abbreviations. FPDM, Fukui Prefectural Dinosaur Museum; **GMNH-PV,** Paleo-Vertebrate Collection of the Gunma Museum of Natural History, Tomioka, Gunma, Japan; **HEC,** Karl Hirsch Eggshell Collection housed at the University of Colorado Museum of Natural History, Colorado, United States of America; **IVPP,** Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **KDC-PV,** Paleo-Vertebrate Collection of Kanna Dinosaur Center, Kanna, Tano, Gunma, Japan; **LAP,** Laboratorio de Anatomía Patológica y Biología Celular de la Universidad de Cádiz, Cádiz, Spain; **LPUFS,** Laboratório de Paleontologia of the Universidade Federal de Sergipe; **MUPE HB,** Azanak site collection, Museo Paleontológico de Elche, Alicante, Spain; **MUSM,** Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Perú; **UMMP,** University of Michigan Museum of Paleontology, Michigan, United States of America. **XMDFEC,** Xixia Museum of Dinosaur Fossil Eggs of China.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1888
THEROPODA Marsh, 1881
SPINOSAURIDAE Stromer, 1915
Figures 1–6

Referred material. Isolated tooth crowns, MUSM 4269, MUSM 5122; isolated tooth, MUSM 5121. MUSM 4269 and MUSM 5121 were collected by four of us (A.B.-P., J.T., R.S.-G., and P.-O.A.) There is no available information for MUSM 5122.

Geographic occurrence. MUSM 5121 and MUSM 4269 were collected from locality BAG-2016-2 (Fig. 1), located southwest of Bagua and east of the Marañón River (05° 40.641’ S; 078° 33.954’ W). The locality that produced MUSM 5122 is unknown but displays similar preservation features to MUSM 4269 and MUSM 5121 found in BAG-2016-2, notably in the coloration of the enamel (Figs. 2–4) and the color and texture of the original sediment matrix it was originally embedded in.

Stratigraphic occurrence. Locality BAG-2016-2 is located in the upper part of the Fundo El Triunfo Formation (Rentema Member of the Chota Formation *sensu* Chacaltana *et al.*, 2014). All material described in this work that came from this locality, including the teeth MUSM 5121 and 5122, was collected in situ by the MUSM-University of Montpellier expedition, MUSM 5121 was still embedded in rock.

The base of the Fundo El Triunfo Formation was given a maximum depositional age of 81.6 ± 0.3 Ma (early Campanian), based on detrital zircon U-Pb analysis from volcaniclastic sandstones and lithic sandstones (Moreno *et al.*, 2020). These results are in accordance with previous fission track estimations made by Naeser *et al.* (1991) and middle Campanian–early Mastrichtian biostratigraphical ages as estimated by Mourier *et al.* (1988). Accordingly, this formation likely spans all or part of the Campanian–Maastrichtian interval.

DESCRIPTION

General remarks. All teeth are slender and conical in shape, with a circular or subcircular cross-section ('conidont' teeth *sensu* Hendrickx *et al.*, 2015a). The enamel, in the areas where it is preserved, has a distinctive granular surface.

Preservation. The apex of all specimens and the base of the crown of MUSM 4269 and MUSM 5122 are lost. MUSM 5121 preserves most of the crown and root.

MUSM 5121

Crown. The crown is very well preserved, lacking only its apex (Fig. 4). The preserved height of the crown is 56.6 mm, and its preserved base length and width are 18.9 mm and ca. 19 mm, respectively (the width had to be estimated as a portion of the lingual surface is lost). The preserved cross section is circular to subcircular, labiolingually flattened

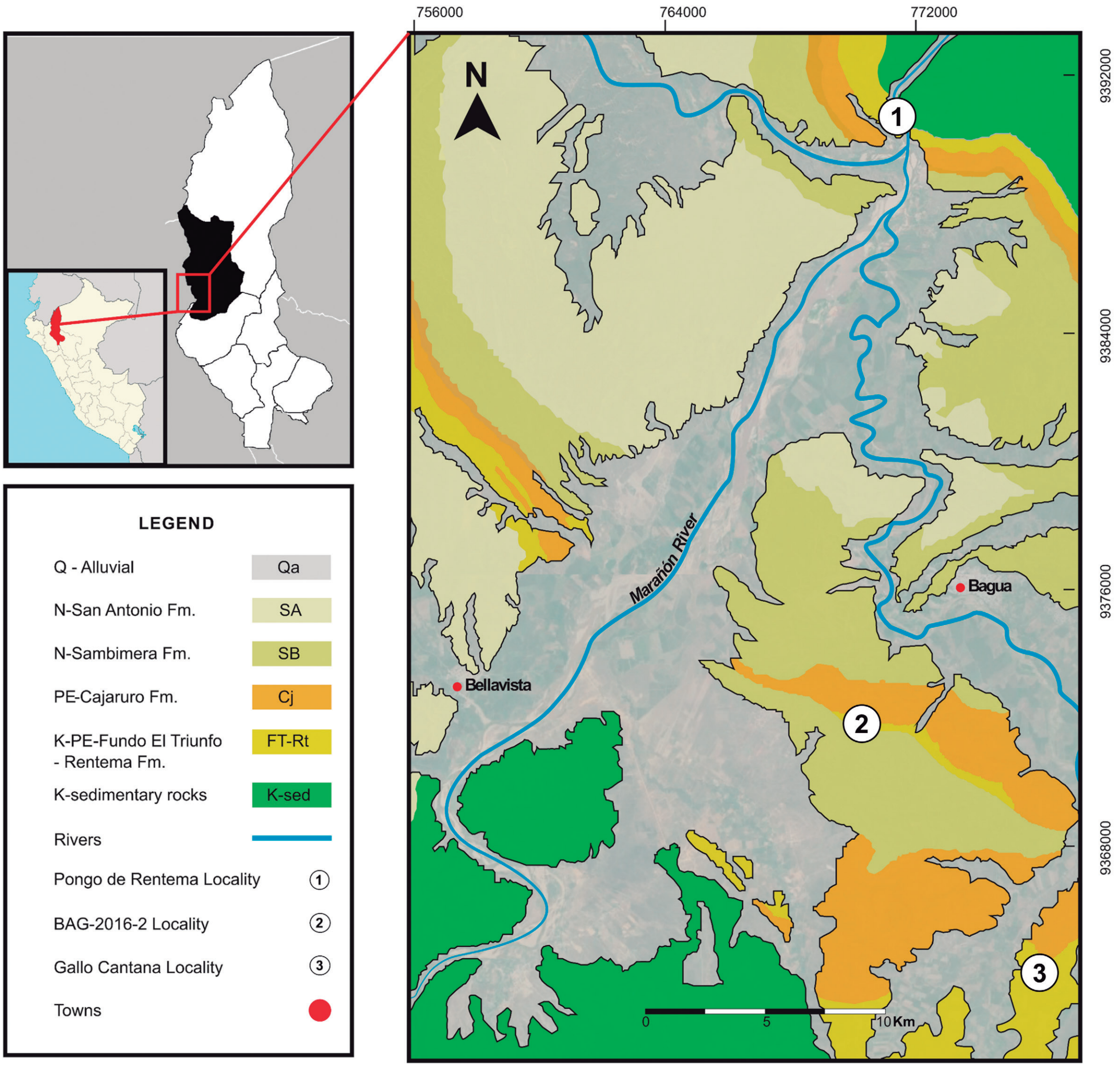

Figure 1. Geologic map of dinosaur fossil localities within the latest Cretaceous (Campanian–Maastrichtian) Fundo El Triunfo Formation (Bagua Basin) referenced in this work. Maps are based on Chacaltana *et al.* (2014) and Moreno *et al.* (2020). Background texture images from AirbusMaxar TechnologiesCNES / Airbus 2021; Google Earth accessed February 2021.

towards the apex of the crown, and progressively mesiodistally compressed towards the root (see Figs. 5, 6). The estimated ratio between mid-crown width and mid-crown length (mid-crown ratio) is 0.85.

Enamel is present on most of the crown except for a portion close to the first breakage point. Two curvatures stand out. The most pronounced curvature follows the labio-lingual axis, but the crown is also curved distally. The crown angle is 77.0°, which is measured between the apical segment (connecting the mesial-most point at the cervix to the apical-most point of the crown) and the crown base (see Hendrickx *et al.*, 2015a). A second angle created by the apical segment and the crown width (to assess the mesiodistal curvature) measured 80.1°. Both carinae are well-preserved, unserrated, and strongly lingually deflected. µCT images show a pattern of apico-basally oriented lines in the dentine that run the length of the tooth, becoming more conspicuous towards the apex. These probably represent incremental lines of von Ebner (Erickson, 1996), but the resolution is not high enough to allow us to count them (see Fig. 5).

Denticles. The carinae are unserrated. However, we identified small, parallel dents perpendicular to the distal carina (see Fig. 4). These structures could be remnants of denticles. These structures are not present in the mesial carina. Unlike in MUSM 4269, these structures do not seem

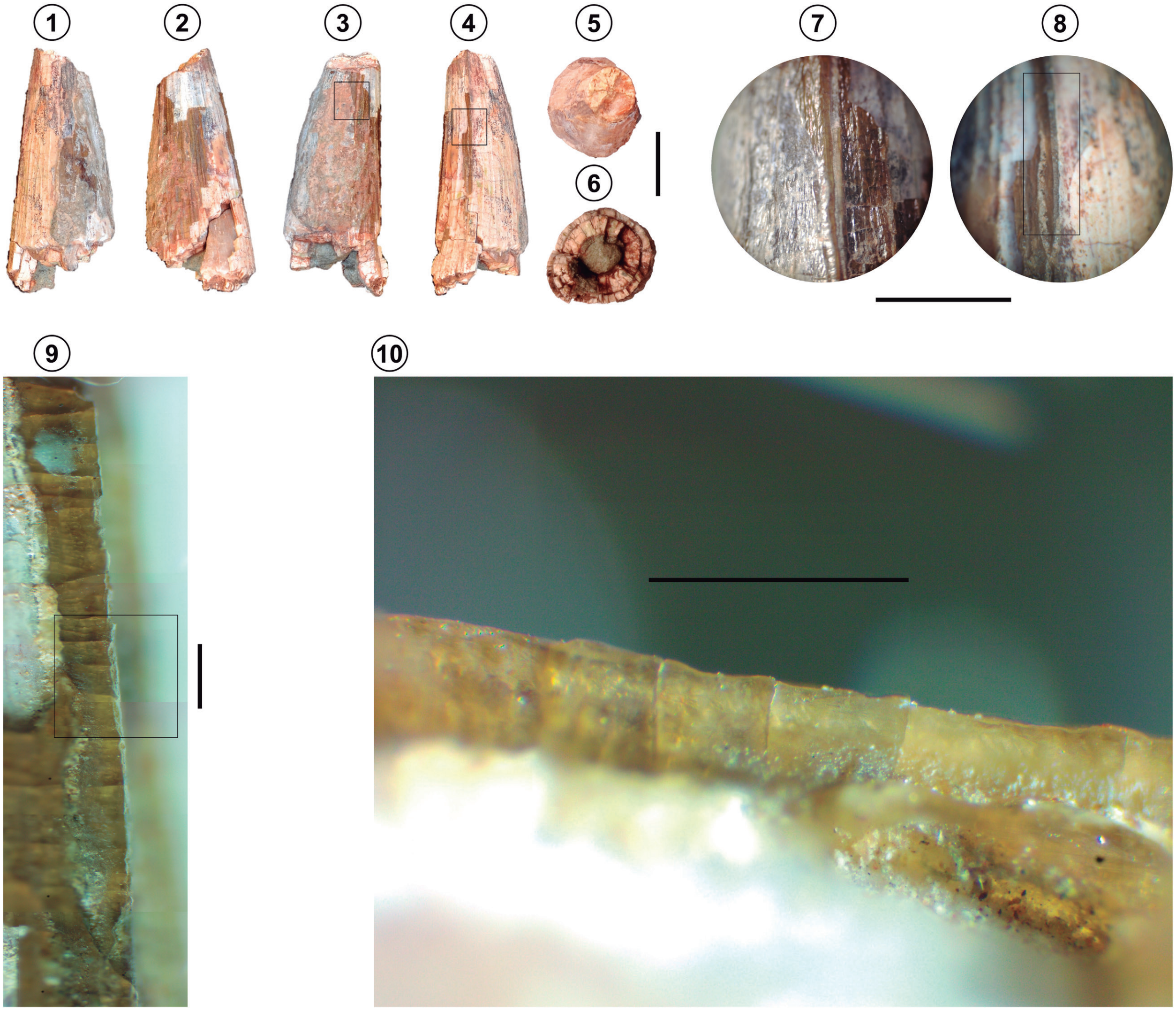

Figure 2. Spinosaurid tooth **MUSM** 4269 in **1,** labial, **2,** lingual, **3,** mesial, **4,** distal, **5,** apical, **6,** and basal, **7** views. **7** and **8** depict stereoscopic micrographs of the mesial and distal carinae, respectively. **9** and **10** are micrographs of the distal carina from the lingual side. Scale bars: **1–6** = 10 mm, **7–8** = 5 mm, **9–10** = 1 mm.

TABLE 2. Morphometric measurements of the root of MUSM 5121. S1-3 represent transverse sections of the tooth taken at different distances from the preserved base of the root. S1: 34.7 mm, S2: 22.3 mm, S3: 9.8 mm.

Measurements/Sections	S1	S2	S3
DMT (mm)	4.2	4.2	3.4
DDT (mm)	5.2	4.2	3.9
DLIT (mm)	5.4	4.2	3.2
DLAT (mm)	4.6	4	3.8
Length (mm)	18.6	20.3	21.2
Width (mm)	20.1	22.7	26.4*
Length/Width ratio	0.9	0.9	0.8*

Measurements of dentine at the cervix could not be taken as the second point of breakage occurred close to it and portions of the dentine are missing. Abbreviations: **DMT,** dentine thickness mesially; **DDT,** dentine thickness distally; **DLIT,** dentine thickness lingually; **DLAT,** dentine thickness labially. *The length, width and dentine thickness lingually for Section 3 were estimated as most of the lingual dentine of this section was lost (see Fig. 6).

associated at all with the patterns of enamel breakage perpendicular to the direction of the flutes and granules.

Ornamentation. Both the labial and lingual surfaces are fluted and possess granular enamel. The flutes are less prominent in areas devoid of enamel. We count nine flutes on the lingual surface and 16 flutes on the lingual surface. The granules closest to the carinae are not oriented at a 45-degree angle with respect to either carinae.

Root. The preserved root is 59.7 mm long, similar in length to the crown. Several portions of the preserved base of the root were broken off, possibly during diagenesis. The surface of the dentine is relatively smooth. It has a subcircular cross-section at the level of the cervix but gets progressively flattened mesiodistally and becomes more oval-like into moving onto the base of the root (see Fig. 6). As would be expected, the thickness of the dentine gets progressively thinner, too (see Table 2 and Fig. 6).

Through the µCT images, we identified a replacement crown within the pulp cavity that is 47.5 mm long (Fig. 5). Seven flutes are present on the lingual surface of the crown; flutes were not identifiable on its labial surface, although this may be a result of the relatively low resolution of the model.

The replacement tooth occupies much of the pulp cavity but is not yet detached from the functional tooth, and most of the root remains. We place the family unit of both teeth between the initiation and growth stages of crocodylian

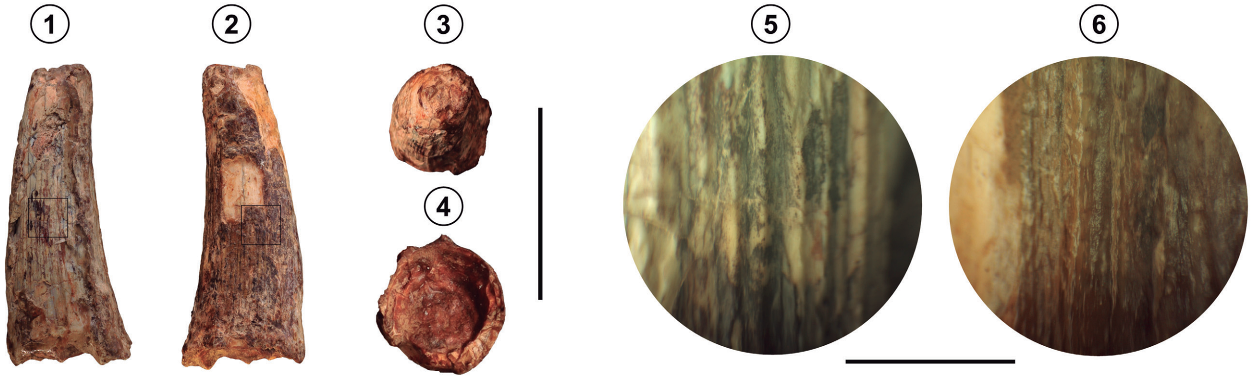

Figure 3. Spinosaurid tooth **MUSM** 5122 in **1,** labial, **2,** lingual, **3,** apical, and basal, **4** views. **5** and **6** depict stereoscopic micrographs of the labial and lingual faces, respectively. Scale bars: **1–4** = 10 mm, **5–6** = 5 mm.

TABLE 3. Linear morphometric measurements of MUSM 5121, MUSM 4269 and MUSM 5122.

Measurement/Specimen	MUSM 5121	MUSM 4269	MUSM 5122
Preserved CH (mm)	56.6	38	44
Preserved CBW (mm)	18.9	14.9	21
Preserved CBL (mm)	19	18.1	21
Preserved CHR	0.99	0.83	1
MCL	15.4	-	-
MCW	12.85	-	-
MCR	1.20	-	-
Labial Flutes	16	12	16
Lingual Flutes	12	6	9

Abbreviations: **CBL,** Crown base length; **CBW,** crown base width; **CH,** crown height; **CHR,** crown height ratio; **MCL,** mid-crown height; **MCR,** mid-crown ratio; **MCW,** mid-crown width.

Figure 4. Spinosaurid tooth **MUSM** 5121 in **1,** labial, **2,** mesial, **3,** distal, **4,** apical, **5,** and basal, **6** views. **7** and **8** depict stereoscopic micrographs of the small marked areas of the labial and lingual faces, respectively. **9** and **11** are micrographs of the mesial and distal carinae taken from the labial side. **10** and **12** are micrographs of the mesial and distal carinae in mesial and distal view, respectively. The white rectangles in **9** and **11** represent the areas from which micrographs **10** and **12** were taken. Scale bars: **1–6** = 20 mm, **7–8** = 5 mm, **9–12** = 1 mm.

teeth proposed by Wu *et al.* (2013) and between the ontogenetic stages IV and V of the crocodylian tooth cycle developed by Hanai & Tsuihji (2019) for *Tarbosaurus bataar*.

MUSM 4269

Crown. This partial, fragmentary crown lacks most of its enamel, although some patches remain (Fig. 2). The preserved height of the crown is 38 mm; its preserved length and width (towards the base) are 18.1 mm and 14.9 mm, respectively. The crown has two main curvatures associated with the mesiodistal and labio-lingual axes. The most conspicuous curvature follows the labio-lingual axis; the crown is curved lingually, accentuated towards the apex. Another less pronounced curvature follows the mesiodistal

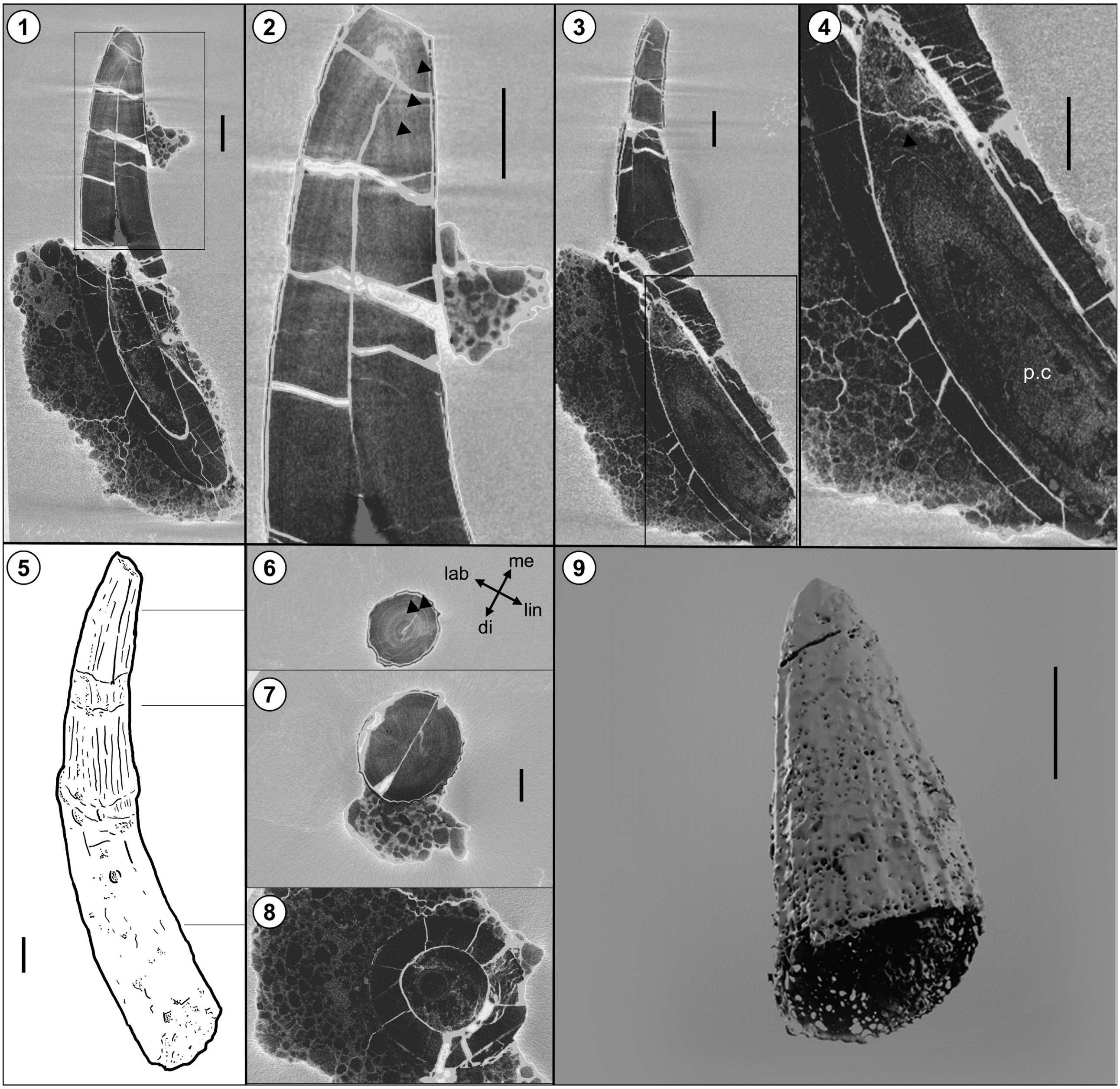

Figure 5. Spinosaurid tooth **MUSM** 5121 in **1–4, 6–8,** µCT scans, **5,** line drawing, and, **9,** three-dimensional segmentation. **1** and **2** show the incremental lines of von Ebner (daily growth lines; indicated by arrows). **3** and **4** show an inner replacement tooth in the pulp cavity. A possible set of von Ebner lines in **4** is indicated by an arrow. µCT images in **6–8** depict the labio-lingual flattening of the tooth towards the root; lines of von Ebner are visible in **6**. The three-dimensional segmentation of the inner tooth in labial view, **9,** was extracted via 3D Slicer. It lacks its most basal portion because the lingual side was extremely eroded and added noise to the reconstruction. Abbreviations: me, mesial; di, distal; lab, labial; lin, lingual. Scale bars: **1–4** = 10 mm, **5** = 20 mm, **6–8** = 5 mm, **9** = 10 mm.

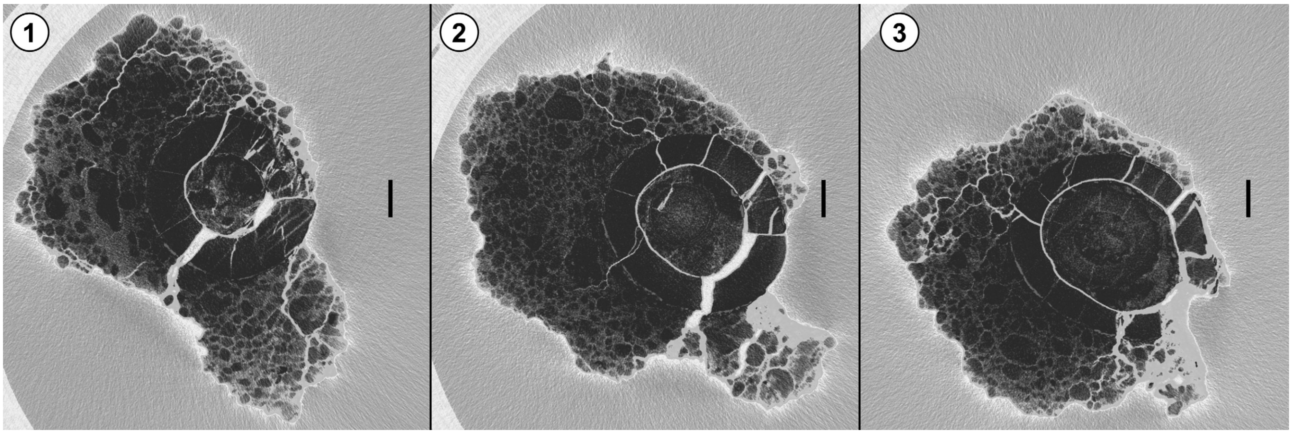

Figure 6. Transverse sections of **MUSM** 5121 at different distances from the preserved base of the root. **1,** S1: 34.7 mm, **2,** S2: 22.3 mm, **3,** S3: 9.8 mm. Scale bars= 5 mm.

axis. In cross-section, the tooth is subcircular, slightly flattened labio-lingually. The distal and mesial carinae are deflected lingually, both are conspicuous and unserrated.

Denticles. The carinae are unserrated. However, we identified sequences of parallel, transverse lines across the length of the preserved distal carina that may be consistent with patterns of enamel breakage but may also represent incipient denticles (Fig. 2).

Ornamentation. Both the labial and lingual surfaces are fluted. The flutes are less prominent in areas devoid of enamel. We count six flutes on the lingual surface and 12 flutes in the patches of the lingual surface that still preserved enamel and/or were not covered by the matrix.

MUSM 5122

Crown. The preserved height of this fragmentary crown is 44 mm, its preserved length and width are 21 mm. The preserved cross-section is subcircular and slightly flattened labio-lingually (Fig. 3).

The crown features two curvatures, we interpret the most prominent one as following the mesiodistal axis. Most of the crown surface is damaged and consequently, most of the enamel has been lost. The areas that are more well-preserved are those parallel to the axis of the main curvature and do not evidence the presence of carinae. The enamel in the remaining areas (that would have had the carinae), is lost. Thus, we interpret the surfaces alongside the less pronounced curvature as the labial and lingual surfaces. The labial face is eroded and has no remaining enamel.

Denticles. Both carinae are lost, and consequently, the presence of denticles cannot be assessed.

Ornamentation. Even though both labial and lingual surfaces have flutes, enamel is lost in most of the lingual surface and in all of the labial surface. Consequently, assessing the number of flutes is especially challenging. We counted at least 14 flutes on the labial surface and seven on the lingual surface.

SAUROPODA Marsh, 1878
MACRONARIA Wilson & Sereno, 1998
TITANOSAURIA Bonaparte & Coria, 1993
(sensu Wilson & Sereno, 1998)
Figure 7

Referred material. Axial skeleton: MUSM 4672, a series of proximal caudal vertebrae; MUSM 4671, a partial caudal vertebra; MUSM 4680, possible partial vertebrae or portion of a phalanx (Fig. 11, see description); MUSM 4675, MUSM 4676, MUSM 4678 and MUSM 4679, rib fragments; MUSM 4677, MUSM 4669, flat bones, possibly a piece of a scapula and pelvic element respectively. Appendicular skeleton: MUSM 4667, a virtually complete humerus; MUSM 4673; a right fibula; MUSM 4674, the proximal extremity of a left tibia; MUSM 4670, the distal extremity of a left tibia; MUSM 4681, the distal portion of the femur.

Geographic occurrence. MUSM 4672, MUSM 4673 and MUSM 4670 were collected from the Pongo de Rentema Locality. MUSM 4674 and MUSM 4671 came from the Gallo Cantana and BAG-2016-2 localities, respectively. The localities that produced MUSM 4680, MUSM 4676, MUSM 4678, MUSM 4679, MUSM 4677, MUSM 4669, MUSM 4667, and MUSM 4681 are unknown.

Stratigraphic occurrence. Pongo de Rentema, Gallo Cantana, and the BAG-2016-2 localities are found within the Campanian–Maastrichtian Fundo El Triunfo Formation (Rentema Member of the Chota Formation *sensu* Chacaltana *et al.*, 2014).

DESCRIPTION

Axial skeleton

Caudal vertebrae (MUSM 4672). This sequence of four incomplete caudal vertebrae currently represents the only dinosaur material from the Bagua Basin found in association and assigned to the same individual. The interpretation of the position of each individual vertebra can be seen in Figure 8. Neural spines and most vertebral processes were not preserved (Fig. 10). Although the vertebrae were first mentioned by Mourier *et al.* (1986), only one of the vertebrae in the series was cleaned and prepared in a laboratory at the time of publication of that work (the one we interpret to be the first on the sequence). The illustration of that element in Mourier *et al.* (1986: Fig. 3) appears to be reversed because it depicts the left transverse process as absent and the right transverse process as incomplete. In fact, the specimen lacks its right transverse process and

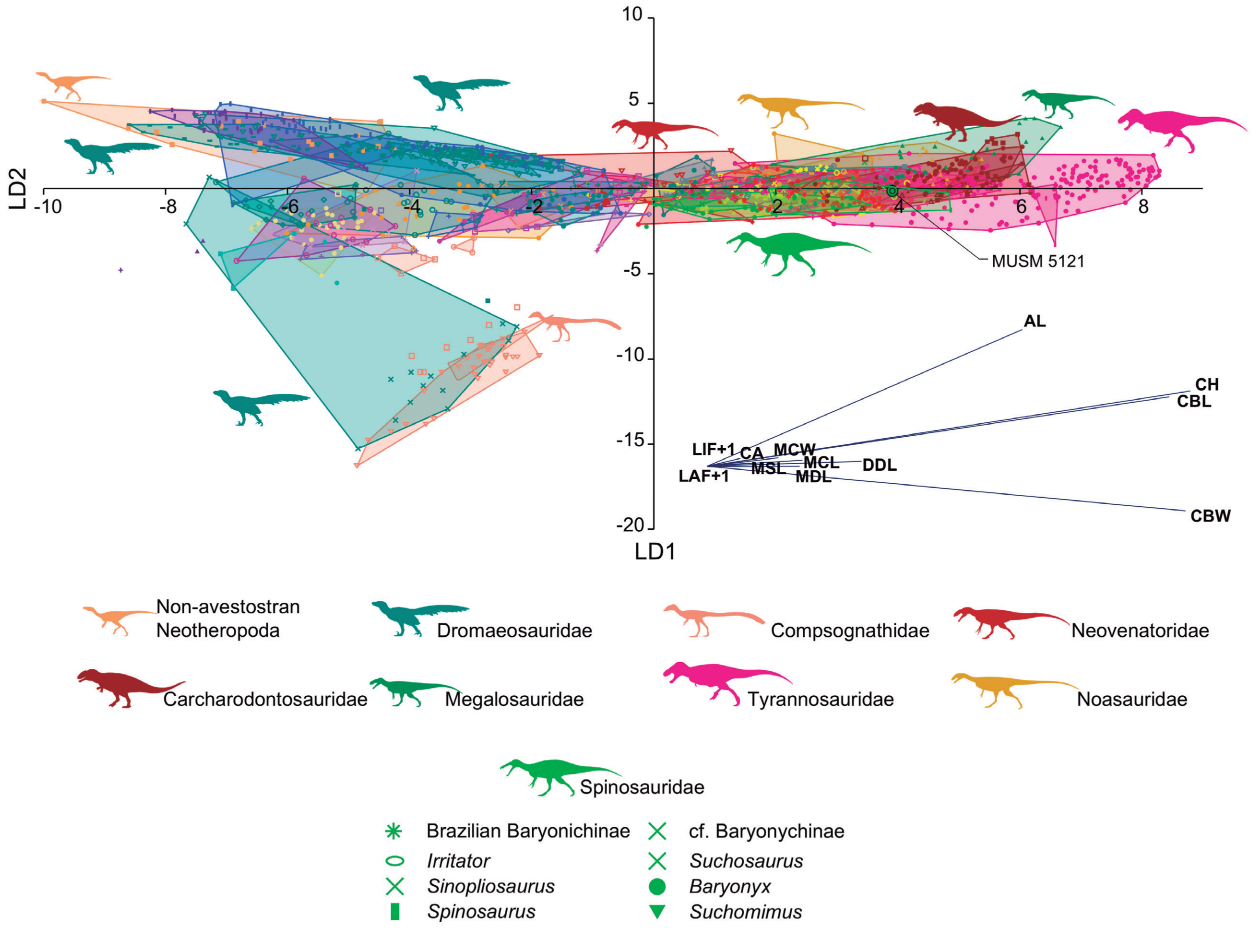

Figure 7. Graphical results of LDA and placement of MUSM 5121 along two axes: LD1 and LD2. Together, both axes represent 59.55% of the variance (LD1 = 43.34%, LD2 = 16.21%; see Supplementary Online Information). MUSM 5121 occupies the morphospace of Spinosauridae, though overlapping that of Carcharodontosauridae and Tyrannosauridae. Abbreviations: **AL,** apical length; **CA,** crown angle; **CBW,** crown base width; **CH,** crown height; **DDC,** distal denticle length; **LAF+1,** number of labial flutes plus one; **LIF+1,** number of lingual flutes plus one; **MCL,** mid-crown length; **MCW,** mid-crown width; **MDL,** mesial denticle length. Silhouettes correspond to the better-represented theropod taxa, with an emphasis on Spinosauridae. For specific information on all taxa included in this work, as well as all symbols and colors for each taxon, consult the Supplementary Online Information. Silhouettes taken from Phylopic.org. Licenses and artist credits can be found in the Acknowledgments section.

features an incomplete left transverse process.

The rest of the vertebrae in the series were not prepared in a laboratory until the onset of this work. The preparation process allowed for the recovery of the articular surfaces, some nutrient foramina (*e.g.*, four on the ventral surface of the fourth vertebra in the sequence), and nearly complete neural arches in two of the vertebrae. The orientation of all four vertebrae was inferred through the position of the ventral chevron facets. Their position caudally from the centra means that the vertebrae are strongly procoelous, which is a diagnostic character for Titanosauria, contrasting with the plesiomorphic amphiplatyan condition for the group (Mourier *et al.*, 1986; Salgado, 1993; Wilson, 2002; Wilson & Sereno, 1998). The posteroventral rims of the condyles are flattened and strongly tilted posteriorly, as in the anterior caudal vertebrae of *Bonatitan reigi* (Salgado *et al.*, 2015).

Figure 8. Proximal caudal vertebrae MUSM 4672 in lateral left view, arranged in the sequence proposed in this work. Scale bar= 5 cm.

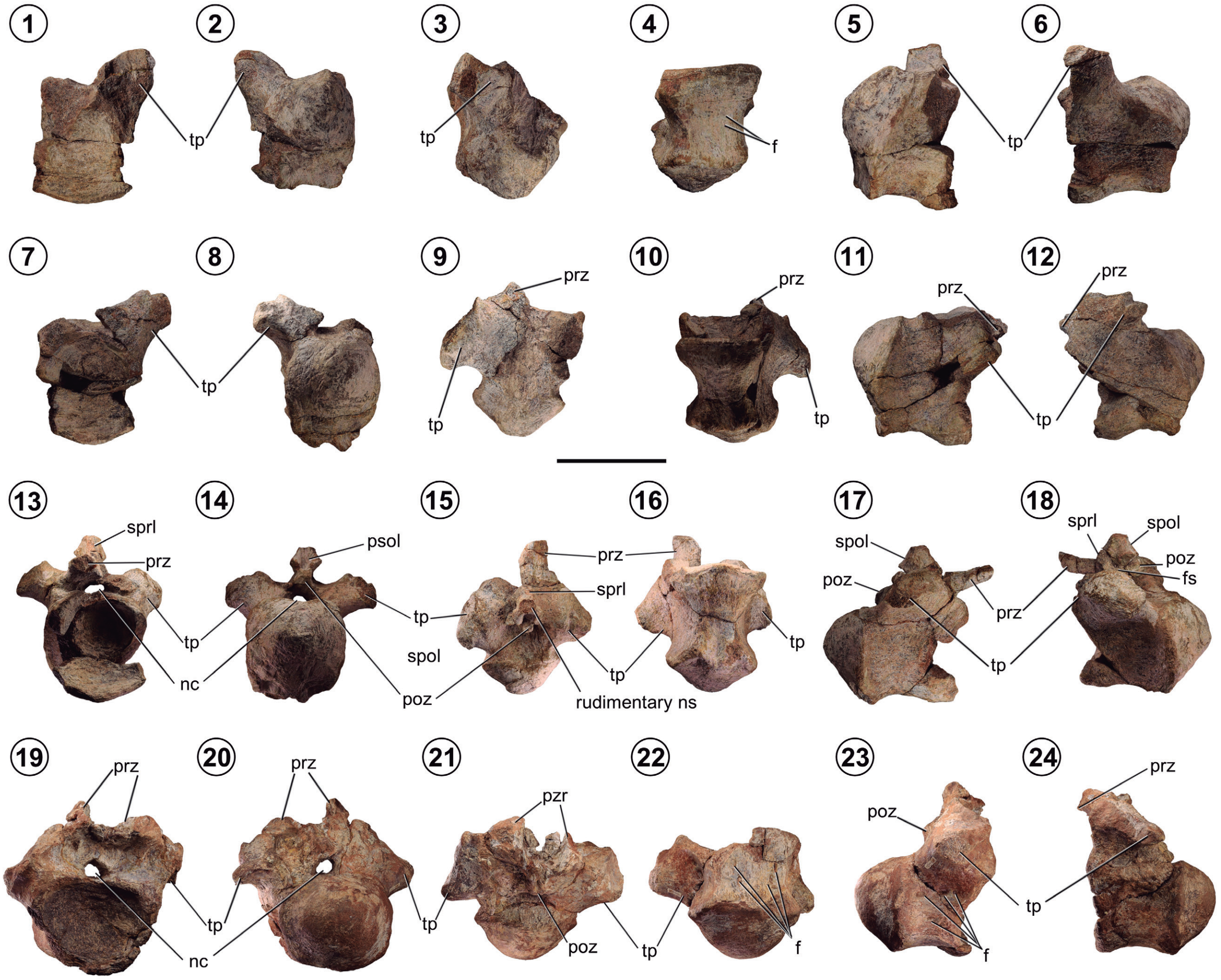

Figure 9. Caudal vertebrae MUSM 4672 in anterior, **1, 7, 13, 19,** posterior, **2, 8, 14, 20,** dorsal, **3, 9, 15, 21,** ventral, **4, 10, 16, 22,** right lateral, **5, 11, 17, 23,** and left lateral, **6, 12, 18, 24** views. Abbreviations: **f,** foramina; **fs,** fossa; **nc,** neural canal; **ns,** neural spine; **poz,** postzygapophysis; **prz,** prezygapophysis; **psol,** postspinal lamina, **spol,** spinopostzygapophyseal lamina; **sprl,** spinoprezygapophyseal lamina; **tp,** tranverse process. Scale bar= 10 cm.

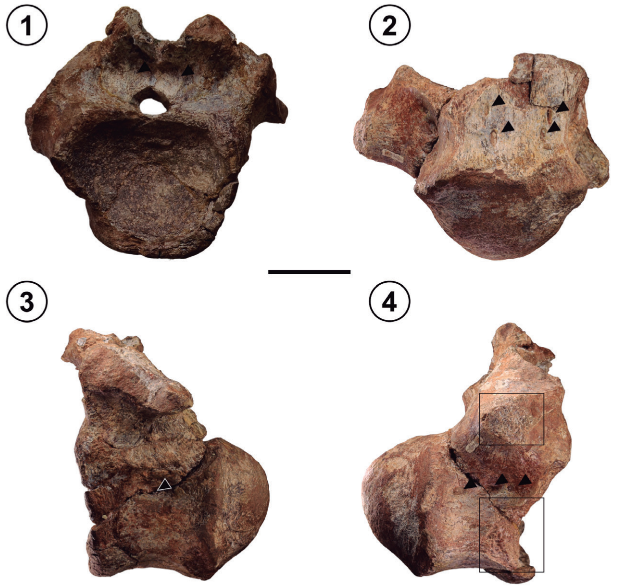

Figure 10. Caudal vertebra **MUSM** 4672. Possible pneumatic features of the fourth vertebra of the series in anterior, **1,** ventral, **2,** left lateral, **3,** and right lateral, **4** views. Foramina are indicated by arrows. Boxes in (4) highlight broken areas where normal spongy bone is present, rather than the camellate pneumaticity that is common in saltasaurines. Scale bar= 5 cm.

This incomplete set of vertebrae is also the material most similar to that of another named titanosaur taxa: the contemporary saltasaurine *Yamanasaurus lojaensis*, as the condyle of the last vertebra of the series is relatively spherical (the previous three vertebrae have taller, narrower condyles) and the posterior end of all condyles is elevated with respect to the vertebral midlines. Additionally, the many points of breakage reveal no camellate pneumaticity but instead a normal, spongy pattern on its inner structure. There are, however, identifiable pneumatic foramina on the neural arch and the upper, lateral portions of the centrum, adjacent to the transverse processes and on the ventral surface of the last vertebra of the series (Fig. 10). These sets of characteristics are not common in saltasaurines, but similar to that of *Neuquensaurus australis* and the aforementioned *Yamanasaurus lojaensis* (Apesteguía *et al.*, 2020; Zurriaguz & Cerda, 2017).

Caudal vertebra (MUSM 4671). This incomplete vertebra lacks the neural spine, along with most of the neural arch and portions of the transverse processes (Fig. 11). The material exhibits a conspicuous mediolateral deformation in an inclined plane. As a result, the lateral left side is much more flattened than the right side. As with MUSM 4672, a pair of well-developed chevron facets indicate the procoelous nature of the vertebra. This vertebra also features two more similarities to those of MUSM 4672, no pneumaticity is found on various broken surfaces and the posterior rim of the conical condyles is flattened postero-ventrally.

MUSM 4680. Extremely eroded and fragmentary material. The lack of identifiable characters other than a concave face on one of the surfaces makes it particularly difficult to interpret.

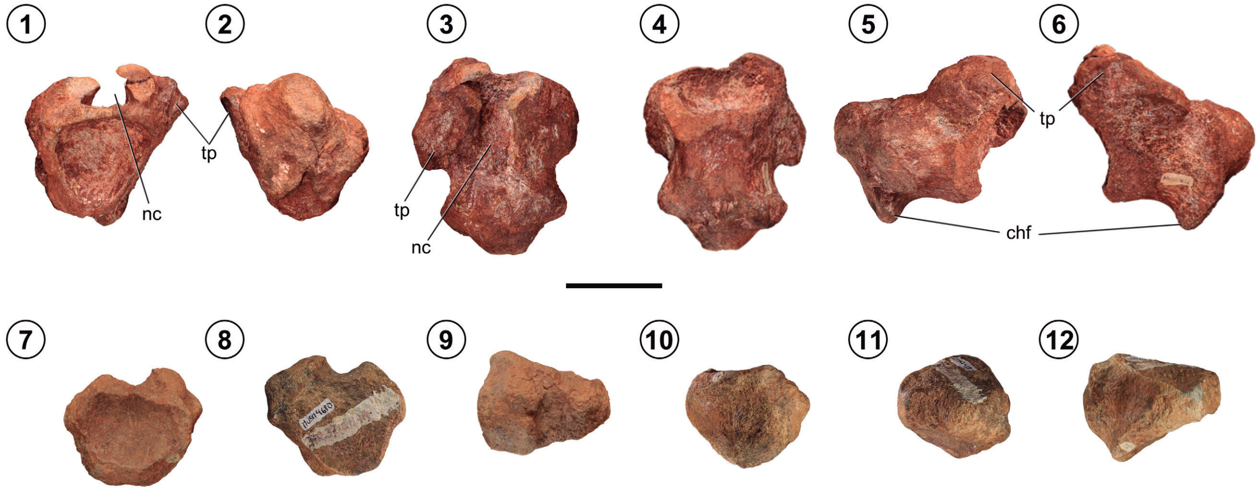

Figure 11. Caudal vertebra **MUSM** 4671, **1–6,** and **MUSM** 4680, **7–12.** Each vertebra is in its own row in anterior, **1, 7,** posterior, **2, 8,** dorsal, **3, 9,** ventral, **4, 10,** right lateral, **5, 11,** and left lateral, **6, 12** views. Scale bar= 5 cm. Abbreviations: **chf,** chevron facet; **nc,** neural canal; **tp,** transverse process.

Dorsal rib fragments (MUSM 4675, 4676, 4678, 4679). Portions of several dorsal ribs are preserved. The fragments are small and lack structures that can bear diagnostic characters such as preserved articular surfaces. The points of breakage also show no pneumatic cavities within them. Pneumatized dorsal ribs have been suggested to be a general diagnostic character for Titanosauriformes (Wilson, 2002; Wilson & Sereno, 1998), but generally, pneumaticity extends through the proximal portion of the element. The absence of pneumaticity in these dorsal rib fragments could be due to true absence, or the specimens could correspond to the non-pneumatized distal portions of the dorsal rib. At present, we cannot definitively rule out either interpretation, although the presence of pneumatized pelvic elements (see below) favors the latter interpretation.

Appendicular skeleton

Scapular fragment (MUSM 4677). This fragmentary, flat bone is likely a portion of the scapula blade. The specimen does not possess camellate pneumaticity. Instead, its inner structure presents a common spongy bone pattern.

Pelvic fragment (MUSM 4669). Although the fragmentary nature of the material precludes an assignment of the material to a specific component of the pelvis, the broken sections exhibit a pattern of camellate pneumaticity consistent with a titanosaurian origin. However, such pattern pneumaticity is partial, as half of the available portion of the bone has a normal spongy texture, whereas the other presents the big cells characteristic of camellate pneumaticity. It is most likely this element pertains to an ilium, given the frequency of pneumatized bone in that element (see Zurriaguz, 2024).

Figure 12. Scapular fragment **MUSM** 4677, **1–3,** pelvic fragment **MUSM** 4669, **4–6,** and dorsal rib fragments **MUSM** 4675, 4676, 4678, 4679, **7–10**. The scapular fragment is shown in presumed medial, **1,** lateral, **2,** and transverse section, **3** views. Section **3** is taken from the top of the image, **2**. The pelvic element fragment is shown in lateral, **4,** and transverse , **5, 6** views. Sections **5** and **6** are taken from the left and bottom of image, **4** respectively. Both show a pattern of camellate pneumaticity with enlarged air cavities; **6** shows a portion of the cross section that features both apneumatic (left side) and pneumatic (right side) inner structure. Dorsal rib fragment **MUSM** 4679, **7** is embedded in matrix. **MUSM** 4676, 4675, and 4678, **8–10** are shown in anteromedial (top right), lateral (bottom right), and transverse (top and bottom left) views. Scale bars: **1–3** = 10 mm, **4–6** = 5 mm, **7–10** = 5 mm.

Right humerus (MUSM 4667). An almost complete, well-preserved right humerus measuring 86 cm long (Fig. 13). We interpret the specimen to represent an adult or sub-adult individual based on the presence of well-developed regions for muscle attachment, such as a conspicuous bulge or tuberosity near the medial portion of the proximal fossa (Rigby *et al.*, 2021), but histological data would be required to confirm that. Some portions of the bone are lost and reconstructed with resin, such as the lateralmost portion of the proximal end (including the most proximal deltopectoral

Figure 13. Right humerus **MUSM** 4667. Photographs **1–6** and three-dimensional models, **7–10,** and serial cross-sections, **11** in anterior, **1, 7,** medial, **2, 8,** posterior, **3, 9,** lateral, **4, 10,** proximal, **5,** and distal, **6** views. Cross sections are oriented so that the anterior and lateral regions face up and right, respectively. The position of the cross sections is indicated by the tick marks next to them. Hatched lines on the 3D models represent the areas that were lost and subsequently filled with resin. Abbreviations: **cbb,** coracobrachialis muscle scar; **cf,** cuboid fossa; **dpc,** deltopectoral crest; **f,** foramen; **hh,** humeral head; **of,** olecranon fossa; **rac,** radial articular condyle; **suc,** supracoracoideus muscle scar; **ulc,** ulnar articular condyle. Scale bar= 10 cm.

crest), a narrow area around the midpoint between the radial and ulnar condyle, and most of the radial condyle, (except for its most medial portion in anterior view). Additionally, the bone appears to be broken into two portions along the proximal portion of the diaphysis. The fracture is more conspicuous posteriorly. Other regions with minor resin additions include the distal section of the deltopectoral crest and a small portion of the bone over the cuboid fossa in anterior view, as well as the posterior of the deltopectoral crest. Both distal condyles are well defined; the distalmost section of the ulnar condyle is lost, but no resin was added to the region.

The well-developed deltopectoral crest and proximal fossa make the humerus mediolaterally concave anteriorly. At the midpoint, the cross-section of the diaphysis becomes D-shaped. Distally, the differentiated condyles create a figure eight-shaped cross-section (Fig. 13). The diaphysis is relatively straight but presents a medial tilt along its axis, towards the proximal end, where it also expands moderately. The diaphysis does not appear to be twisted along its length.

The lateral edge of the deltopectoral crest is nearly straight in anterior view, and its lateral corner projects anteriorly and medially, like those of most titanosaurs (González-Riga *et al.*, 2019; Mannion *et al.*, 2013). The region of the crest with the most anterior projection is both flattened and beveled, as in *Jainosaurus* and *Mendozasaurus* (González-Riga *et al.*, 2019; Wilson *et al.*, 2009). The general anterior orientation of both distal condyles is consistent with that of the more derived saltasaurine titanosaurs (Novas, 2009; Wilson, 2002). MUSM 4667 is comparatively relatively slender and anteroposteriorly flattened (see Table 4). The humeral robustness index (*sensu* Wilson & Upchurch, 2003) is estimated at 0.24 (even when assuming the greatest lateral projection of the proximal section of the deltopectoral crest), similar to those of humeri of relatively gracile proportions, such as those of *Antarctosaurus septentrionalis* (0.24) and *Phuwiangosaurus sirindhornae* (0.25), more slender than that of the much more robust *Neuquensaurus* (0.3–0.34) and *Opisthocoelicaudia skarzynskiii* (0.37); though it does not reach the slenderness of *Muyelensaurus* (0.18) (Otero, 2010; Wilson & Upchurch, 2003).

The humerus features some prominent surface markings, such as a relatively conspicuous nutrient foramen at the cuboid fossa and a posterolateral bulge that exhibits a muscle scar possibly for the insertion of the M. supracoracoideus (Meers, 2003; Otero, 2018; Otero *et al.*, 2020). The loss of the lateral section of the proximal margin of the humerus impedes us from evaluating characters such as the flatness of the proximal section, as occurs in most titanosaurs (González Riga *et al.*, 2019) or the presence of a rounded projection in the proximolateral corner that defines a slight sigmoid curvature in anterior view, as seen in the saltasaurines *Saltasaurus* or *Opisthocoelicaudia* (González Riga *et al.*, 2019; Upchurch *et al.*, 2004).

Proximal femur (MUSM 4681). This eroded articular surface

TABLE 4. Humeral morphometric measurements of MUSM 4667.

LCB (cm)	14.1
MCB (cm)	12.9
MAD (cm)	7.1
HAL (cm)	16.4
GPW (cm)	32.5
GDW (cm)	21.7
MB (cm)	11.2
MC (cm)	32.6

Abbreviations: **LCB,** lateral condyle breadth; **MCB,** medial condyle breadth; **MAD,** maximum anteroposterior diameter; **HAL,** head anteroposterior length; **GPW,** greatest proximal width; **GDW,** greatest distal width; **MB,** minimum breadth; **MC,** minimum circumference.

of a long bone is possibly a femur. The material is eroded, and extensive portions of its surface are covered by resin. The surface is extremely fragile. We refer the material to the proximal extremity of a femur based on the progressive widening of the bone in cross-section towards what we interpret to be its most medial portion. No detailed morphometric data can be extracted.

Right fibula (MUSM 4673). This nearly complete fibula lacks only a portion of its proximal and distal ends. The bone is broken into at least three sections on its distal half and into two sections on its proximal portion. These sections were then glued together in the preparation process. Portions around the midpoint of the element have also been filled with resin (Fig. 14). Due to the absence of much of the proximal and distal ends, a robustness index for the fibula cannot be calculated.

The diaphysis is mostly straight, with little twisting or mediolateral curvature throughout its length. However, the

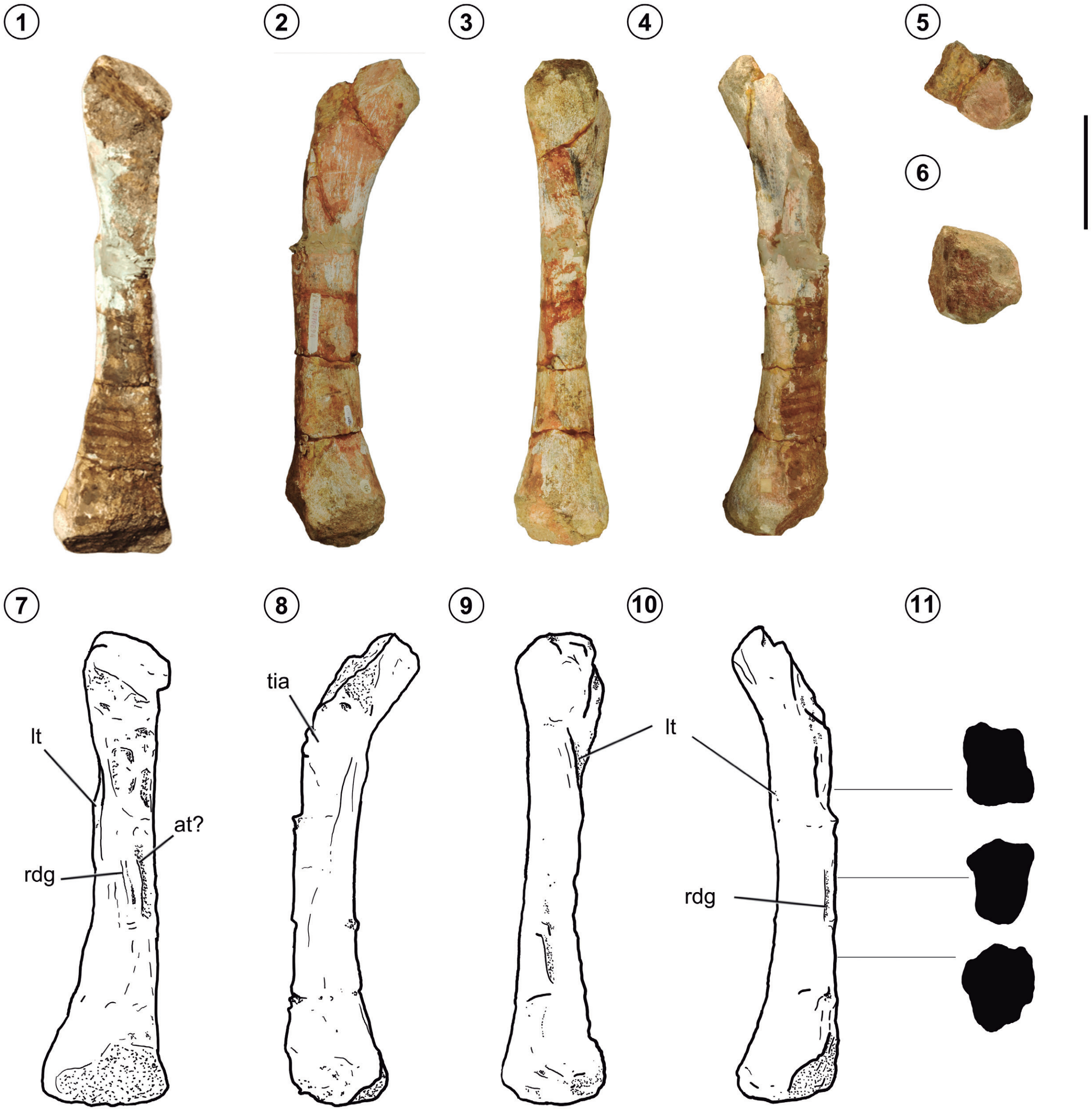

Figure 14. Right, fibula **MUSM** 4673. Photographs **1–6,** interpretive drawings, **7–10,** and serial cross-sections, **11,** in anterior, **1, 7,** medial, **2, 8,** posterior, **3, 9,** lateral, **4, 10,** proximal, **5,** and distal, **6.** Cross sections are oriented so that the anterior and lateral regions face up and right, respectively. The position of the cross sections is indicated by the tick marks next to them. Abbreviations: **at,** anterior trochanter; **lt,** lateral trochanter; **rdg,** ridge; **tia,** tibial articular surface. Scale bar= 20 cm.

preserved proximal and distal portions of the bone exhibit a prominent posterior expansion; thus, when observed in lateral or medial view, the diaphysis of the fibula shows a moderate curvature. The preserved distal extremity is mostly rounded and slightly flattened on its medial surface (Fig 14). The tibial articular surface is relatively flat, with a small medial projection towards the proximal extremity.

Compared to other titanosaur fibulae, MUSM 4673 is relatively small—similar in size and robustness to *Laplatasaurus* (Gallina & Otero, 2015; González-Riga *et al.*, 2019) and larger and more robust than that of *Lirainosaurus* (Diez Díaz *et al.*, 2012). It is also of similar size but stouter than that of *Bonitasaura* (Gallina & Apesteguía, 2015), though, due to the absence of much of the proximal and distal ends, a robustness index for the fibula cannot be calculated. The tibial articular surface is relatively flat, with a small medial projection towards the proximal extremity. The lateral trochanter is conspicuous and extends laterally, though it does not do so as prominently, nor is it as robust as that of *Laplatasaurus*, *Uberabatitan*, or *Neuquensaurus* (González-Riga *et al.*, 2019). An additional ridge is present anterolaterally and is particularly conspicuous in lateral view (see Fig. 14). The lateral trochanter is conspicuous and extends laterally, although it does not do so as prominently, nor is it as robust as that of *Laplatasaurus*, *Uberabatitan*, or *Neuquensaurus* (González-Riga *et al.*, 2019).

Proximal right tibia (MUSM 4674). Some areas of the surface of the tibia, particularly in the periphery of a prominent cnemial crest, are lost. The preserved articular surface has a much rougher texture compared to that of the rest of the surface of the bone. The preserved regions appear to be mostly straight and of similar dimensions to that of the contemporary saltasaurine *Yamanasaurus* (Apesteguía *et al.*, 2020).

Distal right tibia (MUSM 4670). Much of the surface over the articular surfaces was lost and subsequently covered

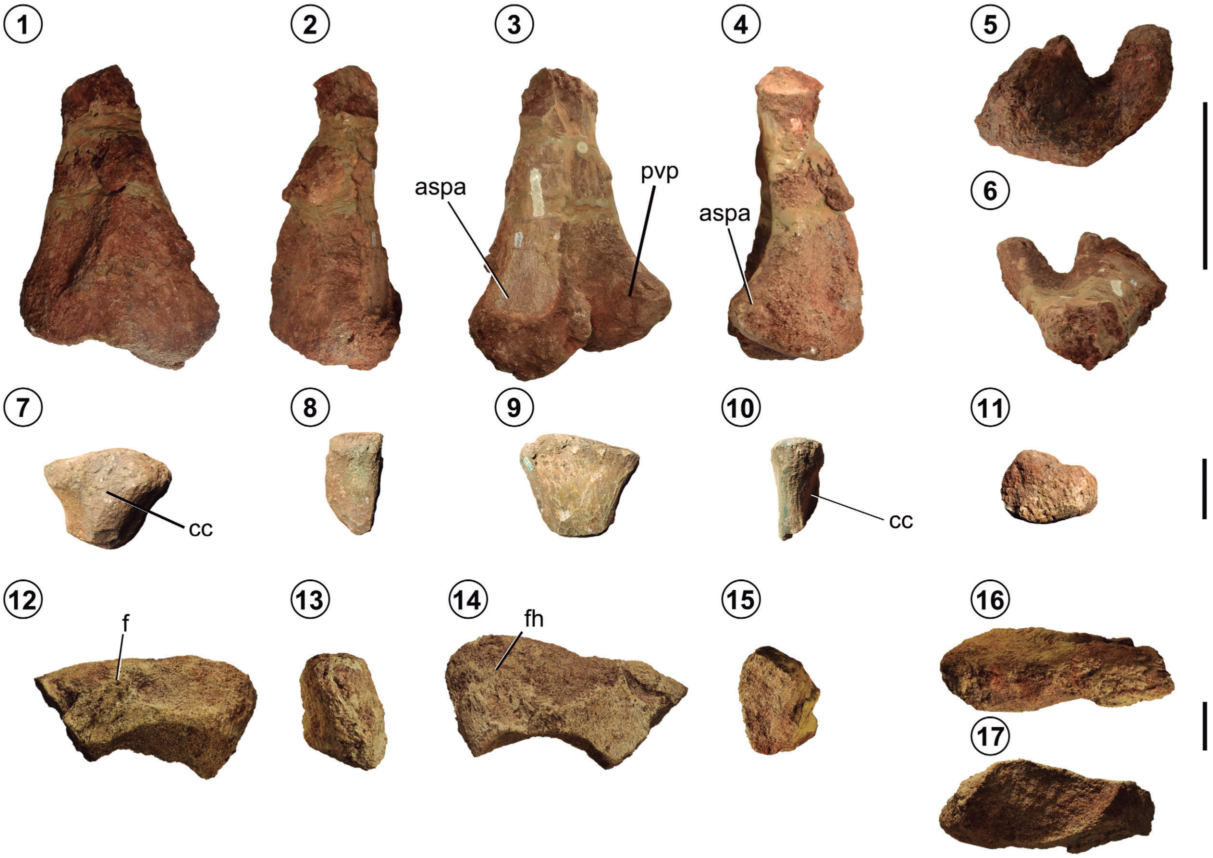

Figure 15. Distal left tibia **MUSM** 4670, **1–6,** proximal left tibia **MUSM** 4674, **7–11,** and proximal femur **MUSM** 4681, 13–16, in anterior, **1, 7, 13,** medial, **2, 8, 13,** posterior, **3, 9, 14,** lateral, **4, 10, 15,** distal, **5, 17,** and proximal, **6, 11, 16** views. Abbreviations: **aspa,** ascending process for the astragalus; **cc,** cnemial crest; **f,** foramen; **fh,** femoral head; **pvp,** posteroventral process. Scale bars: **1–6** = 10 cm, **7–11** = 5 cm, **12–17** = 5 cm.

Figure 16. Map showing Formations that bear titanosaurian remains of latest Cretaceous age (Campanian–Maastrichtian) (1, 6–22), and spinosaurid remains from Berriasian to Cenomanian age (2–5) in South America. **For titanosaurian remains:** Ecuador: 1, Río Playas Formation. Bolivia: 6, Chaunaca and El Molino Formations (both have yielded prints). Brazil: 7, Marilia Formation; 8, Adamantina Formation. Chile: 9, Tolar Formation; 12, Hornitos Formation. Argentina: 10, Yacoraite Formation; 11, Lecho Formation; 14, Ciénaga del Río Huaco Formation; 17, Loncoche Formation; 18, Colorado Formation; 19, Allen Formation; 20, Anacleto Formation; 21, Angostura Colorada Formation; 22, Chorillo (has yielded skeletal and eggshell remains) and Cerro Fortaleza (has yielded skeletal remains) Formations. Uruguay: 13, Guichon (has yielded skeletal and eggshell remains) and Queguay (has yielded eggshell remains) Formations; 15, Asencio Formation; 16, Asencio Formation. **For Spinosaurid remains:** Brazil: 2, Itapecuru Formation; 3, Alcantara Formation; 4, Santana Formation; 5, Feliz Deserto Formation. **Titanosaurian remains:** Skeletal remains: Santucci & Filippi (2022), Soto *et al.* (2012), Soto *et al.* (2022), Soto *et al.* (2024); eggshell remains: Fernández *et al.* (2022); fossil prints: Calvo *et al.* (2022). **For spinosaurid remains:** Kellner & Campos (1996), Medeiros & Schultz (2001), Machado (2010), Kellner *et al.* (2011), Medeiros *et al.* (2014), Hone & Holtz (2017), Aureliano *et al.* (2018), de França *et al.* (2022), Lacerda *et al.* (2023). Silhouettes were made by the authors of this work except for that of the Spinosaurid head (Phylopic.org). Licenses and artist credits can be found in the Acknowledgments section.

with resin. The condyles are well-defined, though, as in MUSM 4674, they exhibit a rough texture on the articular surfaces. The medial condyle is much more robust. The transverse width being larger than the anteroposterior diameter (see Fig. 15) is also diagnostic for Titanosauria (Novas, 2009).

Though the condyles expand both mediolaterally and anteroposteriorly, the loss of most of the diaphysis makes it impossible to determine whether a diagnostic ratio for lithostrotian titanosaurs between the anteroposterior diameter of the condyles and that of the shaft exists (following Wilson, 2002). The dimensions of those elements, however, are similar to those of *Bonitasaura* (Gallina & Apesteguía, 2015).

DISCUSSION

The remains described in this work contribute to a better understanding of the faunal assemblage of northern South America during the Campanian–Maastrichtian. Furthermore, they represent the product of collective efforts done by many different people involved in their collection, processing, and safeguarding. However, because of the difference in timing of the collection of different materials and the loss of data regarding the localities in which many fossils were found, it will be important to conduct future expeditions and collect new material with adequate surveying as to improve the quantity and quality of information of the deposits of the Mesozoic deposits of the Bagua Basin.

Taxonomic implications. The position of MUSM 5121 within the LDA supports the interpretation that it and the other teeth described in this work pertain to Spinosauridae. Our results indicate that the main contributors to the variance are the crown height, crown base length, crown base width, and apical length. Out of these, crown base length and crown base width are strongly linked to the shape of the cross-section of tooth crowns. This helps to explain the relatively discrete morphospace of spinosaurids. Regarding the LDA classification at the level of taxon, MUSM 5121 was classified as ‘Brazilian baryonychinae’; the classifier we gave to the teeth referenced in Lacerda *et al.* (2023) when the space for ‘taxon’ was left blank for those specimens, the classification given for both the Brazilian specimens and MUSM 5121 was *Suchomimus*. The reclassification rate for the taxon level was 59.18%. When classifying at the clade level, MUSM 5121 was included in Spinosauridae both when the Brazilian specimens were given that classification *a priori*, as when the space for clade was left blank. The reclassification rate at the Clade level was 60.58%. The classification of both MUSM 5121 and the Brazilian specimens within *Suchomimus* is consistent with those provided by Lacerda *et al.* (2023). Across the LD2 axis, MUSM 5121 was closer to *Spinosaurus* and *Suchomimus* than to most teeth of *Baryonyx* or the Brazilian specimens. In both taxon and clade level reclassifications, the classification rate was low, though this is not unusual for these analyses (see Lacerda *et al.*, 2023; Hendrickx *et al.*, 2020); additional factors need to be taken into consideration for a more robust conclusion. This is especially relevant because, as previously mentioned, teeth similar to those found in Spinosaurid theropods have appeared many times in different groups of fish-eating vertebrates (Bertin, 2010; Hasegawa *et al.*, 2010).

Besides the linear measurements used in the LDA, some of which can be used to assess the circular cross-section of teeth (characteristic of teeth of conical shape), the relatively straight shape of the crowns and the presence of flutes and a granular enamel are consistent with Spinosauridae (Hasegawa *et al.*, 2010; Kubota *et al.*, 2017; Mateus *et al.*, 2011; Naish *et al.*, 2004; Sereno *et al.*, 1998). The subcircular basal cross-section and the presence of apicobasally oriented flutes distinguish the teeth from those of most other theropods, except unenlagiine theropods (Brum *et al.*, 2021; Kubota *et al.*, 2017; Hendrickx *et al.*, 2015a). However, the Bagua Basin teeth are different from those of unenlagiines in possessing carinae (except MUSM 5122) and granular enamel. With regards to other sauropsids, even though fluted crowns have been identified in crocodylomorphs and marine reptiles (Hasegawa *et al.*, 2010; Gasca *et al.*, 2011), the relatively minor distal recurvature, the slender nature of the crown and the particular pattern of the granular, vein-like enamel of MUSM 4269, MUSM 5121 and MUSM 5122, as well as the estimated temporal range of the collected material, distinguishes them from these sauropsid groups. Because the findings reported in this work correspond to a maximum age within the Campanian (81.6 ± 0.3 Ma following Moreno *et al.*, 2020), a thalattosuchian, pliosaurid, or icthyosaurian origin would be less likely. The slender crowns and relatively minor distal curvature also distinguish the teeth from Bagua from those of sebecid crocodylomorphs, and the granular enamel distinguishes it from that of both crocodylomorphs and elasmosaurid plesiosaurs (Buffetaut *et al.*, 2019; Hasegawa *et al.*, 2010).

For the comparative analysis of the preserved teeth with regards to previous findings of teeth classified as spinosaurids, we used the character evaluation of spinosaurid teeth by Mateus *et al.* (2011), later expanded by Kubota *et al.* (2017). Such evaluation provides general descriptions and includes a list of base characters to compare new discoveries with reference spinosaurid taxa. These are: (1) a suboval or subcircular crown in cross-section, (2) presence of vertical parallel grooves, (3) carinas with six or more denticles per millimeter, (4) exceptionally long and thin roots, (5) smooth or striated enamel surface, (6) denticles of irregular size, (7) number of grooves, (8) 45-degree angled orientation of enamel sculptures near interdenticular grooves, (9) well-pronounced carinae, and (10) curvature of the crown.

Following these criteria, we compared the Peruvian material with: (a) spinosaurids from northern Africa, Europe, South America and Asia, with *Torvosaurus* as outgroup (following Mateus *et al.*, 2011 and Kubota *et al.*, 2017); (b) two recently reported teeth from Japan (Hattori & Azuma, 2020); and (c) one spinosaurid tooth from the Kem Kem Beds from the collection of the Laboratorio de Anatomía Patológica y Biología Celular—Universidad de Cádiz, Spain (LAP) (see Supplementary Online Information). A tooth reported by Hone *et al.* (2010), previously included in the expanded Table 2 of Kubota *et al.* (2017), is not included in this work as, following the observations made by Hasegawa *et al.* (2010) and Kubota *et al.* (2017) (*i.e.*, a slender laterally compressed tooth with no visible fluting or granules). Although in the case of *Irritator*, some of the teeth that are positioned more posteriorly in the holotype do appear more labio-lingually flattened and non-fluted (GJOR pers. obs.), we think that, in isolation, the classification criteria should prevail and teeth with those features should not be assigned to Spinosauridae.

The unserrated carinae distinguishes MUSM 5121 and MUSM 4269 from the finely denticulated teeth found in baryonychines (Kellner *et al.*, 2011; Gasca *et al.*, 2011; Hendrickx *et al.*, 2015a; Kubota *et al.*, 2017). Based on these characteristics, we tentatively refer MUSM 4269, MUSM 5121 and MUSM 5122 to Spinosauridae; however, due to the recent discoveries of isolated spinosaurid teeth that bear characteristics of Spinosaurinae and Baryonychinae (*e.g.*, teeth reported by Hattori & Azuma [2020]) and the inherent difficulties of classifying isolated teeth material, we do not extend the classification beyond the aforementioned rank.

Assignment of the fossil material to the Titanosauria was made on the basis of strong diagnostic characters (*e.g.*, as for MUSM 4667, MUSM 4671, MUSM 4672, MUSM 4669), or due to reasonable inferences regarding the age and size of the remains, associations based on location and preservation patterns. Additionally, the rough texture identified in the distal extremities of the available long bones is consistent with the loss of identity of the bone around the articular surfaces as ossification is suppressed in favor of cartilage around those areas (Wilson & Sereno, 1998). The presence of some limited camellate pneumaticity identified on MUSM 4669, identified as a portion of a pelvic element, as well as some pneumatic foramina on the last element of the series of proximal caudal vertebrae (MUSM 4672), also adds some nuances to the nature of the loss of pneumaticity amongst small titanosaurs. Additional analysis of the inner structure of the available vertebrae material via CT-scan would shed more light on the inner bone structure of these elements.

The age, size, relative stoutness of the limb bones and partial pneumaticity of the proximal caudal vertebrae (MUSM 4669) are consistent with saltasaurine titanosaurs, among which *Yamanasaurus lojaensis*, recently described for the Late Cretaceous of Ecuador (Apesteguía *et al.*, 2020) and which, geographically and temporally, is the closest to the Peruvian titanosaurs mentioned in the present work. Geologically, both the Río Playas Formation (Lancones Basin) that yielded the remains of *Y. lojaensis* and the Fundo El Triunfo Formation that yielded the titanosaur bones of the Bagua Basin are part of the Andean Margin (Río Playas Formation being within the arc zone and Fundo El Triunfo Formation, within the backarc zone; Jaillard *et al.*, 2005). Despite having a different lithological composition (Apesteguía *et al.*, 2020; Chacaltana *et al.*, 2014; Jaillard *et al.*, 2005; Moreno *et al.*, 2020), both units span a similar timeframe: the Campanian–Maastrichtian interval and have been tentatively linked on the basis of the sequences of marine transgressions in the latest Cretaceous (Jaillard *et al.*, 2005).

Although there is not sufficient evidence to claim the congenerity of the Peruvian material to that of the holotype of *Yamanasaurus lojaensis*, we suggest that the similar paleoenvironmental conditions between Río Playas and Fundo El Triunfo Formations (numerous archipelagos and coastal environments that came as a result of marine transgressive events, Jaillard *et al.*, 2005) could have produced habitats that were favorable for the colonization of small titanosaurs.

Paleobiogeographical Implications

The biogeographical distributions of Baryonychinae and Spinosaurine appear distinct, with the former more prominent in Laurasia and the latter in Gondwana—but neither group being exclusive to either area. Although the spinosaurid teeth described in this work appear to be consistent with a relatively late colonization of western Gondwana by spinosaurids, as suggested by Milner's (2001) paleogeographical hypothesis (see also Barker *et al.*, 2021), the discovery of baryonychine teeth in the Berriasian–Valanginian of Brazil (Lacerda *et al.*, 2023) complicates this paleobiogeographical scenario. Considering such new discoveries, it may be necessary to rethink the current paleobiogeographical hypotheses for the origin and distribution of Spinosauridae.

The teeth described in this study possibly expand the geographical and temporal range of Spinosauridae. As stated before, the maximum age of the teeth would be Campanian, even if we assigned them to the most basal levels of the Fundo El Triunfo Formation. The spinosaurid fossil record in South America was understood to be limited to Brazil, possibly making these fossils both the first record of the group in western South America and the youngest record for the group worldwide. Moreover, these findings suggest that there was at least one additional group of large theropods, besides the known abelisaurids in the Latest Cretaceous of South America, following the disappearance of carcharodontosaurid tetanurans from the fossil record after the Cenomanian.

The absence of skeletal remain-yielding Cretaceous beds of post-Cenomanian, pre-Campanian age in western South America generates a 10-million year-long gap in the evolution of dinosaur assemblages in that region (~94–83.6 Ma). Although informative, the theropod ichnofossils reported for the Valanginian Carhuaz Formation and the Berriasian Hualhuani Formation cannot be confidently assigned to any lower-level taxon. The affinities of the ichnotaxon *Ornithomimipus jaillardi* reported from Vilquechico require additional scrutiny because no ornithomimid taxon has been identified from South America. In Gondwanan landmasses, the phylogenetically-closest taxon to Ornithomimidae is the ornithomimosaur *Nqwebasaurus thwazi* De Klerk *et al.*, 2000 from the Berriasian of present-day South Africa. Other fossil material previously classified under Ornithomimosauria in the African continent were subsequently reassigned to other theropod clades (Cerroni *et al.*, 2019; Sereno, 2017).

Because of the uncertain dinosaur status and stratigraphical age of the lost eggshell material originally thought to come from Laguna Umayo, the deposits of the Fundo El Triunfo Formation in the Bagua Basin yield the only osteo-dental non-avian dinosaur remains in Perú so far.

CONCLUSIONS

While evidently fragmentary in nature, the findings presented in this work possibly expand the geographical and temporal range of spinosaurids and provide additional information on the size and distribution of titanosaurs in northern South America during the latest Cretaceous. The presence of both identified taxa is consistent with the interpretation of the Bagua Basin as a mainly fluvial system with occasional marine incursions. Such environment would have allowed for the non-avian dinosaur fauna to thrive, so more findings are to be expected in Peruvian foreland basins.

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