Rev. Mus. Argentino Cienc. Nat., n.s.
26(2): 205-215, 2024
ISSN 1514-5158 (impresa)
ISSN 1853-0400 (en línea)

Returning the dragon to its cave: the spinosaurid nature of the purported ornithopod materials from the 'Middle' Cretaceous Alcântara Formation, northeastern Brazil

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Abstract: We have conducted a reassessment of dinosaur caudal vertebrae from the Cenomanian Alcântara Formation in the Maranhão State, northeastern Brazil. These elements were originally described as belonging to the coeval African theropod *Sigilmassasaurus*. Subsequently, they were reassigned to a large ornithopod similar to the slightly older *Ouranosaurus*, representing the first occurrence of a basal hadrosauriform in South America. Here we review the anatomy of the caudal vertebrae from the Alcântara Formation, emphasizing comparisons with both spinosaurid theropods and hadrosauriform ornithopods to re-evaluate their taxonomic assignment between these two distantly related groups. Characters such as centra with subrectangular lateral walls, ventral surface bearing a longitudinal depression, low base of the neural arches, rod-shaped neural spines and transverse processes not reaching the anterior and posterior borders of the centra, among others, allow referral of these vertebrae to Spinosaurinae. The only nominal spinosaurid described for the Alcântara Formation is *Oxalaia quilombensis*. However, the absence of overlapping material precluded the referral of the Maranhão caudal vertebrae to this species. Furthermore, the existence of multiple dental morphotypes in the Alcântara Formation that suggests a greater diversity of spinosaurids opens the possibility of those vertebrae belonging to a different species. Nevertheless, the reassignment of the Maranhão caudal vertebrae to Spinosauridae nullifies the evidence of ornithopod remains in the Alcântara Formation and limits its record in northeastern South America to footprints from Cenomanian strata.

Keywords: Spinosauridae, Ornithopoda, Laje do Coringa, Alcântara Formation, Cenomanian, Brazil

Resumen: ***Devolviendo el dragón a su cueva: la naturaleza espinosáurida de los materiales de un supuesto ornitópodo de la Formación Alcântara del Cretácico 'Medio', noreste de Brasil.***
Hemos llevado a cabo una reevaluación taxonómica de vértebras caudales de dinosaurios de la Formación Alcântara del Cenomaniano en el estado de Maranhão, noreste de Brasil. Estos elementos fueron descritos originalmente como pertenecientes al terópodo africano contemporáneo *Sigilmassasaurus*. Posteriormente, fueron reasignados como un ornitópodo grande similar a *Ouranosaurus*, un poco más antiguo, representando entonces la primera aparición de un hadrosauriforme basal en América del Sur. Aquí revisamos los materiales publicados más vértebras caudales adicionales inéditas de la Formación Alcântara. Además, se realizaron comparaciones con terópodos espinosáuridos y ornitópodos hadrosauriformes para dilucidar su asignación taxonómica entre estos dos grupos de dinosaurios distantemente relacionados. Los rasgos anatómicos observados en las vértebras caudales, incluidos los centros con paredes laterales subrectangulares, la superficie ventral que presenta una depresión longitudinal, la base baja de los arcos neurales, una espina neural en forma de varilla y una apófisis transversal que no alcanza los bordes anterior y posterior del centro vertebral, entre otras características, permiten asignar los especímenes a terópodos espinosáuridos, particularmente Spinosaurinae. El único espinosáurido nominal descrito para la Formación Alcântara es *Oxalaia quilombensis*, aunque su asignación a los especímenes aquí estudiados está excluida por la ausencia de elementos comparables y la existencia de múltiples morfotipos dentales en esta unidad litoestratigráfica, lo que sugiere una mayor diversidad de espinosáuridos. La asignación actual anula la evidencia

de restos de ornitópodos en la Formación Alcântara y limita su registro en el noreste de América del Sur a huellas de depósitos cenomanianos.

Palabras clave: Spinosauridae, Ornithopoda, Laje do Coringa, Formación Alcântara, Cenomaniano, Brasil

INTRODUCTION

The composition of the 'Middle' Cretaceous terrestrial faunas of the low latitudes of South America involves the interaction of multiple paleobiogeographic traits, such as the break-up of Gondwana and the consequent isolation or dispersion patterns raised from this geological event. In this regard, the fauna of the early Cenomanian Alcântara Formation is key to understand the diversity and composition of terrestrial faunas during this interval in northern South America, since it preserves one of the richest terrestrial fossil records for this age (*i.e.,* Lindoso et al., 2012, 2013, 2019; Medeiros et al., 2014; Medeiros & Lindoso, 2022; Carvalho & Lindoso, 2024). Paleobiogeographically, several of the tetrapod terrestrial components of the Alcântara Formation appear to reflect close relationships with coeval faunas from Africa, like the candiodontid zyphosuchians, nigersaurine rebbachisaurids, basal titanosaurians, unenlagiines paravians, carcharodontosaurids, bahariasaurids, spinosaurids and other fragmentary theropods, as previously suggested (*i.e.,* Medeiros *et al*., 2007, 2014, 2019; Kellner *et al*., 2011; Martin and De Lapparent de Broin, 2016; Lindoso *et al*., 2019; Letizio *et al*., 2022; Medeiros & Lindoso, 2022). Among the more intriguing fossil materials from the Alcântara Formation are a pair of caudal vertebrae that were originally described as the first occurrence of the theropod *Sigilmassasaurus* outside Africa (Medeiros & Schultz, 2001, 2002), a taxon of uncertain affinity at that time but recently considered as a derived spinosaurid (see below). Subsequently, these materials were regarded as representing a large basal hadrosauriform ornithopod, akin to *Ouranosaurus* (*i.e.,* Novas *et al*., 2005; Novas, 2009; Rozadilla *et al*., 2021). This reassignment carried significant implications for South American paleogeography, as it suggested the presence of the first large-sized hadrosauriform on this continent during the Cenomanian, aligning again with the 'Middle' Cretaceous faunas from Africa.

The increase in the fossil record from the Cenomanian of Gondwana during the last two decades resulted in significant progress in the understanding of dinosaur systematics and their phylogenetic relationships (*i.e.,* Ibrahim *et al*., 2014, 2020), prompting reconsideration of the taxonomy of this putative ornithopod material from the Alcântara Formation.

In this work, we review previously published and additional novel dinosaur caudal vertebrae from the Alcântara Formation to determine whether they belong to hadrosauriform ornithopods or spinosaurid theropods. Additionally, we discuss the possible assignation of these elements to the previously known taxa from this unit. In doing so, this study contributes to a better understanding of the terrestrial faunal composition of northern South America, in particular from the Alcântara Formation.

MATERIAL AND METHODS

Background of the materials

Field expeditions were conducted between 1994 and 2000 by teams from the Federal Universities of Rio de Janeiro and Maranhão at the Laje do Coringa paleontological site on Cajual Island, São Marcos Bay, Maranhão State, northeastern Brazil. These expeditions resulted in a diverse array of vertebrate fossil remains from the Alcântara Formation of the Itapecuru Group. Based on palynological analyses (Pedrão *et al*., 1993), this formation is of early Cenomanian age. The Alcântara Formation has yielded a rich vertebrate fauna, consisting of various fish species, possible plesiosaurs and mosasaurs, turtles, crocodilians, pterosaurs, and a variety of dinosaurs, including sauropods, theropods, and putative ornithopods (Carvalho & Pedrão, 1998; Carvalho, 2001, 2004; Dutra & Malabarba, 2001; Medeiros & Schultz, 2001, 2002; Vilas Bôas & Carvalho, 2001; Castro et al., 2004; Sousa et al., 2004; Toledo et al., 2005, 2011; Elias et al., 2007; Lindoso et al., 2011, 2012, 2013, 2019; Medeiros et al., 2014, 2019; Letizio et al., 2022; Medeiros & Lindoso, 2022). As previously noted, this fauna bears similarities to that found in northern Africa during the same time interval (Medeiros *et al*., 2007, 2011, 2014).

An important issue concerning the theropod fauna from the Alcântara Formation is the current assignment of some caudal vertebrae discovered in the bone bed Laje do Coringa. Initially,

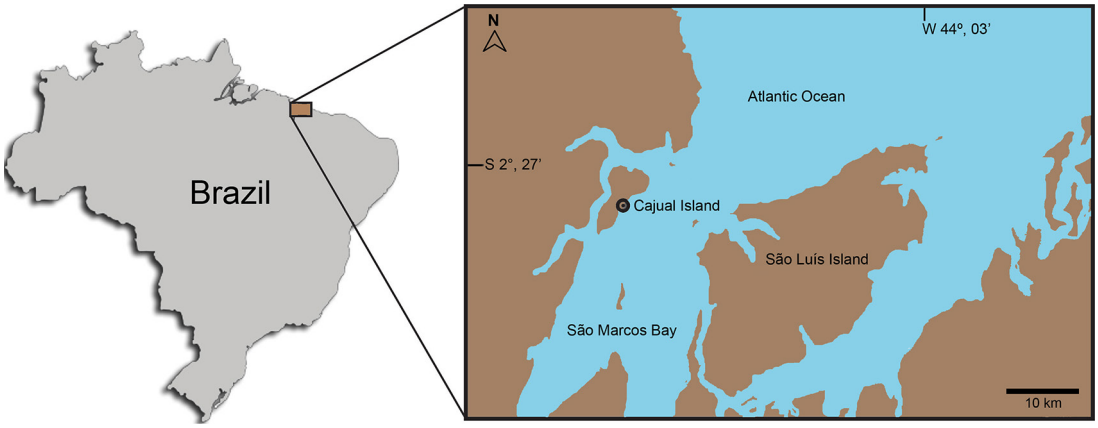

Figure 1. Map showing the fossiliferous locality where the materials were found.

these vertebrae were attributed to *Sigilmassasaurus brevicollis* by Medeiros & Schultz (2001, 2002), a theropod taxon with uncertain affinities at that time (*e.g.,* Holtz *et al*., 2004). *Sigilmassasaurus brevicollis* was previously described from the Cenomanian of Morocco by Russell (1996), primarily based on isolated elements. Russell (1996) also associated with this taxon partial skeletons from Egypt previously identified as *Spinosaurus* B by Stromer (1934) (see below).

The similarity between the Brazilian and African materials supports affinities among Cenomanian faunas of equatorial western Gondwanan regions. However, the referral of various axial elements of *Sigilmassasaurus brevicollis* to a single taxon was surrounded by uncertainty, and whether all these elements represented the same theropod clade remained unclear. Consequently, Novas *et al*. (2005) proposed that the caudal elements formerly attributed to *Sigilmassasaurus*, including those of Spinosaurus B described by Stromer (1934), belonged to an ornithopod resembling the long-spined *Ouranosaurus* from the Aptian of Africa. The implication of the Brazilian material belonging to an *Ouranosaurus*-like ornithopod was briefly suggested by these authors and supported by Novas (2009) and Rozadilla *et al*. (2021).

In recent years, additional discoveries and taxonomic reappraisals of spinosaurids have resulted in a substantial increase in the knowledge of the tail morphology of these animals (i.e., Ibrahim *et al*., 20 14; 2020; Samathi *et al*., 2021; Mateus & Estraviz-López, 2022). This has provided the context and opportunity to reevaluate the identity of the Brazilian material and, in turn, attempt to clarify its relationships.

Description and comparisons

Multiple taxa preserving overlapping homologous elements pertaining to Spinosauridae and Hadrosauriformes were considered for comparisons and are listed in Table 1.

Here we opted to use anterior and posterior definitions instead of cranial and caudal to avoid confusion regarding caudal elements.

Additionally, we adhere to the phylogenetic interrelationships obtained from one of the most recent analyses of spinosaurids (Sereno *et al*., 2022). Similarly, we follow the phylogenetic framework of the recent analysis based on an updated dataset by Prieto-Márquez & Wagner (2023).

Validity of *Sigilmassasaurus brevicollis*

Recently, *Sigilmassasaurus brevicollis* has been considered as a valid taxon within Spinosauridae, closely related to *Spinosaurus* (*i.e.*, Evers *et al*., 2015; Barker *et al*., 2021). However, other studies considered it a junior synonym of either *Spinosaurus marrocanus* (Mahler, 2005) or *Spinosaurus aegyptiacus* (*e.g.,* Ibrahim *et al*., 2014; Smyth *et al*., 2020; Sereno *et al*., 2022). Because the validity of *Sigilmassasaurus brevicollis* is beyond the scope of the present study, we refer to the materials described by Russell (1996) as *Sigilmassasaurus brevicollis* for comparative purposes only.

Institutional abbreviations. MN, Museu Nacional/UFRJ, Departamento de Geologia e Paleontologia. Quinta da Boa Vista, São Cristóvão, Rio de Janeiro, Brazil; UFMA, Universidade Federal do Maranhão, State of Maranhão, Brazil.

Taxon		Source
Spinosauridae	*Baryonyx walkeri*	Mateus *et al.*, 2011
	Camarillasaurus cirugedae	Sánchez-Hernández & Benton, 2014 Rauhut *et al.*, 2019 Samathi *et al.*, 2021
	*Ceratosuchops inferodios (*including *Riparovenator milnerae j.s.)*	Barker *et al.*, 2021 Sereno *et al.*, 2022
	Iberospinus natarioi	Mateus & Estraviz-Lopez, 2022
	Protathlitis cinctorrensis	Santos-Cubedo *et al.*, 2023
	Sigilmassasaurus brevicollis	Russell, 1996 McFeeters *et al.*, 2013
	Spinosaurus aegyptiacus	Ibrahim *et al.*, 2020
	Suchomimus tenerensis	Sereno *et al.*, 1998, 2022
	Phuwiang spinosaurid	Samathi *et al.*, 2021
	Santana spinosaurid	Bittencourt & Kellner, 2004
Hadrosauriformes	*Altirhinus kurzanovi*	Norman, 1998
	Iguanodon bernissartensis	Norman, 1980 Verdú *et al.*, 2017
	Mantellisaurus atherfieldensis	Norman, 1986 Bonsor *et al.*, 2023
	Ouranosaurus nigeriensis	Taquet, 1976 Bertozzo *et al.*, 2017

Table 1. List of taxa used for comparison and bibliographical sources in which it was based.

RESULTS

Systematic paleontology
Dinosauria Owen, 1842
Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
Megalosauroidea Huxley, 1869
Spinosauridae Stromer, 1915
Spinosaurinae gen. et sp. indet.

Referred material. The originally published elements (*i.e.*, UFMA 1.10.229 and 1.10.240) and seven additional caudal vertebrae not previously described by Medeiros and Schultz (2001, 2002), which are herein referred to as the "Alcântara form". The additional caudal elements included in this study are: UFMA 1.10.311, 1.10.540, 1.10.887, 1.10.1511, 1.10.1653, 1.10.1783, and 1.10.1785, all of which are deposited in the Uni-

versidade Federal do Maranhão fossil collection (see Fig. 2).

Locality and horizon. Laje do Coringa paleontological site, Cajual Island, Maranhão

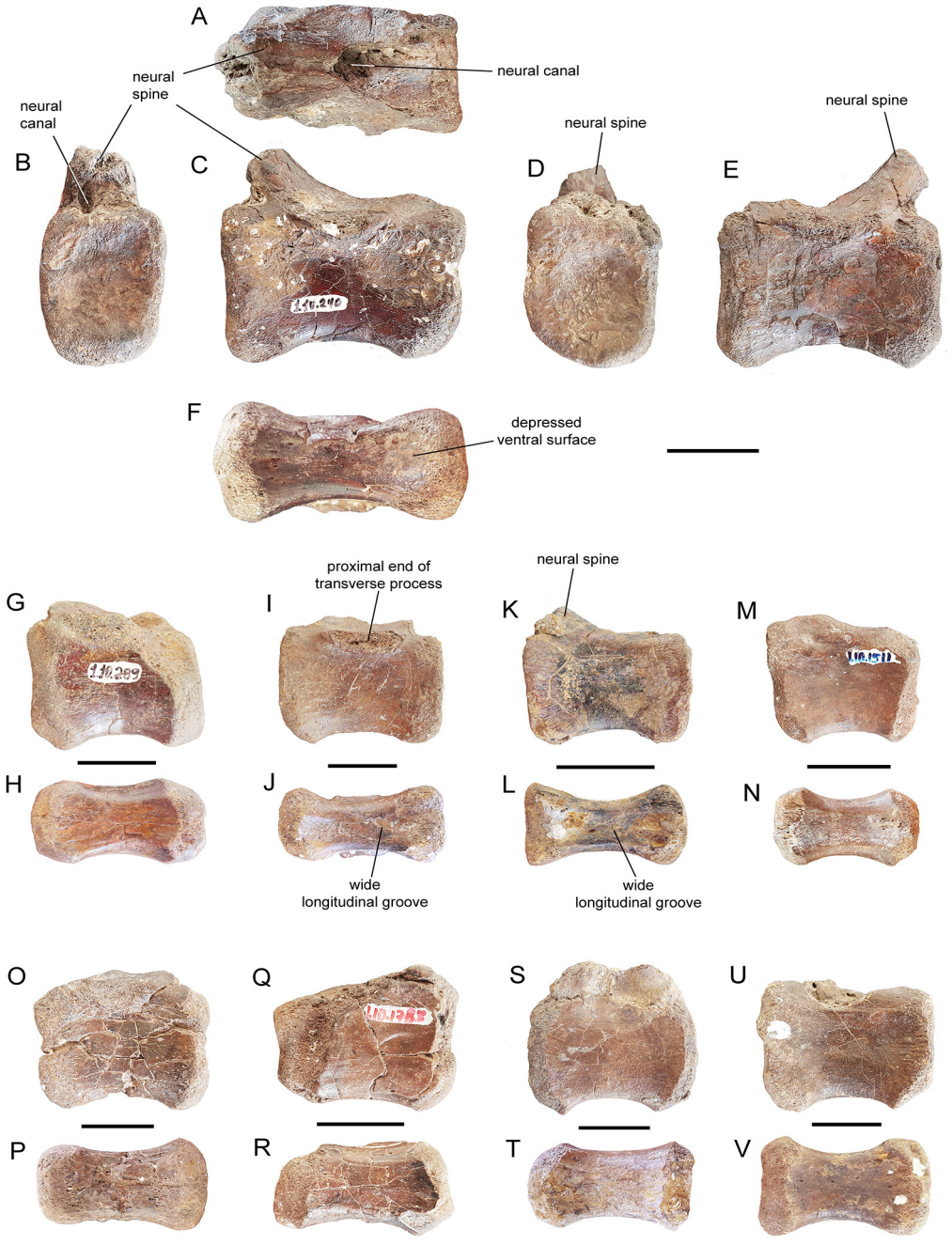

Figure 2. Spinosaurid partial caudal vertebrae collected in the Laje do Coringa flagstone, Alcântara Formation. UFMA 1.10.240 in dorsal (A), posterior (B), right lateral (C), anterior (D), left lateral (E) and ventral (F) views; UFMA 1.10.289 in lateral (G) and ventral (H) views; UFMA 1.10.311 in lateral (I) and ventral (J) views; UFMA 1.10.887 in lateral (K) and ventral (L) views; UFMA 1.10.1511 in lateral (M) and ventral (N) views; UFMA 1.10.1653 in lateral (O) and ventral (P) views; UFMA 1.10.1783 in lateral (Q) and ventral (R) views; UFMA 1.10.1785 in lateral (S) and ventral (T) views; UFMA 1.10.540 in lateral (U) and ventral (V) views.

State, northeastern Brazil. Alcântara Formation, Itapecuru Group, early Cenomanian (Late Cretaceous).

Description. These elements are considered to belong to the caudal series of the vertebral column because they possess articular facets for the haemal arches. None of the caudal vertebrae are complete, preserving the vertebral centra and the base of the neural arch in most cases, and occasionally the base of the transverse processes and neural spine (Fig. 2). It is uncertain whether these elements represent a single individual or not, as well as the precise position of each vertebra along the caudal series, because they were found isolated. However, some traits such as the proportions of the centra and the presence of transverse processes may be indicative of the approximate position of these vertebrae in the caudal axial skeleton.

UFMA 1.10.1785 is the most proximal vertebrae from the available sample. It shows a dorsoventrally higher and anteroposteriorly shorter centrum than other preserved elements. This is consistent with the variation evidenced in the more proximal caudal series of both hadrosauriforms (Bertozzo *et al*. 2017) and spinosaurids (Ibrahim *et al*., 2020). Two additional characters worth noting are, the hexagonal morphology of their articular facets and the more dorsal position of the base of the transverse process relative to the base of the neural arch (see below). However, the absence of laminae connecting the transverse process with the centrum supports a more posterior position within the proximal series, nearer the mid-caudals.

All centra are slightly amphicoelic, except UFMA 1.10.1785, which presents a concave anterior and a planar posterior facets, taller than wide, and anteroposteriorly longer than high. The length/height ratio of the centra ranges from 1.26 (UFMA 1.10.1785) to 1.51 (UFMA 1.10.887). Furthermore, the anterior and posterior articular facets are subvertically oriented and parallel to each other, with the exception of UFMA 1.10.511 and 1.10.887, where the posterior facet is posterodorsally inclined. In lateral view, all the centra have an arched ventral edge related to the articular surfaces for the haemal arches (Fig. 2C, E, G, I, K, M). The lateral surfaces of the centra are slightly concave, but more pronounced in UFMA 1.10.240, 1.10.540 1.10.887 and 1.10.1511. Both the anterior and posterior surfaces of the centra show straight ventral margins. In some elements, like UFMA 1.10.1785, the hexagonal contour of the posterior surface is approximately twice taller than wide.

UFMA 1.10.887 displays a variation of the latter contour, in which the ventral part of the hexagonal profile is taller than the dorsal one. Finally, some elements, like UFMA 1.10.240 (Fig. 2B, D) have centra with a trapezoidal posterior profile in which the dorsal margin is slightly wider than the ventral one.

The ventral surfaces (Fig. 2F, H, J, L, N, P, R, T, V) of these vertebrae vary from being gently concave in UFMA 1.10.1785 to show a longitudinal sulcus flanked by two lateroventral crests in UFMA 1.10.240 and 1.10.881.

The neural arches are separated from the anterior articular surface of the centrum by a narrow space and from the posterior articular surface by a subtle constriction. The neural canals are dorsoventrally short.

The bases of the transverse processes are preserved in UFMA 1.10.240, 1.10.311, 1.10.540, and 1.10.1785. In the most proximal element of the axial series (UFMA 1.10.1785), the transverse process is located dorsally in the neural arch, unlike the condition present in the other vertebrae, where it is located at the neurocentral junction. The base of the transverse process occupies more than fifty percent of the length of the centra. There is no evidence of laminae connecting the transverse process with the zygapophyses or the neural spine (Fig. 2A-F, I-J, S-T, U-V). UFMA 1.10.511 and 1.10.887 lack transverse processes, having been replaced by a slightly developed lamina. The poor preservation of the remaining elements precludes ascertaining the presence of transverse processes.

The prezygapophyseal processes can be partially observed only in UFMA 1.10.240 and 1.10.887, which originate on the anterior half of the vertebra. The neural spine is partially preserved in UFMA 1.10.240, 1.10.540 and 1.10.887 and it appears to be restricted to the posterior region of the vertebra. The neural spine is posterodorsally oriented, angled about 45 degrees relative to the dorsal surface of the centrum. There is no evidence of postzygapophyses raising from the neural arch, because only the preserved neural arches are restricted to the most proximal section (Fig. 2). The morphology of the base of the neural spine is rod-shaped, transversally wider than anteroposteriorly elongated in UFMA 1.10.240. It appears to be more subcircular in UFMA 1.10.887, where the structure is poorly preserved (Fig. 2A-F and 2K-L).

DISCUSSION

Comparison with hadrosauriform caudal vertebrae

The Alcântara form differs from basal hadrosauriforms in a suit of characters. First, the centra are longer than tall. In contrast, in hadrosauriforms the middle and proximal distal caudal vertebra centra are taller than long or subequal in height and length. In addition, the presence of a ventral concavity in the middle and distal vertebrae of the Alcântara vertebrae, differs from the condition of *Iguanodon*, *Mantellisaurus*, *Althirinus*, and *Ouranosaurus*. Similarly, the presence of lateral excavations in the vertebral centrum of the specimens of Alcântara, contrasts with the observed in such forms which lacks these structures. Furthermore, in the Alcântara form the transverse processes are located in the central area of the dorsal edge of the centrum, not reaching further than three quarters of its length. On the contrary, the transverse processes appear to occupy the entire length of the dorsal border of the centrum in hadrosauriforms, such as *Ouranosaurus* and *Mantellisaurus*. In the Alcântara form, the neural arches are lower than those of hadrosauriforms. In addition, in the Alcântara form, the neural spines have rounded cross sections, whereas in hadrosauriforms these are laminar and anteroposteriorly elongated. Finally, in the Alcântara vertebrae the neural spines are posterodorsally directed, but subvertically oriented in hadrosauriforms.

Comparison with spinosaurid caudal vertebrae

Among the most relevant features that confidently allow the referral of the Alcântara form to Spinosauridae is the rod-shaped and posterodorsally directed neural spines, restricted to the posterior half of the vertebra. This condition is present on the middle and distal sections of the tail of *Spinosaurus aegyptiacus* (Ibrahim *et al*., 2020: fig. 1). In addition, the lateral and ventral excavations in the centra (Fig. 2K) are shared by *Spinosaurus aegyptiacus* (Ibrahim *et al*., 2020), including the longitudinal sulcus delimited by lateral crests. The presence in more distal elements with posterodorsally oriented posterior articular faces of the centra, as well as transverse processes replaced by a poorly developed laminae, are features shared with spinosaurids, such as *Iberospinus natarioi* (Mateus & Estraviz-López, 2022: figs. 20 and 21). The Alcântara form lacks laminae connecting the neural spine and the postzygapophyses. This is more similar to the caudal vertebrae of *Spinosaurus* and *Sigilmassasaurus* than those of the basal spinosaurid *Camarillasaurus* and baryonychines (*i.e.,*, *Ceratosuchops*, *Baryonyx*). However, the Alcântara form differs from *Spinosaurus aegyptiacus* in the absence of deep perforations in the dorsal surface of the mid and distal caudal centra (Ibrahim *et al*., 2020: figs 2d and 2e).

Comparisons with Brazilian spinosaurid materials and the genera *Irritator* and *Angaturama* (from the slightly older Romualdo Formation of the Araripe Basin) are currently not possible because these are solely known from cranial elements (Kellner & Campos, 1996; Martill *et al*., 1996). Similarly, the Alcântara form cannot be compared with the Santana spinosaurid (MN 4743-V; Bittencourt & Kellner, 2004), since this specimen preserves the most proximal elements of the caudal series, which are absent in the Alcântara form. Likewise, the spinosaurid material of the Itapecuru Formation of Aptian-Albian age is restricted to appendicular elements (França *et al*., 2022).

Apart from the material studied here, other spinosaurid materials have been described for the Alcântara Formation (*i.e.,* Medeiros, 2006), including *Oxalaia quilombensis* that was based in the rostral tip of the snout (Kellner *et al*., 2011). As occurs with *Sigilmassasaurus*, *Oxalaia quilombensis* has been proposed as a junior synonym of *Spinosaurus aegyptiacus* (Smyth *et al*., 2020), although some anatomical differences appear to support its validity as a proper genus, possibly more related to *Irritator* or *Angaturama* than to *Spinosaurus* (see Terras *et al*., 2022 and references therein). Referral of UFMA 1.10.240 to *Oxalaia* has also been suggested based on their provenance (Terras *et al*., 2022). Although it is possible, the evidence based on isolated teeth suggests the presence of more than one spinosaurid morphotype in the Alcântara Formation (Medeiros, 2006), preventing the assignment of non-overlapping material to any of these particular morphotypes. Therefore, we consider the Alcântara form as an indeterminate Spinosaurinae.

CONCLUSIONS

We present a thorough systematic re-evaluation of the caudal vertebra from the Alcântara Formation in the Maranhão State, northeastern Brazil, previously described by Medeiros & Schultz (2001, 2002). We added detailed descriptions of

additional caudal vertebrae collected in the same locality. UFMA 1.10.240, 1.10.229, 1.10.311, 1.10.887, 1.10.1511, 1.10.1785, 1.10.1783, 1.10.1653, and 1.10.540 share several characters with spinosaurids, such as a rod-shaped and posterodorsally directed neural spine and a ventral surface lacking a deep median concavity. Collectively, these osteological attributes strongly support the hypothesis that these vertebrae are not related to Hadrosauriformes, but should be referred to Spinosaurinae. The assignment of the Alcântara form to *Oxalaia* is hindered by the presence of more than a tooth morphotype in this lithostratigraphic unit.

ACKNOWLEDGEMENTS

The authors deeply thank Manuel Alfredo Medeiros (Universidade Federal do Maranhão) for his kind willingness to provide the photographs and granting permission to study the material. We also to the editor Agustín Martinelli, Jhonatan Alarcón Muñoz and an anonymous reviewer for providing valuable suggestions for improvements to the manuscript, Jorge Bar for facilitating valuable access to scientific research for this manuscript, and Jennifer Yebra Escorcia for technical support in the draft of the manuscript. The Fundation Nothos was supported via project FN.IP-PA.2024-001. Work by A.P-M. (part of the Reptilian Ecosystems Research Group of the Generalitat de Catalunya, 2021 SGR 0119) was supported by the grant PID2020-119811GB-I00 funded by MCIN/AEI/10.13039/501100011033 from the Ministerio de Innovación y Universidades, Gobierno de España and the CERCA Programme/Generalitat de Catalunya.

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Doi: 10.22179/REVMACN.26.863

Recibido: 09/06/2024
Aceptado: 26/06/2024