

A new rebbachisaurid (Sauropoda: Diplodocoidea) from the middle Cretaceous of northern Brazil

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ABSTRACT

A new genus and species of Rebbachisauridae sauropod from the Cenomanian of the São Luís Basin, Alcântara Formation, *Itapeuasaurus cajapioensis* gen. et sp. nov., is described, the first from this temporal interval in northern Brazil. It is characterized by the presence of large and deep fossae on ventro-lateral aspect of the dorsal neural arch split by laminae obliquely oriented; posterior centrodiaphyseal lamina forked ventrally forming the dorsal edge of the centrodiaphyseal fossa; dorsal and ventral components of anterior caudal transverse process thinner than the usual bony bar. This latter feature is associated with the presence of a prezygodiaphyseal centrodiaphyseal fossa accessory lamina. The phylogenetic analysis performed herein identifies the subclade Nigersaurinae as a South American – African/European clade, suggesting a vicariant event before Cenomanian times. In addition, continental vertebrate taxa recorded in the Alcântara Formation offer support to a minor evolutionary change after major vicariant event in Western Gondwana.

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1. Introduction

One of the most interesting subjects concerning the Mesozoic continental faunas is the identification of events of vicariance and

dispersal throughout the history of Gondwana. In this sense, Rebbachisauridae is paleobiogeographically relevant, a clade formed by all diplodocoids more closely related to *Rebbachisaurus garasbae* than to *Diplodocus longus* (*sensu* Salgado et al., 2004).

Anatomical Abbreviations: acpl, anterior centroparapophyseal lamina; cprf, centroprezygapophyseal fossa; di, diapophysis; cdf, centrodiaphyseal fossa; med.cprf, medial centroprezygapophyseal lamina; med.sprf, medial spinoprezygapophyseal lamina; nc, neural canal; ns, neural spine; pa, parapophysis; pacdf, parapophyseal centrodiaphyseal fossa; pcdl, posterior centrodiaphyseal lamina; pf, pneumatic fossa; pfl, pneumatic fossa lamina; prcdf, prezygapophyseal centrodiaphyseal fossa; prcdf1, prezygapophyseal centrodiaphyseal fossa lamina; prcdfal, prezygodiaphyseal centrodiaphyseal fossa accessory lamina; prdl, prezygodiaphyseal lamina; prsl, prespinal lamina; prpl, prezygoparapophyseal lamina; prz, prezygapophysis; posl, postspinal lamina; poz, postzygapophysis; spdl, spinodiaphyseal lamina; sprf, spinoprezygapophyseal fossa; sprl, spinoprezygapophyseal lamina; spzal, spinopostzygapophyseal accessory lamina; s-cprf-d, subfossa centroprezygapophyseal dorsal; tp, transverse process; tprl, intraprezygapophyseal lamina.

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Their records have been useful for ascertaining the moment of definitive separation between South America and Africa (Carballido et al., 2010). Recently, phylogenetic analysis has emphasized a marked provincialism among members of Rebbachisauridae, with some of them restricted to Europe and northern Africa (e.g. *Nigersaurus*, *Demandasaurus*, *Rebbachisaurus*) and others only composed by Upper Cretaceous South American taxa (e.g. *Limaysaurus*, *Cathartesaura*, *Nopcsaspondylus*, El Chocon rebbachisaurid) (Sereno et al., 2007; Whitlock, 2011; Fanti et al., 2013; Wilson and Allain, 2015; Mannion et al., 2019). This group of neosauropods also reveals extreme adaptations for herbivory and high temperatures in habitats at tropical and subtropical paleolatitudes (Sereno et al., 2007; Ibíricu et al., 2017).

In South America, Rebbachisauridae is diverse and frequently recorded in an interval extending from the Barremian to Turonian, particularly in Argentina. Additionally, their remains are composed mainly of postcranial elements (Calvo and Salgado, 1995; Bonaparte, 1996; Calvo, 1999; Salgado et al., 2004; Gallina and Apesteguía, 2005; Apesteguía, 2007; Carballido et al., 2010, 2012; Haluza et al., 2012; Ibíricu et al., 2012, 2013). This diversity has been also complemented by a few cranial remains (Calvo and Salgado, 1995; Carabajal et al., 2016; Canudo et al., 2018). Other records of Rebbachisauridae in South America occur only in northern-northeastern Brazil (Carvalho et al., 2003; Medeiros and Schultz, 2004; Castro et al., 2007; Medeiros et al., 2014).

In the São Luís Basin, Cretaceous outcrops are mainly Cenomanian in age (Klein and Ferreira, 1979; Pedrão et al., 1993). For over 20 years, the most important fossiliferous outcrop in this basin has been the Laje do Coringa bone-bed, which records the Alcântara Formation (lower Cenomanian), at Cajual Island, São Marcos Bay (Corrêa-Martins, 1996; Medeiros and Schultz, 2001, 2002) (Fig. 1). Therein, a noteworthy paleocommunity including crocodyliforms, fishes, dinosaurs, plants remains, invertebrates, and pterosaurs has been recorded (Medeiros et al., 1995, 1996, 2014; Corrêa-Martins, 1996; Vilas-Bôas et al., 1999; Vilas-Bôas and Carvalho, 2001; Medeiros and Schultz, 2001, 2002; Elias et al., 2007; Pereira and Medeiros, 2008; Araújo et al., 2011; Lindoso et al., 2012, 2013a).

The Alcântara Formation records both Titanosauria and Diplodocoidea remains, although the former is less frequent in the Laje do Coringa bone bed (Medeiros et al., 2007, 2014). The fragmentary state of these materials has precluded the proposition of any nominal species, except for a few teeth tentatively assigned to *Malawisaurus* (Freire et al., 2007). Some rebbachisaurid remains (e.g. caudal vertebrae/neural spine) have been tentatively assigned to a more specific taxonomic level, cf. *Limaysaurus tessonei* (Medeiros and Schultz, 2004).

In the Parnaíba sedimentary Province (which also include the São Luís Basin to the north), Diplodocoidea remains has been found in a better preservation state, with a unique nominal species described so far, *Amazonsaurus maranhensis* Carvalho et al. (2003). This rebbachisaurid was described based on a partial postcranial skeleton in Lower Cretaceous (Aptian-Albian) strata of the Itapecuru Formation, southern Maranhão State, northern Brazil (Carvalho et al., 2003). Many common taxa are recorded in the Alcântara and Itapecuru formations (e.g. Theropoda and fishes), suggesting a homogeneous paleocommunity inhabiting the northeastern Brazil throughout the Albian and early Cenomanian (Medeiros and Schultz, 2002; Medeiros et al., 2007, 2014).

In the present study, a new genus and species of rebbachisaurid dinosaur is described from lower Cenomanian strata of Brazil, the first nominal diplodocoid from the Alcântara Formation. It comes from a new fossiliferous locality in Maranhão State and may help to increase our understanding concerning this sauropod group during the mid-Cretaceous worldwide.

2. Geological setting

The São Luís Basin is a marginal basin located in the north portion of South America. It has a total area of 18.000 km² and its genesis is related to the Equatorial Atlantic opening initiated during the Late Jurassic and Early Cretaceous (Szatmari et al., 1987; Góes and Rossetti, 2001; Carvalho, 2001a). This basin represents one sub-basin on a larger intracratonic sedimentary area, the Parnaíba Province, tectonically reactivated in the Mesozoic during the South America and Africa breakup (Góes, 1995; Góes and Coimbra, 1996; Góes and Rossetti, 2001). The São Luís Basin is limited by the following structural arches: the Xambioá-Alto Parnaíba Antecline to the south, the Capim Arch to the northwest, and the Rio Parnaíba Lineament to the east (Góes, 1995).

The sedimentary record of the São Luís Basin can be divided into three depositional sequences *sensu* Rossetti (2001): S1, S2 and S3. The S1 sequence accumulated during the upper Aptian and lower Albian, and includes about 450 m of sandstones, shales and limestones deposited in shallow marine, lacustrine and fluvio-deltaic environments that make up the Grajaú and Codó formations. The S2 sequence, lower-middle Albian, consists of about 500 m of sandstone and pelitic deposits attributed to shallow marine and fluvio-deltaic environments that make up the Itapecuru Formation (Campbell, 1949) or Undifferentiated Unit (Rossetti and Truckenbrodt, 1997). The S3 sequence accumulated between the middle Albian and the Upper Cretaceous. It comprises 600–800 m of sandstones and pelitic deposits referred to the Alcântara and Cujupe formations (Rossetti and Truckenbrodt, 1997; Paz and Rossetti, 2001).

The new sauropod described herein comes from a new locality in the Itapeua beach, Cajapió municipality, northern Maranhão State, Brazil (Fig. 1). This locality is part of the Alcântara Formation, São Luís Basin (Medeiros et al., 2015). Its sedimentary succession includes around 2,5 m of reddish argillaceous levels at the base, being immediately overlaid by centimetric levels of fine to medium silty sandstones, laterized, where dinosaur bones and teeth remains are found. These layers are superposed by reddish argillite strata intercalated by greenish siltite mottled with reddish coloring. Additionally, mud crack, fluidization and elephant skin structures are observed in plan view (Medeiros et al., 2015). The diplodocoid remains comes from greenish argillaceous siltic levels 20 cm thickness (Fig. 2B). The Alcântara Formation records a diverse biota comprising plants, fishes, turtles, dinosaurs, pterosaurs, vertebrate and invertebrate ichnofossils (Medeiros and Vilas-Bôas, 1999; Carvalho, 2001b; Dutra and Malabarba, 2001; Medeiros and Schultz, 2001; Moraes-Santos and Carvalho, 2001; Elias et al., 2007; Freire et al., 2007; Pereira and Medeiros, 2008; Lindoso et al., 2012, 2013a; Medeiros et al., 2014).

3. Material and methods

The fossils described herein are housed at the fossil collection of the Universidade Federal do Maranhão (UFMA). They were localized by a fisherman on a beach in the Cajapió municipality, Maranhão State, subsequently being recovered by a team of paleontologists of the Universidade Federal do Maranhão (UFMA), Universidade Federal do Rio de Janeiro (UFRJ), Centro de Pesquisa de História Natural e Arqueologia do Maranhão (CPHNAMA) and Universidade Estadual do Maranhão (Fig. 2A). As the specimen was exposed on the intertidal area, it was necessary to develop a stabilization technique under flood conditions, using wire, splints and impermeable polyurethane foam, before and after the total removal of each bony element, which often took more than one daily tide cycle (Medeiros et al., 2015). Considering the tidal cycles and the stabilization technique, the effective working time was reduced to less than 4 h per day.

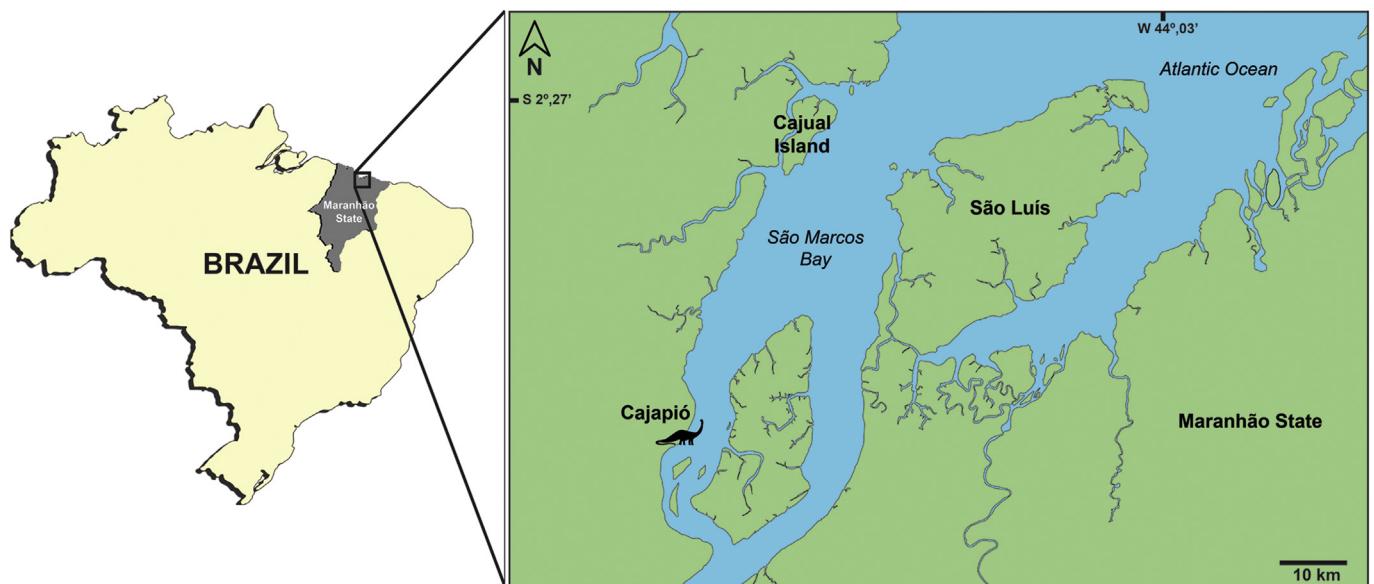


Fig. 1. Location of Itapeua beach, Cajapió municipality, northern Maranhão State, Brazil. The sauropod silhouette indicates the area where the material was collected.

Mechanical conventional techniques of fossil preparation were performed at the laboratory of the CPHNAMA. The phylogenetic analysis conducted herein is detailed in a specific section. For the nomenclature of vertebral laminae and fossae we followed Wilson (1999), Wilson et al. (2011) and Carballido et al. (2012).

4. Systematic paleontology

SAURISCHIA Seeley, 1887

SAUROPODOMORPHA Huene, 1932

SAUROPODA Marsh, 1878

DIPLODOCOIDEA Marsh, 1884 (*sensu* Upchurch, 1995)

REBBACHISAURIDAE Bonaparte, 1997

***Itapeuasaurus cajapioensis*, gen. et sp. nov.**
(Figs. 3–9)

Diagnosis. Rebbachisauridae distinguished by the following combination of characters on the dorsal and caudal vertebrae (autapomorphies are marked with an asterisk): Presence of three shallow pneumatic fossae disposed vertically on the dorsal surface of the neural arch, which are separated by the spinoprezygapophyseal lamina and spinopostzygapophyseal accessory lamina; large and deep fossae on the ventro-lateral aspect of the dorsal neural arch split by laminae obliquely oriented*; posterior centrodiapophyseal lamina forked ventrally forming the dorsal edge of the centrodiapophyseal fossa*; dorsal and ventral components of anterior caudal transverse process thinner than the usual bony bar associated to the presence of a prezygapophyseal centrodiapophyseal fossa lamina and prezygodiapophyseal centrodiapophyseal fossa accessory lamina*.

Holotype. An incomplete dorsal neural arch (UFMA. 1.10.1960–01); three anterior caudal vertebrae (UFMA. 1.10.1960–03, 1.10.1960–04, UFMA. 1.10.1960–05); and two middle caudal vertebrae (UFMA. 1.10.1960–07, 1.10.1960–08).

Paratype. A summit of dorsal neural spine (UFMA. 1.10.1960–02); an anterior caudal vertebra (UFMA. 1.10.1960–06); two chevrons (UFMA. 1.10.1960–10, 1.10.1960–11); an incomplete ischium (UFMA. 1.10.1960–09)

Stratigraphic horizon. Alcântara Formation, São Luís Basin, lower Upper Cretaceous (Cenomanian).

4.1. Comparative description

4.1.1. Dorsal vertebrae

Two elements comprise the dorsal vertebrae of *Itapeuasaurus cajapioensis*. However, only the most well preserved is described herein (Fig. 3). UFMA 1.10.1960–01 represents a large, partially preserved middle-posterior dorsal neural arch. Most of the neural spine and right costal articulations are not preserved. The left parapophysis is missing and only the base of the right diapophysis is preserved. The left diapophysis is almost completely preserved; it is broad and laminar, forming an angle of almost 90° relative to the neural spine. Although the centrum is missing, large fossae on the ventrolateral aspect of neural arch are deep and internally partitioned by a thin, obliquely oriented lamina (Fig. 3D). Its unusual position does not allow comparisons with other rebbachisaurids.

In UFMA 1.10.1960–01, the parapophysis is above the zygapophysis level, a position observed in *Rebbachisaurus*, *Nigersaurus*, *Histriasaurus* and *Demandasaurus* (Dalla Vecchia, 1999; Sereno et al., 2007; Fernández-Baldor et al., 2011; Wilson and Allain, 2015), but not shared with *Comahuesaurus* and *Limaysaurus* [= *Rebbachisaurus tessonei*] (Calvo and Salgado, 1995; Carballido et al., 2012). In these latter rebbachisaurids, the parapophysis is far below the level of the zygapophysis. Otherwise, the leveling parapophysis/zygapophysis is present in the Rebbachisauridae MMCH-Pv 49/17 (Haluza et al., 2012).

The lateral aspect of neural arch display two fossae (centrodiapophyseal fossa, **cdf**; parapophyseal centrodiapophyseal fossa, **pacdf**; fig. 3C), which differ from all others rebbachisaurids known. For example, in *Katepensaurus* the parapophyseal centroprezygapophyseal fossa (**pacprf**) and (**pacdf**) are subdivided by laminae (Ibiricu et al., 2013; fig. 7C), and in *Histriasaurus* it forms a complex latticework of thin bone laminae (Dalla Vecchia, 1998; fig. 9C). Otherwise, *Limaysaurus*, *Nopcsaspondylus*, *Nigersaurus* and *Demandasaurus* present a reduction in complexity in these fossae (Nopcsa, 1902, fig. 2; Calvo and Salgado, 1995, fig. 8D; Sereno et al., 2007, fig. 3C; Fernández-Baldor et al., 2011, fig. 9B). In UFMA 1.10.1960–01, the posterior centrodiapophyseal lamina (**pcdl**) is forked in the middle region of the neural arch toward the centrum. These two new laminae form the border of the **cdf** and partially the **pacdf**. We consider it an autapomorphy for *Itapeuasaurus cajapioensis*.

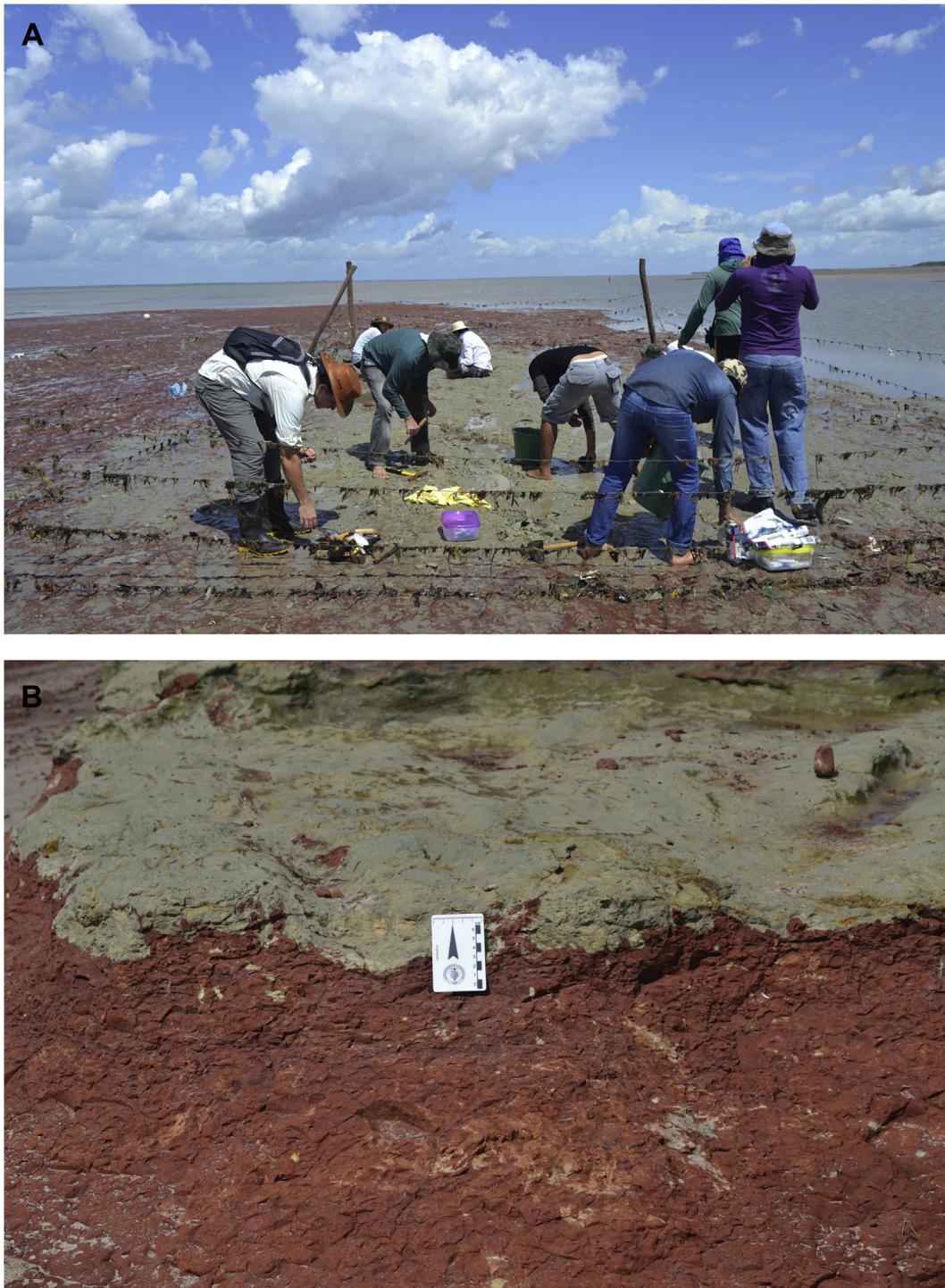


Fig. 2. Photographs of the excavation and geological context of *Itapeuasaurus cajapioensis* at Cajapió municipality, northern Maranhão State. **A)** View of the Itapeua beach during the removal of the material between tidal cycles; **B)** Section of an outcrop of the Alcântara Formation (São Luís Basin) at Itapeua beach revealing reddish/greenish pelitic deposits.

The surface framed by the prespinal (**prsl**), prezygaparapophyseal (**prpl**), and spinodiapophyseal (**spdI**) laminae is well delimited by three shallow fossae disposed vertically, increasing in size toward the apex (Fig. 4B). These fossae are subdivided by the spinoprezygapophyseal lamina (**sprl**) and spinopostzygapophyseal accessory lamina (**spzal**). *Limaysaurus tessonei* possesses apparently the same complex of fossae/lamina, but at a number of two (Calvo and Salgado, 1995; fig. 8). Although *Nigersaurus* also have dorsal vertebrae with paired pneumatic spaces at the

base of the neural spines, Sereno et al. (1999) does not offer information regarding its compartmentalization. In *Rebbachisaurus*, the pneumatic fossae are irregularly distributed along the inferior margin of the diapophysis, margin of the spinodiapophyseal lamina and neural spine (Wilson and Allain, 2015; figs. 8B, 9).

The neural canal is almost circular in anterior and slightly elliptical in posterior view. It is bordered by the medial centroprezygapophyseal lamina (med. **cprl**) into a large fossa in a drop

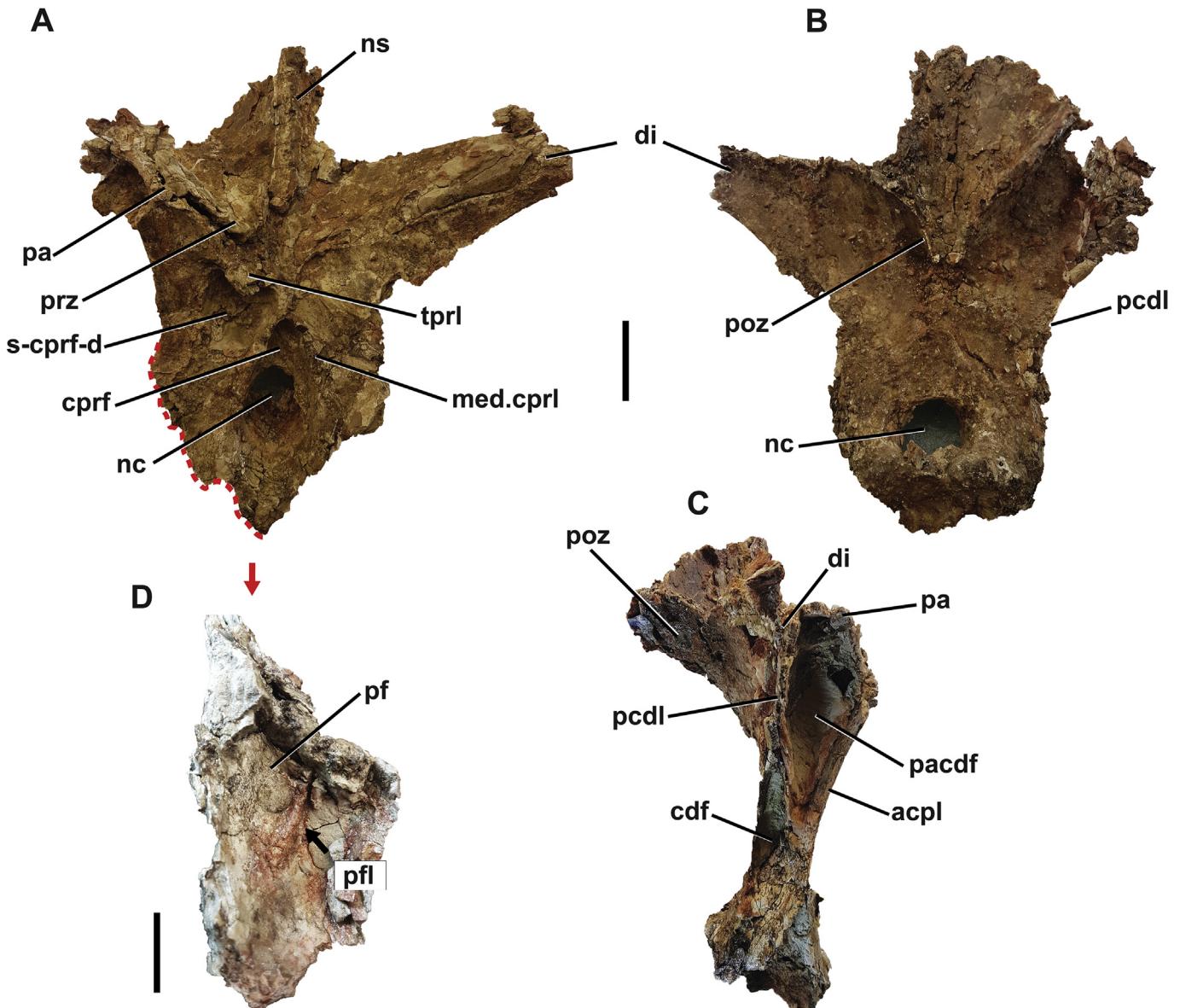


Fig. 3. Holotype of *I. cajapioensis*. Dorsal vertebra (UFMA 1.10.1960–01) in anterior (A), posterior (B), right lateral (C) and latero-ventral views (D). The scale bar represents 10 cm.

shape in anterior view (centroprezygapophyseal fossa - **cprf**). Both the med. **cprl** and the intraprezygapophyseal lamina (**tprl**) border the subfossa centroprezygapophyseal dorsal (**s-cprf-d**, *sensu* Carballido et al., 2012; fig. 4B), which is large in *Itapeuasaurus cajapioensis*. (Fig. 3A). In fact, the complex lamina/fossae in the infraprezygapophyseal region of UFMA 1.10.1960–01 is distinct from all other Rebbachisauridae known.

4.1.2. Caudal vertebrae

Six caudal vertebrae almost complete are preserved (four anterior and two middle). The most anterior of them, UFMA 1.10.1960–03 is 540 mm high being 95% complete (Table 1; Fig. 5). The centrum is anteroposteriorly short, subcircular in shape, with lateral and ventral sides concave. The ventral concavity has a mediolateral direction without the presence of lateral ridges. There is no sign of lateral pneumatic cavities and both articular faces are amphicoelous. Subcircular anterior caudal centrum is present in *Cathartesaura*, but along with amphiplatyan articular faces (Gallina and Apesteguía, 2005).

The neural arch is reduced and positioned on the anterior half of the centrum. In UFMA 1.10.1960–03 the neural spine is slightly inclined posteriorly (Fig. 5C). Otherwise, the neural arch in anterior caudals of *Limaysaurus* is twice higher than the height of the centra (Calvo and Salgado, 1995: 22) and in *Cathartesaura* a neural spine S-shaped is present (Gallina and Apesteguía, 2005; fig. 3A).

The transverse process is a laminar complex dorsoventrally short and slightly oriented upward (a slight variation from the morphological type ‘complex’ termed by Gallina and Otero, 2009). Instead, in *Histriasaurus* the transverse process is laterally and backwardly directed (Dalla Vecchia, 1998). In UFMA 1.10.1960–03 both the dorsal and ventral component of the transverse process are laminar rather than bar shaped; the ventral component is parallel to the dorsal one rather than oblique as in most rebbachisaurids (e.g. *Katepensaurus*, *Limaysaurus*, *Rebbachisaurus*, *Cathartesaura*). The isolated anterior caudal vertebrae from Kem Kem bed (NHMUK R36636) bears limited similarities with UFMA 1.10.1960–03, including dorsal and ventral components parallel to each other in its dorsolateral plan. Most laminar anterior caudal

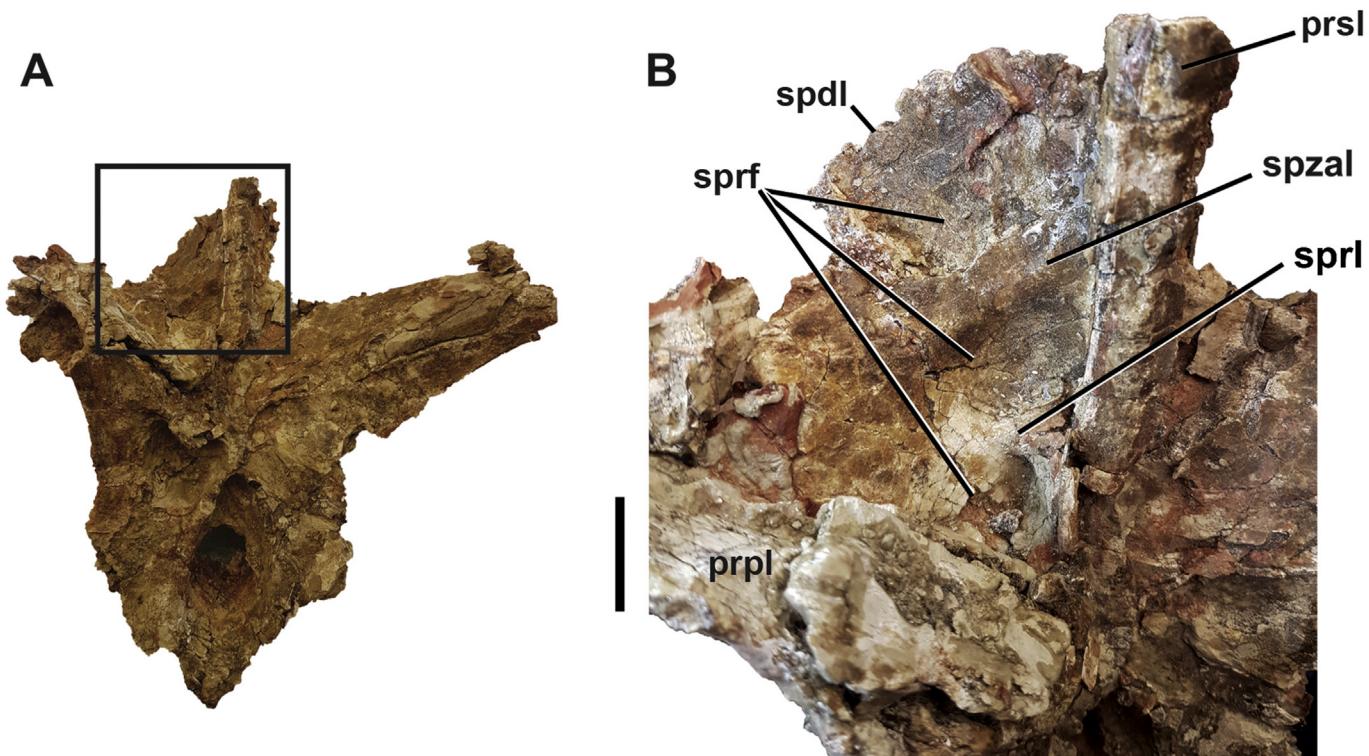


Fig. 4. Holotype of *I. cajapioensis*. Dorsal vertebra (UFMA1.10.1960–01) in anterior (A) and detail of the right base of the neural spine (B) views. The scale bar represents 5 cm.

transverse processes put UFMA 1.10.1960–03 apart from diplodocids, which have dorsal components well developed (bony bars). Although *Comahuesaurus* shares with *Itapeuasaurus cajapioensis* a transverse process dorsoventrally short and dorsolaterally deflected, the centroprezygapophyseal fossa (**cprf**) does not span the entire length of the dorsal and ventral components of the transverse process (see Carballido et al., 2012; fig. 6A).

A thin ‘web’ of bone between the dorsal and ventral components is absent in UFMA 1.10.1960–03; instead, a large prezygapophyseal

centrodiapophyseal fossa (**prcdf**) is compartmentalized medially by two short laminae. The first one is positioned more externally into the **prcdf**, obliquely oriented (prezygapophyseal centrodiapophyseal fossa lamina [**prcdfl**]) (Fig. 5A). As in *Katopensaurus*, the **prcdfl** arises from the dorsolateral margin of the centrum and isolates the dorsomedial corner of the **prcdf**. However, this lamina continues a trajectory under the dorsal component (= prezygodiapophyseal lamina [**prdl**]) performing an arc until contacting the ventral component (Fig. 5A). The second lamina, herein termed

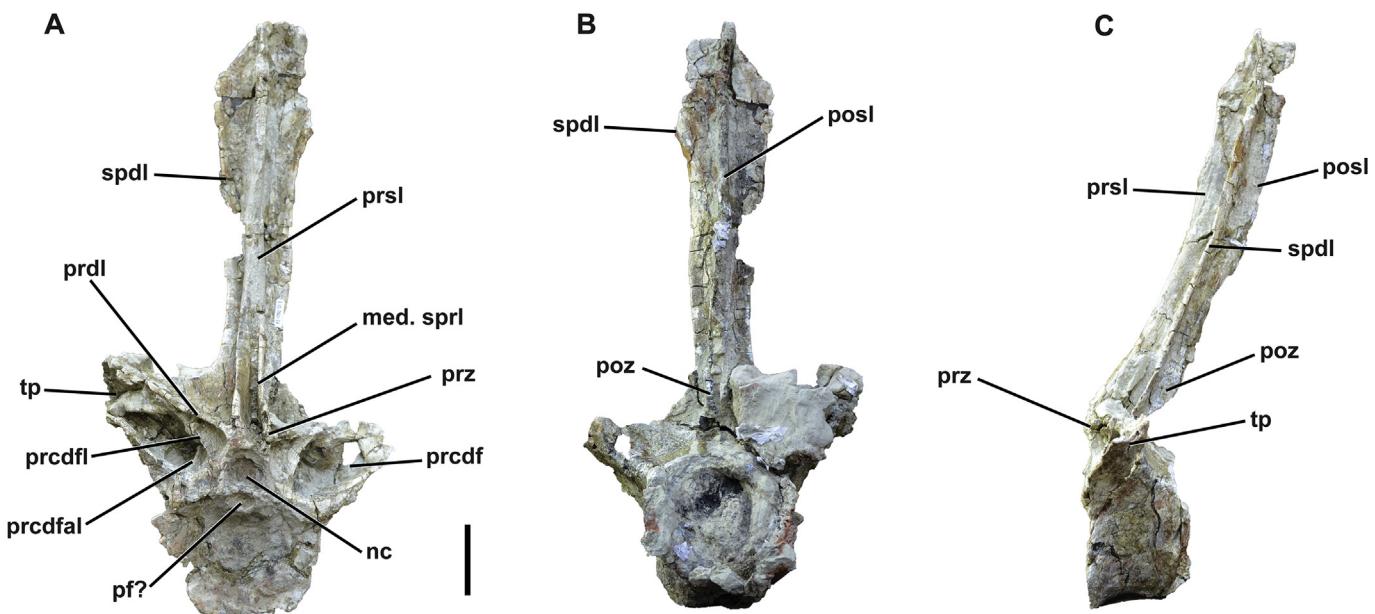


Fig. 5. Holotype of *I. cajapioensis*. Anterior caudal vertebra (UFMA 1.10.1960–03) in anterior (A), posterior (B) and left lateral (C) views. The scale bar represents 5 cm.

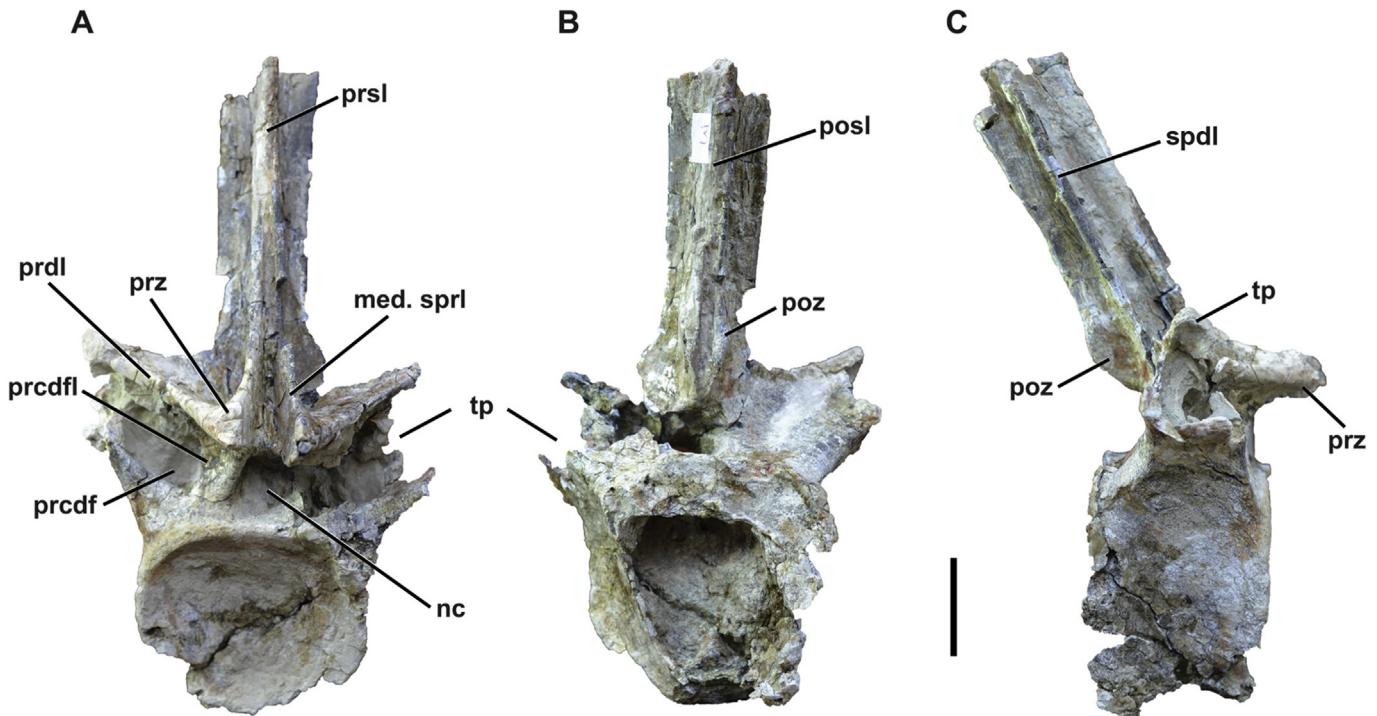


Fig. 6. Holotype of *I. cajapioensis*. Anterior caudal vertebra (UFMA 1.10.1960–04) in anterior (A), posterior (B) and right lateral (C) views. The scale bar represents 5 cm.

prezygodiapophyseal centrodiapophyseal fossa accessory lamina (**prcdfal**), is positioned more internally into the **prcdf**, vertically oriented. This lamina arises from the base of the ventral component toward the **prdl** (Fig. 5A). The presence and symmetrical arrangement of **prcdfi** and **prcdfal** in anterior caudal vertebrae of *Itapeuasaurus cajapioensis* is herein considered an autapomorphy. This condition is not present in others rebbachisaurids (see Pereda Suberbiola et al., 2003; Fernández-Baldor et al., 2011; Fernández-Baldor, 2012). For example, in the Isle of Wight rebbachisaurid

anterior caudal vertebra (MIWG 5384), both right and left **prcdf** are asymmetrically compartmentalized (see Mannion et al., 2011: fig. 1A).

The neural spine possesses spinodiapophyseal lamina (**spdl**), pre- and postspinal lamina (**prsl** and **posl**) well developed. The spinodiapophyseal laminae are posteriorly convex and anteriorly concave, which results in an anterior bending of these laminae, present in *Amazonsaurus* and *Rebbachisaurus garasbae* (Carvalho et al., 2003; Wilson and Allain, 2015), but diverging in *R. tessonei*

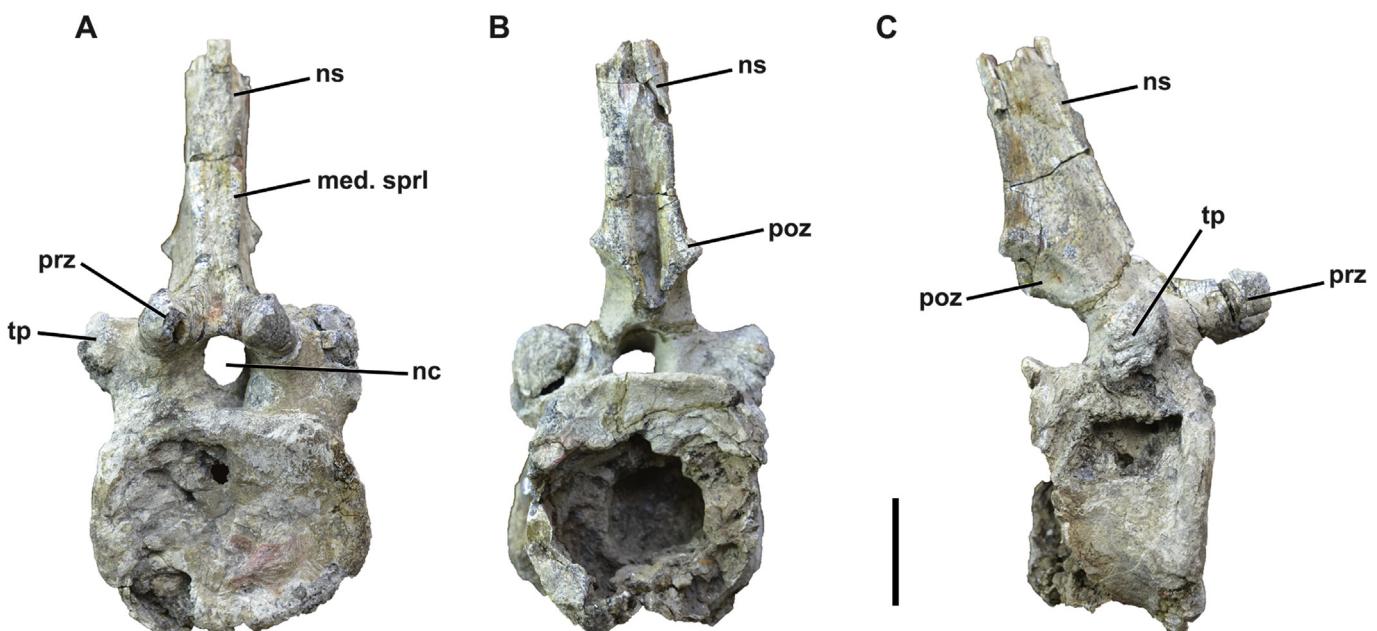


Fig. 7. Holotype of *I. cajapioensis*. Anterior caudal vertebra (UFMA 1.10.1960–05) in anterior (A), posterior (B) and right lateral (C) views. The scale bar represents 5 cm.

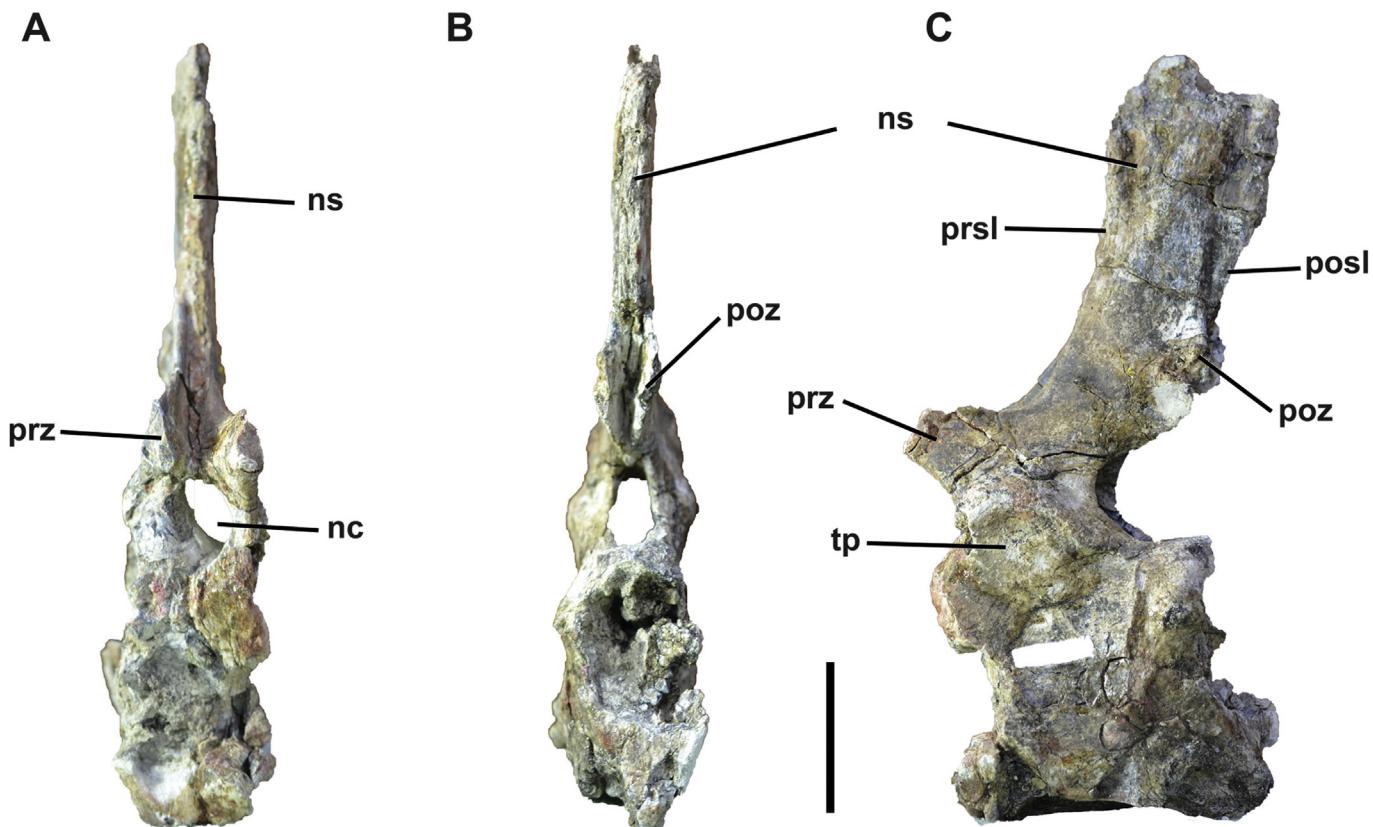


Fig. 8. Holotype of *I. cajapioensis*. Middle caudal vertebra (UFMA 1.10.1960–07) in anterior (A) and posterior (B) and left lateral (C) views. The scale bar represents 5 cm.

(Calvo and Salgado, 1995). According to Sereno et al. (2007), *Nigersaurus* has a characteristic flaring of the lateral lamina at mid length. In *Demandasaurus* and the Isle of Wight rebbachisaurid anterior caudal vertebra (MIWG 5384), the lateral lamina is marked by the small wing-like projections near the top of the neural spine (Pereda Suberbiola et al., 2003; Fernández-Baldor et al., 2011; Mannion et al., 2011). The distal third of the neural spine has a ‘petal-shape’ as a consequence of the expansion of the spinodiapophyseal lamina which is also present in *R. garasbae* (Wilson and Allain, 2015; fig. 9) (Fig. 5). In distal view, the spinodiapophyseal lamina (**spdl**), **prsl** and **posl** form the tetraradiate character typical of Rebbachisauridae (Calvo and Salgado, 1995; Salgado et al., 2004). However, the lateral, anterior and posterior rami are proportional in length.

The pre- and postspinal laminae bifurcate at the median region of the neural spine, continuing toward the neurocentral junction, participating of the formation of the prezygapophysis (medial spinoprezygapophyseal lamina [**med. sprl**]) and postzygapophysis (medial spinopostzygapophyseal lamina [**med. spol**]). This character is absent in *A. maranhensis*, partially present in *R. garasbae* and anterior caudal vertebrae of rebbachisaurids from central Patagonia, UNPSJB-PV 580 and UNPSJB-PV 1004/2. In anterior caudal vertebrae of *Katepensaurus* this character is also distinct, although the specimen UNPSJB-PV 1007/8 may have pre- and postspinal bifurcate lamina once excluded possible diagenetic obliteration or deformation (Ibiricu et al., 2013; fig. 10 C).

In the anterior caudal UFMA 1.10.1960–04 the centrum is amphicoelous. The neural arch is low, which supports prezygapophysis well developed and not wide apart, with its articular facets oriented medially. It is placed beyond the anterior margin of the centrum (Fig. 6). This condition is distinct from *Dicraeosaurus*, *Amazonsaurus* and from the isolated neural arch MCF-PVPH-633.

UFMA 1.10.1960–05 is 84 mm long, missing the distal half of neural spine, most of the transverse process and posterior articular surface (Fig. 7). As in the anterior caudal ones, the centrum is anteroposteriorly short, with lateral sides slightly concave. The ventral side is anteroposteriorly excavated; two discrete articular eruptions close to the anterior edge of centrum is herein interpreted as the haemal articular surfaces. They are ca. 5 cm apart, suggesting opened haemal articulations (not bridged).

As in UFMA 1.10.1960–04, the pedicel is reduced, situated on anterior half of the centrum. The prezygapophysis are placed beyond the anterior margin of the slightly amphicoelous centrum, and there is no prezygodiapophyseal centrodiapophyseal fossa (**prcdf**). The base of the transverse process preserved indicates a fusion of the dorsal and ventral components in a single bony bar. Between the well-developed postzygapophysis, there is a deep groove, which indicates the existence of a forked postspinal laminae. The articular facets of the postzygapophysis form a shallow, elliptic-elongated concavity (Fig. 7 B, C).

In its medium region, the neural spine is pentaradiate in cross-section due the absence of lateral lamina in the proximal half. This topography results of the medial spinoprezygapophyseal (**med.sprl**), prespinal (**prsl**) and postspinal (**posl**) laminae. In *Amazonsaurus* (MN 4555-V), instead, the caudal vertebrae neural spine is more laminar.

UFMA 1.10.1960–07 is 42.4 mm long and is markedly compressed laterally. It is interpreted herein as a middle caudal vertebra (Fig. 8). The centrum is amphicoelous, possessing the lateral faces slightly concave; the ventral one, instead, exhibit a deep notch anteroposteriorly oriented. The ventral margin of the posterior articular surface is slightly bulky than the anterior one, probably as a result of the presence of the haemal articular surfaces. In *Katepensaurus* (UNPSJB-PV 1004) and *Cathartesaura*, the middle caudal centra are similar to UFMA 1.10.1960–07, but the formers are more

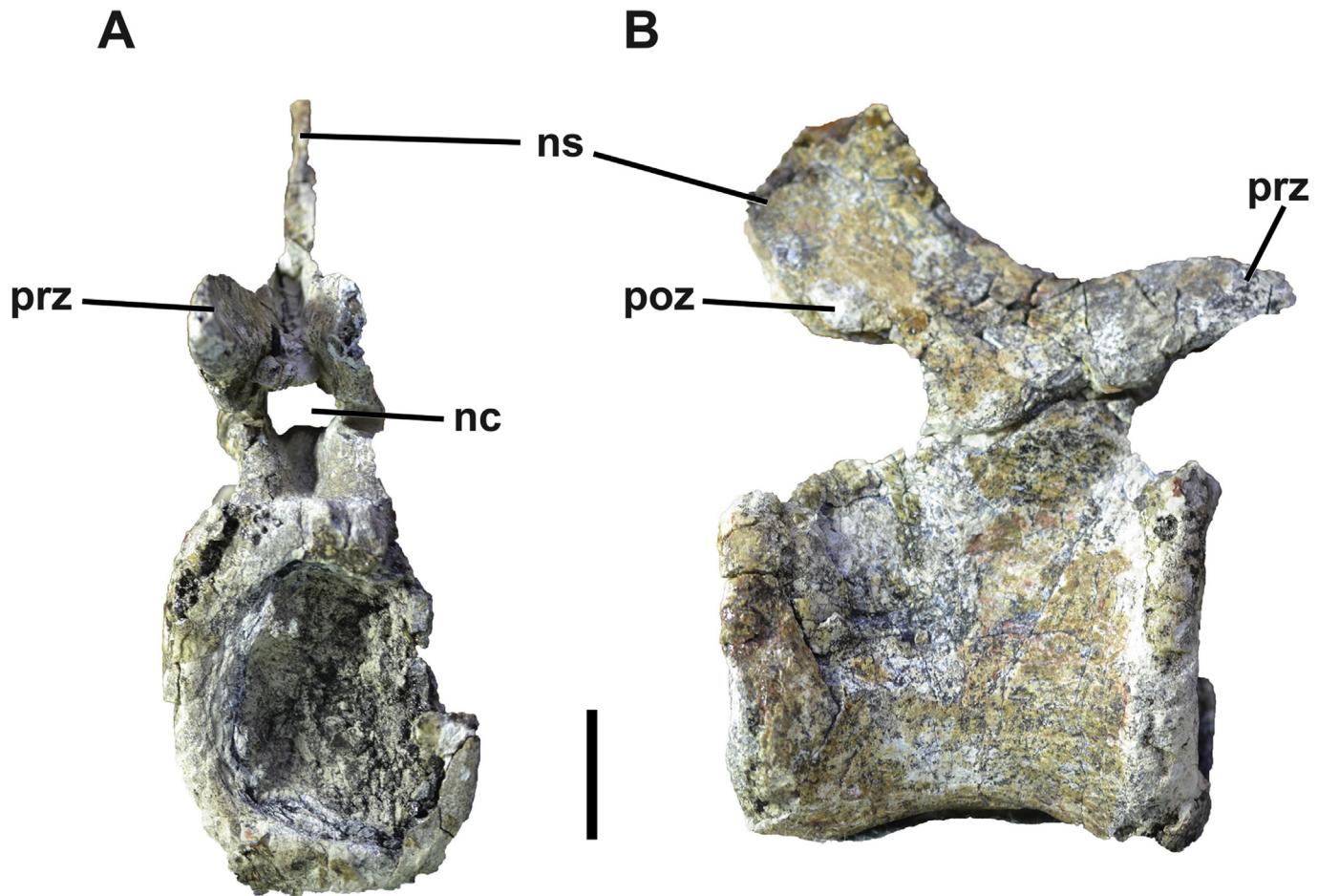


Fig. 9. Holotype of *I. cajapioensis*. Middle caudal vertebra (UFMA 1.10.1960–08) in anterior (A) and right lateral (B) views. The scale bar represents 5 cm.

rectangular in lateral view and have lower neural spines. These differences clearly reflect distinct positions in the caudal series, thus precluding direct comparisons.

The neural arch is positioned on the anterior half of centrum; in this specimen, the transverse process is absent (a common aspect in posterior caudal vertebrae). The neural canal is higher than wide and the pre- and postzygapophysis have a laminar aspect. In lateral view, UFMA 1.10.1960–07 is similar to mid-posterior caudal vertebrae of *Amazonsaurus* (MN 4560-V), but slightly more compressed in anterior/posterior view. The neural spine is slightly oriented posteriorly, only the **prsl** and **posl** being preserved.

UFMA 1.10.1960–07 differs from *Comahuesaurus* (MOZ-PV 6634) by the presence of a ridge on the lateral faces of the centrum, as well as a more excavated ventral surface. Caudal lateral ridges are also present in *Demandasaurus* (Pereda Suberbiola et al., 2003). The mid-caudals of *Zapalasaurus* (Pv-6127-MOZ), mainly the numbers 5 and 6, are remarkably similar to those of *Itapeuasaurus cajapioensis*, but exhibits a slightly greater angle between the prezygapophysis

and the neural spine (Salgado et al., 2006; fig. 2: 5–6). This latter condition, plus the presence of a lateral knob at the base of the neural arch, distances *Histriasaurus* from UFMA 1.10.1960–07.

UFMA 1.10.1960–08 represents a second middle caudal vertebra, posterior to UFMA 1.10.1960–07 in the caudal series (Fig. 9). The centrum is 109,5 mm long and 170,5 mm, the lateral face being strongly excavated and the ventral face slightly concave. The neurocentral junction is placed on anterior half of the centrum. The prezygapophysis is laminar and surpass the anterior edge of the centrum. As in UFMA 1.10.1960–07, there is no an evident transverse process. The neural spine is low and laterally compressed, without evidence of lateral laminae (II).

UFMA 1.10.1960–08 differs from the middle caudals of *Limaysaurus* and *Demandasaurus* in having a wider angle between the postzygapophysis and the centrum, and from *Comahuesaurus* by a smaller neurocentral junction (Fig. 9B). The mid-posterior caudal vertebra of *Amazonsaurus* (MN 4560-V) is more robust, with equivalent prezygapophysis (Carvalho et al., 2003; fig. 11). In the specimen

Table 1

Measurements of the holotype of *Itapeuasaurus cajapioensis* gen. et sp. nov. (in mm). An ** indicates an incomplete measurement.

Specimen	Centrum length	Centrum width	Centrum height	Neural arch, greatest transverse width	Neural arch, height	Neural spine, greatest transverse width	Neural spine, height	Neural canal width	Neural canal height
UFMA.10.1960-01	—	—	—	135,5*	240*	—	—	46,9	45,8
UFMA.10.1960-03	82,9	130,5	112,7*	260*	110	78,4	400*	26,8	21,06
UFMA.10.1960-04	82,2*	118,8*	113,6*	190*	63,3	—	—	27,1*	31,6
UFMA.10.1960-05	82,4	120,1	100,6*	104,2	49,2	37,5	130*	30,7	21,03
UFMA.10.1960-07	95,9*	47,9*	95,4*	48,1	40,4	9,1	170*	22,5	27,4
UFMA.10.1960-08	111,8*	58,6	87,5	33	38,6	—	—	17,4	12,7

Nos IG-1, the centrum has a spool shape, with a lateral knob (**Ik**) at the base of the neural arch (Dalla Vecchia, 1998; fig. 17A), aspects not present in UFMA 1.10.1960–08. In *Tataouinea*, the postzygapophysis are more developed, and the prezygapophysis are slightly oriented upward (Fanti et al., 2015; fig. 13A). The specimen UNPSJB-PV 1004 and mid-posterior caudal vertebrae of *Zapalasaurus* exhibit a neural spine more expanded than UFMA 1.10.1960–08 (Salgado et al., 2006; fig. 5, 7, 8; Ibiricu et al., 2012; fig. 7).

5. Discussion

5.1. Phylogenetic analysis

Rebbachisauridae was defined as all diplodocoids more closely related to *Rebbachisaurus garasbae* than to *Diplodocus longus* (Wilson [pers. comm.] in Salgado et al., 2004). Recent analysis has recovered *Amazonsaurus* as the most ‘basal’ member of this clade, with the European/African *Histriasaurus* its sister taxon. *Histriasaurus* forms a polytomy with the South American *Zapalasaurus* at the base of Rebbachisauridae and *Comahuesaurus* is also placed outside of Khebbashia (Limaysaurinae + Nigersaurinae) (see Whitlock, 2011; Carballido et al., 2012; Wilson and Allain, 2015; Fanti et al., 2015; Mannion et al., 2019).

Nigersaurinae, a clade defined as *Nigersaurus* not *Limaysaurus* by Whitlock (2011), is formed by African (*Nigersaurus*, *Rebbachisaurus*, *Tataouinea*) and European (*Demandasaurus*) taxa (see Wilson and Allain, 2015; Mannion et al., 2019). Rebbachisauridae also includes Limaysaurinae (*Cathartesaura* + *Limaysaurus*). In order to ascertain the probable phylogenetic relationships of *Itapeuasaurus cajapioensis*, a phylogenetic analysis was carried out based on the matrix proposed by Wilson and Allain (2015). This analysis included a few changes in the characters 119 (from Salgado et al., 2006), 124 (from McIntosh, 1990), 131 (from Wilson, 2002), 132 (from Whitlock, 2011), 141 (from Wilson et al., 1999) (Appendix A).

A parsimony analysis was carried out using the software TNT v. 1.1 (Goloboff et al., 2008a, b). The matrix consists of the compiled data from Wilson and Allain (2015) using a data set of 171 characters scored in 27 taxa, plus the inclusion of *Itapeuasaurus cajapioensis*. Additionally, a heuristic tree search of 1000 replicates of Wagner Trees with random addition sequences was performed, followed by TBR branch-swapping. The initial search produced 334 most parsimonious trees (MPTs) of 282 steps (consistency index [CI] = 0.663, retention index [RI] = 0.810). The strict consensus of this analysis recovered a polytomy at the base of Rebbachisauridae (Fig. 10). However, when an agreement subtree analysis is performed, *Itapeuasaurus cajapioensis* is grouped together with *Demandasaurus* and *Nigersaurus* in *Nigersaurinae* (Fig. 11). In our resulting topology, *Histriasaurus* and *Rebbachisaurus* were excluded and *Amazonsaurus*, *Zapalasaurus* and *Comahuesaurus* recovered as successive outgroups to Khebbashia.

5.2. Taxonomy

Itapeuasaurus cajapioensis is the best preserved diplodocoid sauropod from the Alcântara Formation, Cenomanian of the São Luís Basin. We consider it as a Diplodocoidea primarily by the neural arch in the dorsal vertebrae being tall and neural spines very elongated both in dorsal and caudal vertebrae, being tetraradiate in cross-section. Its attribution to Rebbachisauridae is mainly based on dorsal and ventral components of the transverse process supported by a reduced ‘web’ of bone (*sensu* Gallina and Otero, 2009), summit of the anterior caudal neural spine ‘petal-shaped’ (see Wilson and Allain, 2015; fig. 12) as well as absence of hypophene-hypantrum in posterior dorsals (see Calvo and Salgado, 1995). Additionally, the presence of fossae split by an obliquely oriented

internal pneumatic fossa lamina on the dorsals neural arch, posterior centrodiaphyseal lamina forked on the dorsal vertebrae and caudal transverse processes thinner than the usual bony bar characterize it as a new genus and species of Rebbachisauridae.

In Brazil, rebbachisaurids are scarce and only recorded in the Albian-Cenomanian strata of the São Luís and Parnaíba basins (Alcântara and Itapecuru formations, respectively). Until now, solely one nominal species has been described, *Amazonsaurus maranhensis*, from Aptian-Albian Itapecuru Formation (Carvalho et al., 2003). Isolated and fragmentary rebbachisaurids records include materials of few diagnostic value (e.g. fragments of tetraradiate neural spine) from the Alcântara Formation as well as in underlying Undifferentiated Unit deposits (a designation used for Itapecuru Formation by some authors as Rossetti and Truckenbrodt, 1997), lower/middle Albian in age (Medeiros and Schultz, 2004; Castro et al., 2007). Most of the caudal centra from the Alcântara Formation (e.g. Laje do Coringa bone bed) have been related to *Limaysaurus* sp. (Medeiros and Schultz, 2004), but these authors admit that this generic assignment is weakly sustained because of the lack of diagnostic features (M.A. Medeiros, pers. comm., 2015).

5.3. Spatiotemporal context

Prior studies have supported a North America origin for Diplodocoidea, with the surge of diversification in Flagellicaudata occurring in the Kimmeridgian of North America, Europe and Africa, and Tithonian of South and North America (Whitlock, 2011). Recently, discoveries in East Asia have challenged current paleobiogeographic hypotheses concerning the origin and dispersion of Diplodocoidea, estimating an early Middle Jurassic age for the earliest members of the clade (Xu et al., 2018).

New discoveries also have improved our knowledge regarding spatiotemporal context of Rebbachisauridae. After extinction of most flagellicaudata taxa in the Late Jurassic, Rebbachisauridae became the latest-surviving dipodocoids occupying both Laurasian and Gondwanan landmasses during the Early Cretaceous (Wilson and Allain, 2015). The earliest record of this clade is *Maapusaurus*, now dated as Upper Jurassic of North America (Morrison Formation) (Carpenter, 2018). Moreover, the Lower Cretaceous *Xenoposeidon* from Hastings Group of England represents the successive earliest rebbachisaurid known (Taylor, 2018).

The presence of Diplodocoidea in the early Middle – Late Jurassic interval of North America and Asia suggests a global distribution of this clade before the breakup of Pangea. Furthermore, the discovery of the dicraeosaurid *Lingwulong shenqi* in China indicates that many advanced sauropods lineages originated c. 15 million years earlier than previously hypothesized (Xu et al., 2018). According to Carpenter (2018), it is probable that the migration of rebbachisaurids has occurred between North America and Europe during the latest Late Jurassic and earliest Early Cretaceous, reaching South America via Europe and Africa. This scenario has now confronted time-calibrated phylogeny for a South American root of Rebbachisauridae radiation (see Fanti et al., 2015).

Recently, *Rebbachisaurus* has been positioned as sister taxon to *Nigersaurus* and *Demandasaurus* in the subclade Rebbachisaurinae by Wilson and Allain (2015) (herein termed *Nigersaurinae* following recommendation of Mannion et al., 2019) or as sister taxon to *Demandasaurus* and *Tataouinea* by Fanti et al. (2015). In both cases, *Nigersaurinae* is a subclade restricted to Europe and northern Africa. In fact, the oceanic barrier that would have prevented the closer relationship between African and European faunas seems to have been bridged by an intercontinental land passage by means of carbonate platforms in the Tethyan seaway known as the Apulian Route (Dalla Vecchia, 2002; Sereno et al., 2007; Canudo et al., 2009; Fernández-Baldor et al., 2011;

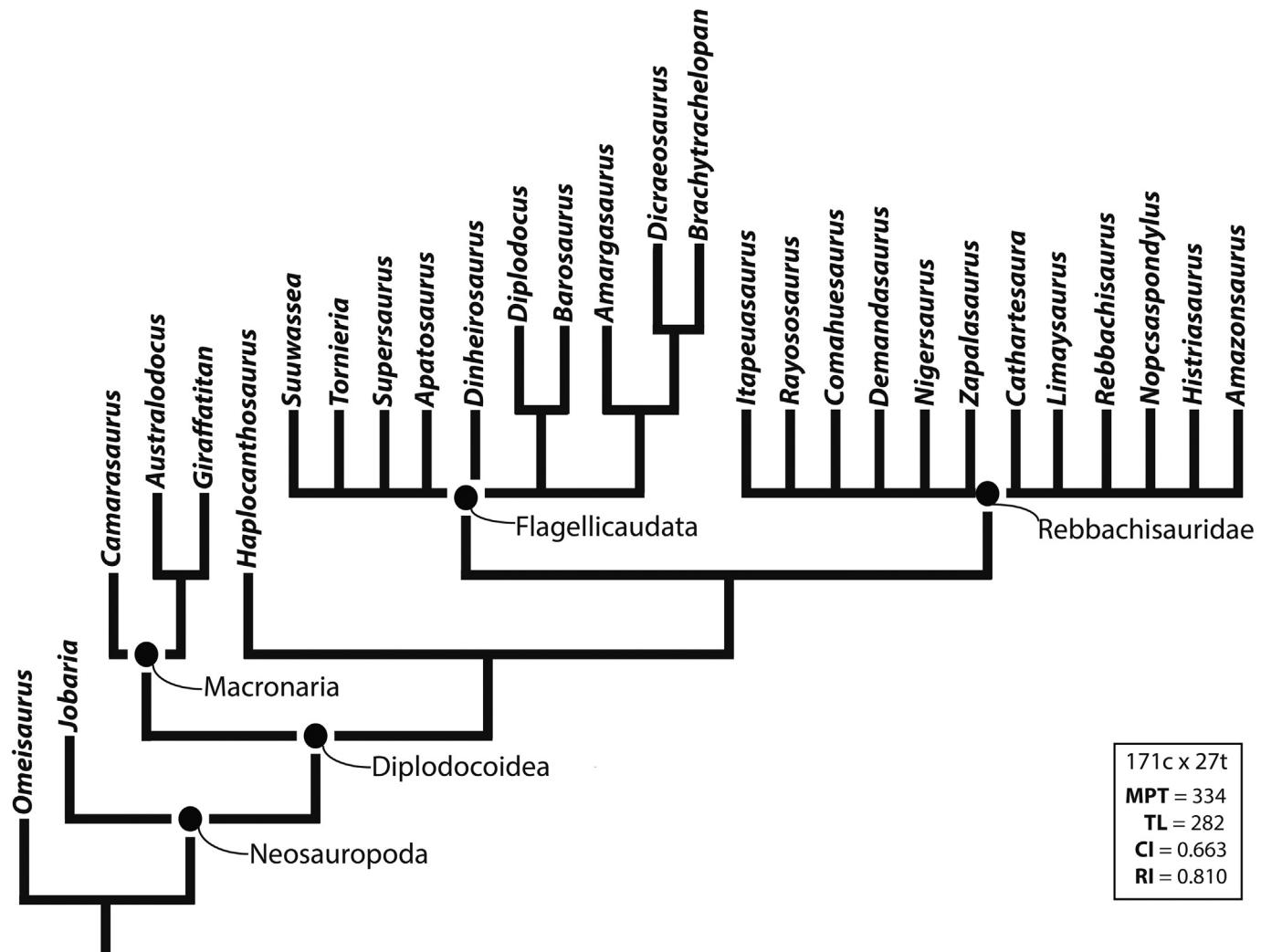


Fig. 10. Phylogenetic relationship among Neosauropoda, including the results for *Itapeuasaurus cajapioensis*. The diagram reflects a strict consensus of 334 most parsimonious trees of 282 steps (MPTs). Abbreviations: c, characters; CI, consistency index; MPT, most parsimonious trees; RI, retention index; t, taxa; TL, tree length.

Holwerda et al., 2018). According to Fernández-Baldor et al., (2011), although the Apulian Route may never have been a continuous land corridor between south Europe and northern Africa, islands appear to have been sufficiently closer to allow faunal interchange. In the present study, the clade formed by *Itapeuasaurus cajapioensis* and *Demandasaurus* suggests that Nigersaurinae was not restricted only to Europe and northern Africa, but also included South American taxa. Similarly, Fanti et al. (2015) also suggest a more widely distributed Nigersaurinae lineage.

In Western Gondwana, especially in the northeastern Brazil, paleobiogeographic patterns are more complex than previously thought. Recent models have suggested the presence of epicontinental seaways on the rift valleys along the Recôncavo-Tucano-Jatobá and Cariri-Potiguar trends during the Aptian (Arai, 1999, 2009, 2014; Maisey, 2000). Maisey (2011) postulated one of these probably separated northeastern Brazil from the rest of South America, but it remained connected with Africa. For this author, another seaway may have left northern Brazil apart from both South America and Africa. As a result, dispersal and vicariance of Early Cretaceous biota of northeastern Brazil do not reflect a conspicuous and unambiguous unique 'event' of breakup between South America and Africa, but complex isolation episodes in parts of Western Gondwana (Maisey, 2011).

The earlier marine incursions along the Equatorial-South Atlantic continental margin of Brazil has been widely recognized as Aptian in age. Undoubted evidences come from Macro- and microfossils records of Sergipe and Parnaíba basins: from the first one, the oldest ammonite assemblages are representatives of the early douvilleiceratid lineage (e.g. *Epicheloniceras*–*Eodouvilleiceras*) and characterize a middle Aptian age, some may even suggest a late early Aptian (e.g. *Dufrenoyia justinae*) (Bengtson et al., 2007). Foraminifera record from oldest marine deposits in the Sergipe Basin confirms a well-developed open connection with low-latitude western Tethyan regions during the late Aptian – late Albian (Koutsoukos, 1992). By the late Coniacian – early Santonian times, the final structural detachment of South America and Africa occurred and consequently the establishment of deep-oceanic conditions in the northern South Atlantic (Koutsoukos, 1998). In the Parnaíba Basin, Maranhão State, marine isopods record is also late Aptian in age (Lindoso et al., 2013b). All these records show faunal Tethyan affinities. In the Cenomanian, however, a permanent oceanic connection seems to have developed, in part as a result of eustatic sea level rising with repeated flooding by ocean waters across most of Saharan region (Maisey, 1991).

The fossil record of the Alcântara Formation has revealed remarkable similarities between the continental faunas of

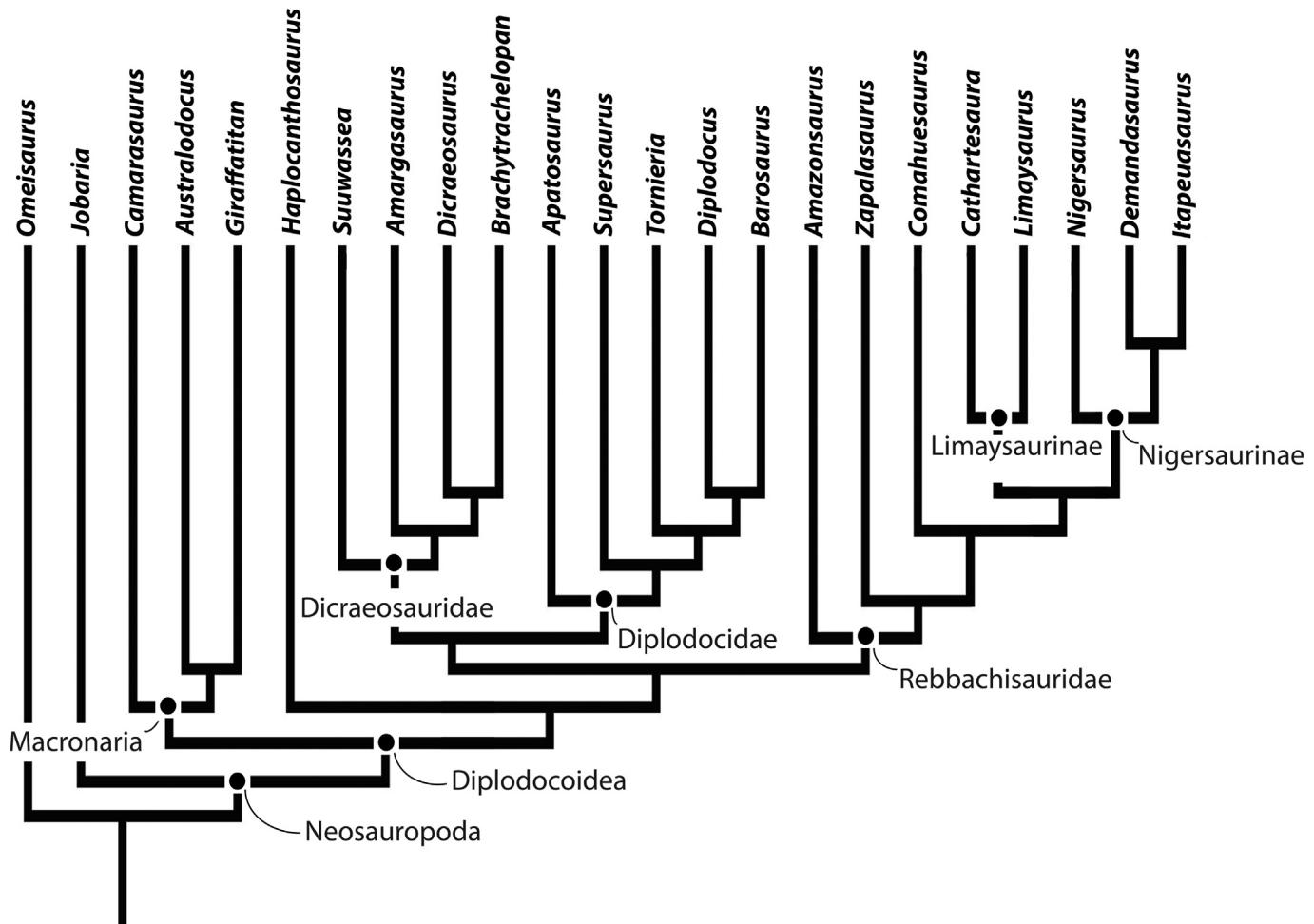


Fig. 11. Phylogenetic relationship among Neosauropoda based on agreement subtree produced in TNT. The resulting topology shows *Itapevasaurus cajapioensis* grouped together with members of Nigersaurinae.

northeastern Brazil and northern Africa during the lower Cenomanian, mainly when compared to the material from southeast Morocco (Medeiros and Schultz, 2001, 2002; Medeiros et al., 2014). The fishes assemblage recorded in the Laje do Coringa bone bed is the most striking element of correlation (see Cavin and

Dutheil, 1999; Cavin et al., 2010), although theropod dinosaurs (e.g. *Carcarodontosaurus*, *Spinosaurus*) are also remarkable. Despite some taxa are restricted to the Alcântara Formation (e.g. *Atlantoceratops equatorialis*, *Equinoxiodus alcantarensis*, *Coringasuchus anisodontis* and *Oxalaia quilombensis*), the similarities of



Fig. 12. Paleoenvironmental context of *Itapevasaurus cajapioensis*. In the background, the Equatorial Atlantic Ocean had already represented a selective barrier on the paleocommunities from the northeastern Brazil and northern Africa. Art by Deverson Pepi.

vertebrate taxa recorded in this lithostratigraphic unit with those of Africa has been claimed as a Gondwanan heritage. For Medeiros et al. (2014), it might be attributed to minor evolutionary changes of the biota after the breakup of South America and Africa.

The presence of a new genus and species of rebbachisaurid in the Alcântara Formation closely related to *Demandasaurus* is another evidence that South America and Africa still shared a faunistic identity during the early Late Cretaceous. Thus, the present data fits well with previous statement of a greater similarity among South America and Africa mid-Cretaceous continental fauna than amongst the southern and northern South American ones (Medeiros and Schultz, 2002; Medeiros et al., 2007, 2014). Before the early Late Cretaceous, dinosaur faunas were relatively cosmopolitan. The isolation of continental landmasses by oceanic barriers led to marked provincialisms (Sereno et al., 1994, 1996).

Since most Alcântara Formation sauropod sampling comes from the Laje do Coringa bone bed, and the skeletal remains collected therein are reworked, fractured and abraded, they are unsuitable for assessing relative diversities. Taphonomic bias is an important factor to be considered in the Laje do Coringa vertebrate assemblage which includes skeletal remains transported and redeposited (Holz, 2003).

Nonetheless, diplodocoid isolated caudal centra are far more numerous than those of titanosaurs, and they certainly would not belong to a single individual. Instead, the fossils from Laje do Coringa represent a sample of a paleocommunity (see Medeiros et al., 2014). However, we consider the Alcântara Formation vertebrate record insufficient to make confident sinecological assessments. The complex pneumaticity observed in *Itapeuasaurus cajapioensis* could be an adaptation for the high temperatures in tropical to subtropical paleolatitudes during the early Late Cretaceous (Fig. 12) (see Ibiricu et al., 2017).

6. Conclusions

Itapeuasaurus cajapioensis gen. et sp. nov. represents the northernmost record of Diplodocoidea in South America and the second nominal Rebbachisauridae for the middle-Cretaceous of Brazil, expanding our knowledge regarding the diversity of this clade in Western Gondwana. Its set of autapomorphies confirm the pneumatic complexity inherent to this neosauropod group. The phylogenetic analysis performed herein identifies Nigersaurinae as a South American – African/European clade more than an exclusively African and European taxa during Cenomanian times. Although this scenario is consistent with previous paleontological data recorded in the lower Upper Cretaceous of the São Luís Basin, recent phylogenetic approaches within Rebbachisauridae precludes a reliable paleobiogeographic hypothesis at this moment. Finally, by now it seems clear that rebbachisaurids outnumbered titanosaurs in the early Late Cretaceous in northern South America right before the steep decline of Rebbachisauridae. New information on several aspects of this remarkable community that lived in northern Brazil depends on better preserved specimens that may be found in the future.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2019.104191>.