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A NEW EARLY CRETACEOUS BRACHIOSAURID (DINOSAURIA, NEOSAUROPODA) FROM NORTHWESTERN GONDWANA (VILLA DE LEIVA, COLOMBIA)

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ABSTRACT—Brachiosaurid sauropods achieved a broad distribution during the Late Jurassic, which has been considered to provide evidence of their origins during the Middle Jurassic, prior to the breakup of Pangea. In contrast to their broad geographic distribution during the Late Jurassic, formally named brachiosaurid species from the Cretaceous have so far been restricted to the Aptian–Albian of North America, which has been interpreted as a signal of differential extinction and/or a bias in the Early Cretaceous fossil record. Here we describe a new brachiosaurid titanosauriform taxon from the Early Cretaceous of Colombia, which is represented by axial elements. The material was recovered from marine sediments of the Paja Formation (Barremian), close to the locality of Villa de Leiva. The weakly laterally expanded and divided transverse processes of the anterior-most caudal vertebrae allows the recognition of a new sauropod taxon, *Padillasaurus leivaensis*, gen. et sp. nov. In order to test the phylogenetic relationships of the new taxon, we performed a cladistic analysis that recovered *Padillasaurus* as a brachiosaurid titanosauriform. This position is supported by a combination of characters, including the presence of blind fossae in anterior caudal vertebrae. Among titanosauriforms, the presence of blind fossae in anterior caudal vertebrae is an apomorphic character that is exclusive to *Giraffatitan*, *Venenosaurus*, *Cedarosaurus*, and *Abydosaurus*. Although more complete remains are needed to test more thoroughly the affinities of the new taxon, the available evidence indicates that brachiosaurids survived at lower latitudes in Gondwana until at least the Early Cretaceous.

<http://zoobank.org/urn:lsid:zoobank.org:pub:652D6B2A-7A8A-4311-8725-279BF2C9E0E3>

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Brachiosauridae is one of the two major clades of Titanosauriformes, a diverse group of sauropods that thrived in the Late Jurassic and Cretaceous in both Laurasia and Gondwana. Brachiosaurids encompass all titanosauriforms more closely related to *Brachiosaurus* than to *Saltasaurus* (Wilson and Sereno, 1998). Definitive brachiosaurid remains are known from the Late Jurassic up to the late Early Cretaceous. During the Late Jurassic, this clade is recorded in both the Northern and Southern Hemispheres, including North America (e.g., *Brachiosaurus altithorax* Riggs, 1903), Africa (*Giraffatitan brancai* [Janensch, 1914]), and possibly Europe and South America (see Discussion; Rauhut, 2006; D’Emic, 2012; Mannion et al., 2013).

After the Jurassic/Cretaceous boundary, finds of brachiosaurids have so far been restricted to the Early Cretaceous (Aptian–Albian) of North America (e.g., *Cedarosaurus* Tidwell et al., 1999, *Venenosaurus* Tidwell et al., 2001, *Abydosaurus* Chure et al., 2010). The absence of this group from other landmasses during the Early Cretaceous has been interpreted either as a product of local extinctions (Wilson and Sereno, 1998; D’Emic,

2012) or as a result of bias in the generally poor Early Cretaceous fossil record (Mannion et al., 2013).

Here we report a new titanosauriform taxon from the Early Cretaceous (Barremian) of Colombia. Dinosaur remains are remarkably scarce in Cretaceous deposits of northern South America, and previous records were limited to isolated theropod teeth from the latest Cretaceous of Colombia (Langston, 1953; Ezcurra, 2009) and dinosaur footprints (Buffetaut, 2000). The remains described here provide information on the virtually unknown dinosaurian faunas of northwestern South America and increase the currently limited knowledge on sauropod diversity from Gondwana during the earliest (pre-Albian) Cretaceous. More specifically, the material here reported is the first phylogenetically informative sauropod record from northern South America, with previous records being restricted to an isolated sauropod vertebra of uncertain affinities (Langston and Durham, 1955). The new taxon is described, its systematic affinities among titanosauriforms (and in particular brachiosaurids) are analyzed through a phylogenetic analysis, and its significance for understanding the paleobiogeographic history of Brachiosauridae is discussed. We discuss alternative hypotheses previously proposed to explain the absence of brachiosaurids outside North America during Early Cretaceous, and suggest that this absence might indeed be a product of the limited sampling of sauropod fossils available from this time period.

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Institutional Abbreviations—**FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **JACVM**, Junta de Acción Comunal Vereda Monquirá, Vereda Monquirá, Colombia; **MB.R**, Museum für Naturkunde, Berlin, Germany; **MPEF**, Museo Paleontológico Egidio Feruglio, Trelew, Argentina.

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1887

SAUROPODA Marsh, 1878

NEOSAUROPODA Bonaparte, 1986

TITANOSAURIFORMES Salgado, Coria, and Calvo, 1997

BRACHIOSAURIDAE Riggs, 1904

PADILLASAURUS LEIVAENSIS, gen. et sp. nov.

(Figs. 2–5)

Etymology—The generic name honors Dr. Carlos Bernardo Padilla Bernal (1957–2013), a paleontological enthusiast who led the creation of the Centro de Investigaciones Paleontológicas de Villa de Leiva (Colombia), promoted paleontological collection and research on the Colombian fossil record, and encouraged the study of this specimen by combining ‘Padilla’ and ‘saurus’ (the Greek word for lizard). The specific name refers to the locality of Villa de Leiva, from which the specimen derives.

Holotype—JACVM 0001, a single specimen that preserves a posterior dorsal centrum, the last presacral vertebra, the two anterior-most and the two posterior-most sacral vertebrae, and the first eight caudal vertebrae.

Diagnosis—Medium-sized titanosauriform characterized by the following autapomorphies: (1) first and second caudal vertebrae with high and dorsally directed prezygodiapophyseal laminae that converge with the centroprezygapophyseal laminae and form the lateroventral ventral margins of the prezygapophyseal processes; (2) anterior caudal vertebrae with weakly laterally expanded transverse processes; and (3) first caudal vertebrae with divided transverse process, the dorsal section of which is posterodorsally directed in the first two caudal vertebrae.

Locality and Horizon—Northeast of Villa de Leiva town, Department of Boyacá, Ricaurte Province, Colombia (Fig. 1). The holotype was collected from the Paja Formation

(Barremian–Aptian). Three ammonite specimens were preserved along with the vertebral remains and extracted during preparation of the specimen. Based on these ammonoids, the new sauropod is here considered to be lower Barremian in age (see Geological Setting).

GEOLOGIC SETTING

The holotype material of *Padillasaurus* was collected by local farmers and subsequently donated and housed at the JACVM. The exact geographic provenance of the material could not be determined. Nevertheless, the information provided by the staff of the JACVM indicates that the material comes from the La Tordolla area, in the Vereda Monquirá, Villa de Leiva (Fig. 1). At this place, the middle member of the Paja Formation crops out. This stratigraphic level has been informally referred to as the ‘miembro de arcillolitas abigarradas’ (variegated claystones member) and considered to be Barremian–Aptian in age (Etayo-Serna, 1968; Forero and Sarmiento, 1985). The Paja Formation is a marine unit deposited during the marine transgression recorded in Colombia during the Early Cretaceous (Etayo-Serna et al., 1976). The middle member of this unit is formed by gypsum-rich claystones with calcareous nodules interbedded with thin calcareous levels with cryptalgal structures (Forero and Sarmiento, 1985), interpreted as deposits formed in tidal salt flats (Forero and Sarmiento, 1985).

The ammonoids preserved with the sauropod specimen consist of fragments of *Gerhardtia galeatoides* (JACVM 2 and JACVM 3) and an almost complete specimen of *Lytoceras* sp. (JACVM 4). This association corresponds to the *Gerhardtia galeatoides* subzone, which represents the lower part of the upper Barremian in the International Union of Geological Sciences (IUGS) biostratigraphic zonation (cf. Reboulet et al., 2009). Therefore, a lower upper Barremian age is assigned to the new sauropod species described here.

DESCRIPTION

In the following description we follow the nomenclature for vertebral laminae proposed by Wilson (1999). The vertebrae of

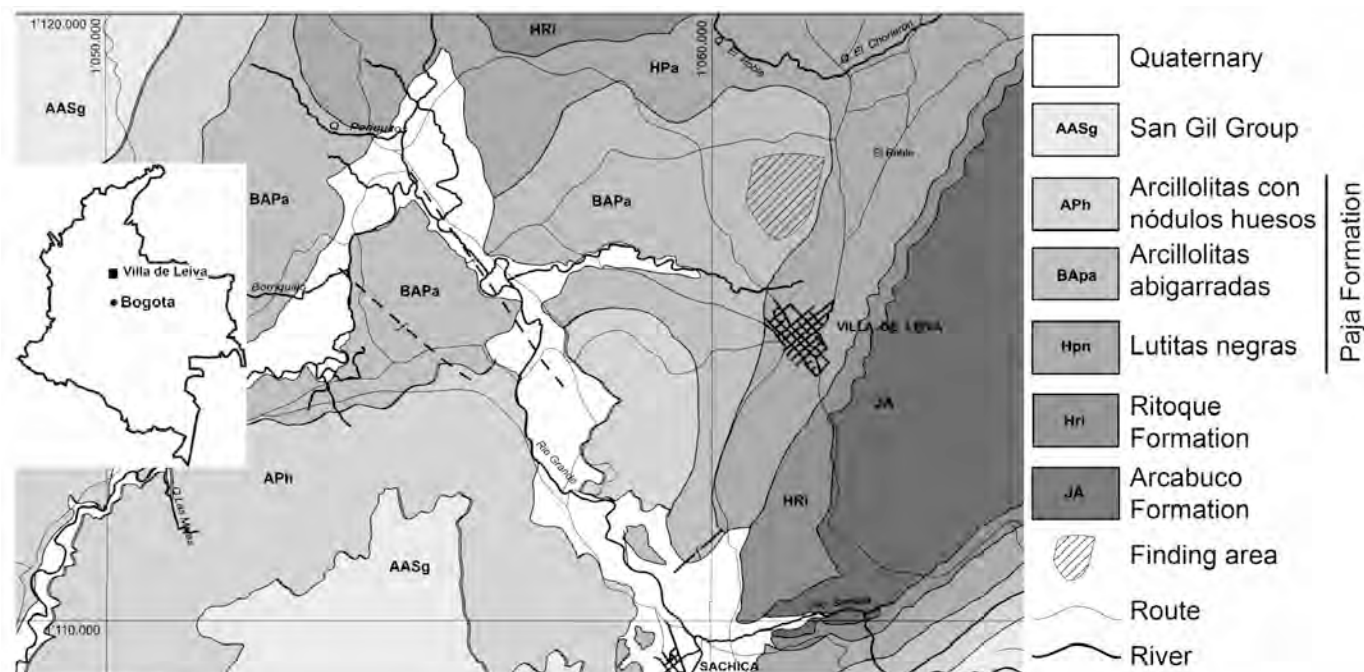


FIGURE 1. *Padillasaurus leivaensis*, location map of holotype specimen (JACVM 0001).

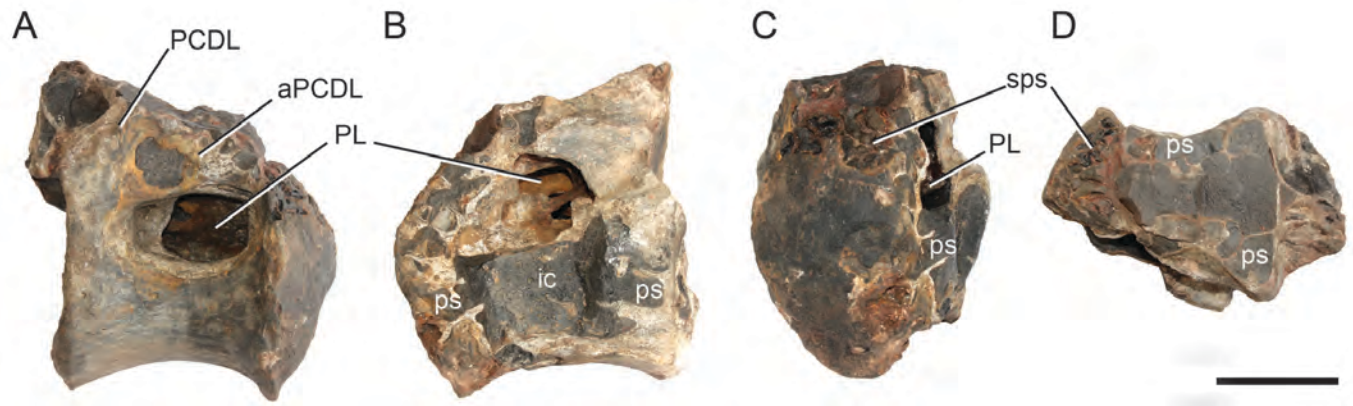


FIGURE 2. *Padillasaurus leivaensis*, JACVM 0001, middle to posterior dorsal vertebra in **A**, right lateral view; **B**, left lateral view; **C**, anterior view; **D**, dorsal view. **Abbreviations:** aPCDL, accessory posterior centrodiapophyseal lamina; ic, internal camera; PL, pleurocoel; ps, pneumatic space; sps, small pneumatic spaces; PCDL, posterior centrodiapophyseal lamina. Scale bar equals 100 mm.

the holotype have been preserved in three different segments that cannot be articulated with each other and include an isolated dorsal centrum (Fig. 2), an as yet unprepared block of three articulated vertebrae (provisionally identified as the last presacral and the two anterior-most sacral vertebrae), and 10 articulated vertebrae (the posterior-most two sacral and the anterior-most eight caudal vertebrae) (Fig. 3).

Dorsal Vertebrae

An almost complete and isolated dorsal centrum (Fig. 2) is here identified as part of a posterior dorsal vertebra. A possible second dorsal vertebra is preserved in a segment of three vertebrae, which are provisionally identified as the last presacral and the two anterior-most sacral vertebrae.

Isolated Dorsal Centrum—The isolated dorsal centrum is better preserved on its right lateral surface. The neural arch is almost entirely missing, exposing the internal pneumatic features of this vertebra (Fig. 2). As is evident on the right lateral surface, the parapophysis was not connected to the centrum, indicating that this element is a middle to posterior dorsal vertebra. The ventral surface of the centrum is slightly convex transversely, and no ventral ridge is present. The centrum is strongly opisthocoelous, with the concave posterior articular surface slightly wider than high (Table 1). The presence of opisthocoelous dorsal centra in mid- to posterior dorsal vertebrae is a synapomorphy of camarasauromorph sauropods (Salgado et al., 1997; Upchurch,

1998; Wilson and Sereno, 1998; D'Emic, 2012; Carballido and Sander, 2014). A marked fossa surrounds, ventrally and posteriorly, the deep pleurocoel, which is longer than high and has a rounded posterior edge (Fig. 2A). This is consistent with the generalized morphology present among non-titanosaur neosauropods. The pleurocoel opens into a large internal camera that communicates with smaller pneumatic spaces, as can be seen in dorsal and left lateral views (Fig. 2B, C). At the anterior-most region of the cotyle, the pneumatic cavities become smaller. The internal pneumatic spaces are very similar in shape and development to those described for the dorsal vertebrae of *Giraffatitan* (Janensch, 1947, 1950; MB.R. 4043) and to a slightly lesser degree those of *Tastavinsaurus*, which seems to have an intermediate condition between the polycamerate and camellate structures (Canudo et al., 2008; Royo-Torres, 2009:figs. 4.15 and 4.17). Considering the classification of pneumatic structures proposed by Wedel et al. (2000b), the morphology of this centrum more resembles the polycamerate system than the less advanced camerate system present in basal camarasauromorphs (e.g., *Camarasaurus*, *Tehuelchesaurus*, *Europasaurus*; Wedel, 2003; Carballido et al., 2011b; Carballido and Sander, 2014) or the more advanced camellate systems of derived somphospondylans (e.g., *Ligabuesaurus*, *Saltasaurus*; Bonaparte et al., 2006; Cerda et al., 2012).

Two single laminae are present in the preserved ventral region of the neural arch. These laminae are the posterior centrodiapophyseal lamina (PCDL), in which an anterior branch is tentatively interpreted as the accessory posterior centrodiapophyseal lamina (aPCDL). The presence of the aPCDL was initially considered a synapomorphy of titanosaur sauropods (Salgado et al., 1997), but its presence in other macronarian sauropods (e.g., *Tastavinsaurus*, *Brachiosaurus*) led to the recognition of a more widespread distribution of this lamina (Carballido et al., 2012; D'Emic, 2012). Some differences in the position of the accessory centrodiapophyseal lamina are observed. In most sauropods, as seems to be the case in *Padillasaurus*, the bifurcation of the PCDL occurs ventrally on the neural arch and the ventral edge of the accessory lamina extends on to the neural arch pedicels (e.g., *Epachthosaurus*, *Malawisaurus*, *Neuquensaurus*, *Tehuelchesaurus*; Martínez et al., 2004:fig. 4; Gomani, 2005:fig. 11; Salgado et al., 2005:fig. 4; Carballido et al., 2011b:figs. 6–8). On the other hand, the bifurcation of the centrodiapophyseal lamina of some sauropods, such as the brachiosaurids *Giraffatitan* (MB. R. 2181) and *Brachiosaurus* (FMNH P 25107), is more dorsally located and the accessory lamina does not reach the neural arch pedicels.

TABLE 1. Measurements (in cm) of the most complete axial elements of *Padillasaurus leivaensis*.

Element	PW	PH	APL	AS	PS	APL/PWH
Dorsal vertebra	25.0	20.0	22.0	CX	FL	0.97
5th? sacral vertebra	21.5	23.5	16.8	?	FL	0.75
1st caudal vertebra	20.5	22.0	11.5	FL	FL	0.55
2nd caudal vertebra	19.5	20.5	13.5	CC	FL	0.67
3rd caudal vertebra	18.5	19.0	11.0	CC	FL	0.58
4th caudal vertebra	17.0	18.0	11.0	CC	FL	0.62
5th caudal vertebra	16.0	17.0	11.3	CC	FL	0.68
6th caudal vertebra	14.5	16.0	11.5	CC	FL	0.75
7th caudal vertebra	13.0	15.0	12.0	CC	FL	0.85
8th caudal vertebra	13.5	13.5	12.5	CC	CC	0.92

Abbreviations: APL, anteroposterior length; AS, anterior articular surface; PH, posterior height; PS, posterior articular surface; PW, posterior width; PWH, average of the posterior width and height. The anterior and posterior articular surfaces can be: CC, concave; CX, convex; FL, flat.

Last Presacral Centrum—The anterior-most element of the segment, composed of three vertebrae, is considered the last dorsal vertebra given that its postzygapophysis is not fused with the prezygapophysis of the first sacral element. As such, this element is here considered as the last dorsal element instead of an unfused anterior sacral, because the degree of fusion present in the other sacral elements indicates an advanced ontogenetic stage (see Carballido and Sander, 2014). This vertebra preserves the posterior half of the centrum and the ventral segment of the neural arch. The preserved centrum does not differ from the isolated element described above, and also possesses large pleurocoels and polycamerate internal pneumatic spaces. The posterior centrodiaepophyseal lamina and the accessory centrodiaepophyseal lamina are also preserved in this vertebra. The development and orientation of these laminae is markedly similar to that of the isolated dorsal centrum, indicating a close position of these elements to one another within the dorsal series of the axial skeleton.

Sacrum

Five sacral vertebrae are commonly present in non-titanosaur sauropods (Salgado et al., 1997; Upchurch, 1998; Wilson and Sereno, 1998), and, based on our identifications and assuming five sacral elements for *Padillasaurus*, the specimen described here preserves remains of the two anterior-most (in one block) and the two posterior-most of these vertebrae (in another block). The centra of the first, second, and fifth sacral vertebrae are complete, whereas the fourth sacral centrum is only represented by a small posterior fragment of its cotyle (Figs. 3, 4). The two anterior centra and the two posterior centra are strongly fused to each other. The limit of each centrum, however, is recognized based on the presence of a slight convexity on its lateral surface (Fig. 4A). The fusion indicates an advanced ontogenetic stage for this individual. The first and second sacral vertebrae have pleurocoels, and



FIGURE 3. *Padillasaurus leivaensis*, JACVM 0001, articulated sequence of the posterior-most two sacral vertebrae (S4 and S5) and the first eight caudal vertebrae (C1–C8), in **A**, left lateral view; **B**, right lateral view. Scale bar equals 100 mm.

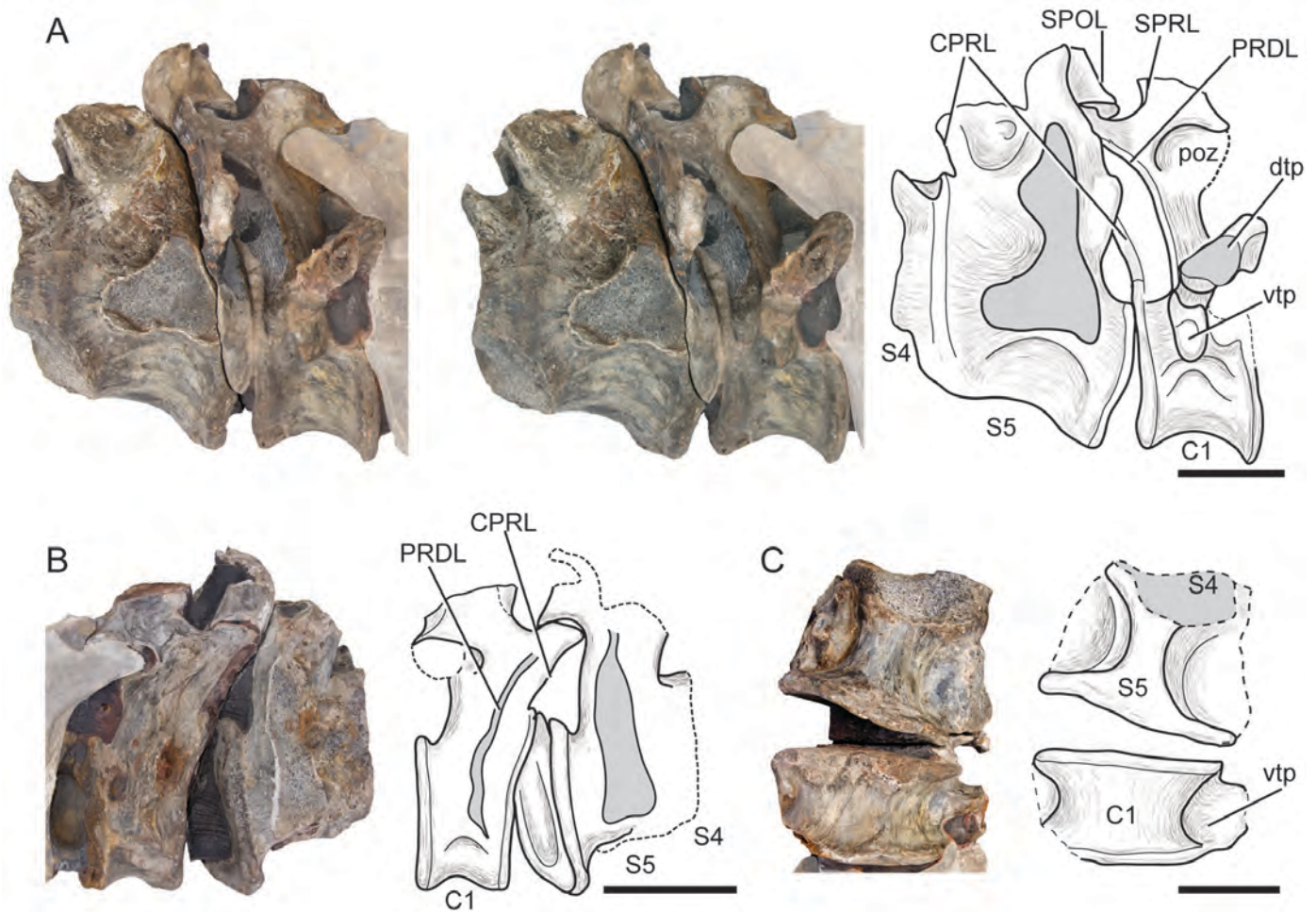


FIGURE 4. *Padillasaurus leivaensis*, JACVM 0001, posterior-most sacral and first caudal vertebrae in **A**, left lateral view; **B**, right lateral view; **C**, ventral view. **Abbreviations:** CPRL, centroprezygapophyseal lamina; **dtp**, dorsal segment of the transverse process; **poz**, postzygapophyses; **PRDL**, prezygodiapophyseal lamina; **SPOL**, spinopostzygapophyseal lamina; **SPRL**, spinoprezygapophyseal lamina; **vtp**, ventral segment of the transverse process. Scale bar equals 100 mm.

the broken surfaces of their neural arches show the presence of polycamerate internal pneumatic cavities (which are virtually identical to those of the isolated dorsal centrum). By contrast, the fourth and fifth sacrals and the caudal vertebrae lack internal pneumaticity. Based on these pneumatic features, the first two sacral elements are here considered as dorsosacral vertebrae. Thus, without taking into account a somitogenetic process in the sacralization of sauropods (Müller et al., 2010; Carballido and Sander, 2014), the morphology of the sacral vertebrae of *Padillasaurus* is congruent with the sacralization process proposed by Wilson and Sereno (1998), in which two dorsals and one caudal vertebra are incorporated into the sacrum alongside the two primordial sacral elements. The recognition of two dorsosacrals and one caudosacral has been relatively common among sauropods, although some taxa seem to have a different pattern (one dorsosacral and two caudosacrals; e.g., McIntosh et al., 1996; Carballido et al., 2011b).

The fifth sacral vertebra lacks the neural spine and the transverse processes (Fig. 4). Its posterior articular surface is flat. The sacral transverse processes are eroded, but their broad base indicates that they extended along most of the centrum and neural arch (Figs. 4A, B). A deep depression is present below the transverse process of the fifth sacral

(Fig. 4A). The ventral surface of this sacral vertebra is narrow and strongly convex transversely (Fig. 4C). The centroprezygapophyseal and prezygodiapophyseal laminae are recognized on the left lateral surface, but both are poorly preserved. Above the postzygapophysis there is a well-developed spinopostzygapophyseal lamina and an anteroposteriorly short but well-defined postspinal lamina.

Caudal Vertebrae

The eight preserved caudals are almost complete except for the dorsal regions of their neural spines and their right transverse processes. All caudals lack any sign of internal pneumaticity, unlike the condition in derived titanosaurs, where caudal pneumaticity is present (Cerdeña et al., 2012).

First Caudal Vertebra—The first caudal vertebra is almost complete except for the dorsal section of its neural spine. Both the anterior and the posterior articular surfaces of the centrum are slightly concave, resembling the platycoelous condition (sensu Romer, 1956) of the first caudal vertebrae of most non-titanosaur and non-diplodocoid sauropods (Salgado et al., 1997; Wilson, 2002; Upchurch et al., 2004). The ventral surface of the centrum is slightly convex transversely (Fig. 4C), differing from the strong convexity of the ventral surface of the fifth sacral

vertebra. The centrum has a deep depression underneath the transverse process, but its margins lack the deep blind fossa present in the second caudal vertebra (see below; Fig. 5A). The transverse process, which extends from the dorsal half of the centrum to the ventral section of the neural arch, is mostly complete (except for the lateral tip of its dorsal segment; Fig. 4A). The transverse process of the anterior caudal of *Padillasaurus* is mediolaterally short, in contrast to most sauropods, which have a mediolaterally extensive transverse process in the anterior caudals (with a mediolateral length that is approximately 50% of the mediolateral width of the centrum; e.g., *Giraffatitan*, *Venenosaurus*, *Europasaurus*; Janensch, 1950:pl. 2; Tidwell et al., 2001: fig. 11.3; Carballido and Sander, 2014:fig. 26). The transverse process is divided into dorsal and ventral branches. These two well-differentiated branches at the lateral end of the transverse process are also well developed in the second caudal (see below). The ventral branch projects laterally, whereas the dorsal branch is posterodorsally directed. The two branches are separated by a well-marked recess or step, which is pronounced in anterior, posterior, and lateral views (Fig. 4A). The presence of laterally forked transverse processes in *Padillasaurus* is here regarded as an autapomorphy of this taxon.

The ventral branch of the transverse process is here interpreted as an extremely developed condition of the ‘ventral bulge’ commonly present among titanosauriform sauropods (Chure et al., 2010; D’Emic, 2012). The presence of a ventral bulge in the transverse process of the first caudal vertebra of *Brachiosaurus* (FMNH P 25107) and *Giraffatitan* (MB.R. 2921) was first noted by Wilson (2002), who considered this bulge to be an apomorphic character of these two taxa (which were referred to the same genus at that time). More recently, Chure et al. (2010) recognized the presence of a ventral bulge in *Abydosaurus* and identified this character as a synapomorphy of Brachiosauridae. Nevertheless, the presence of a ventral bulge in the transverse processes of anterior caudal vertebrae (especially in the first caudal) has been recognized in other titanosauriforms and was most recently proposed as a synapomorphy of Titanosauriformes (with a reversal in derived titanosaurs; D’Emic, 2012; Mannion et al., 2013). Therefore, *Padillasaurus* shares with several basal titanosauriforms the ventral bulge on the transverse process of anterior caudal vertebrae, but has the unique condition of having it much more developed.

The posterior edge of the dorsal branch of the transverse process of *Padillasaurus* almost reaches the level of the posterior articular surface of the centrum. A posterior position of the transverse process is a character shared by titanosauriform sauropods (Mannion and Calvo, 2011; D’Emic, 2012). The posterior orientation of the transverse process in some non-titanosauriforms (e.g., *Europasaurus*, *Galvesaurus*, *Tastavinsaurus*; Mannion et al., 2013; Carballido and Sander, 2014) indicates that this character is in fact shared by camarasauromorph sauropods (Carballido and Sander, 2014). Nonetheless, the dorsal branch of the transverse process of *Padillasaurus* differs from that of other camarasauromorphs (e.g., *Europasaurus*, *Giraffatitan*, *Venenosaurus*, *Cedarosaurus*) in being strongly dorsally orientated in the first two caudal vertebrae.

The neural arch is anteriorly positioned, as in derived camarasauromorph sauropods (Carballido and Sander, 2014). A prominent and well-developed prezygodiapophyseal lamina extends from the anterodorsal section of the ventral bulge of the transverse process up to the prezygapophysis (Fig. 4A, B). Wilson (2002) listed the presence of a prominent prezygodiapophyseal lamina as an autapomorphic character of *Brachiosaurus*, which he considered to include *Brachiosaurus altithorax* and *Giraffatitan brancai* (this character is present and well developed in the first and second caudal vertebrae of *G. brancai* [MB.R. 2921] and in the second caudal of *B. altithorax* [FMNH P 25107]). More recently, Chure et al. (2010) identified the presence of this

lamina as a titanosauriform synapomorphy. A similar development of the prezygodiapophyseal lamina in anterior-most caudal vertebrae (mainly the first two elements) is also present in other camarasauromorphs, such as *Tastavinsaurus* (Royo-Torres, 2009:fig. 4.52) and *Venenosaurus* (Tidwell et al., 1999: fig. 11.3). A subtle difference exists between the condition of *Padillasaurus* and other sauropods with well-developed prezygodiapophyseal laminae. In the former, the lamina does not reach the dorsal margin of the prezygapophysis but converges with the centroprezygapophyseal lamina. The centroprezygapophyseal lamina ventrally supports the prezygapophysis, which extends slightly beyond the anterior articular surface of the centrum (Fig. 4B).

The ventral part of the neural spine is preserved, allowing the recognition of the spinal laminae. The spinoprezygapophyseal lamina extends posterodorsally from the prezygapophysis and vanishes along the anterolateral surface of the neural spine. The prespinal lamina extends dorsally from the base of the neural spine, as in other sauropods. Posteriorly, the neural spine is formed by the spinopostzygapophyseal laminae. The postspinal lamina is absent. The base of the neural spine is positioned posteriorly with respect to the anterior articular surface of the centrum.

Anterior Caudal Vertebrae (Second to Eighth)—In contrast to the slightly concave posterior surface of the first caudal centrum, the posterior surfaces of the second to seventh caudals are flat and the anterior articular surfaces are concave. The anterior articular surface of the eighth caudal vertebra is also concave, but the posterior surface is slightly concave, resembling the platycoelous condition of the first caudal centrum and differing from the flat posterior surface of preceding caudal centra. Based on their articular surfaces, these centra can be identified as procoelous/distoplatyan, as defined by Tidwell et al. (2001). These authors, and more recently González Riga et al. (2009) and Carballido et al. (2011a), considered this character as only occurring in a few camarasauromorph taxa (e.g., *Cedarosaurus*, *Malarguesaurus*, *Chubutisaurus*). Nevertheless, anteriorly concave and posteriorly flat articular surfaces are actually present in other basal camarasauromorphs (e.g., *Giraffatitan*, *Galvesaurus*, *Tastavinsaurus*; Carballido et al., 2012; D’Emic, 2012). In contrast, the derived clade Titanosauria is characterized by the presence of slightly to strongly procoelous (anteriorly concave and posteriorly convex; sensu Romer, 1956) caudal vertebrae (Salgado et al., 1997; González Riga et al., 2009), with the exception of taxa such as *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977), which have opisthocoelous caudals. The centrum length increases slightly along the caudal series, whereas the width of the posterior articular surface decreases. Therefore, the ratio of the anteroposterior length/mediolateral width of the posterior centrum increases posteriorly along the preserved caudal vertebrae (Table 1), a common pattern in sauropod caudal vertebrae (e.g., *Giraffatitan*, *Cedarosaurus*; Janensch, 1950; Tidwell et al., 1999).

As in the first caudal centrum, the anterior caudal vertebrae have lateral depressions underneath the transverse process, which in the second and the fourth caudal vertebrae bear a blind and well-delimited fossa. Therefore, pneumatic hiatuses are recognized throughout the anterior caudal series of *Padillasaurus*, as was also recently noted for *Giraffatitan* (Wedel and Taylor, 2013). In the second caudal centrum, the fossa is 3 cm long, 2 cm high, and 2 cm deep, being slightly smaller in the fourth caudal (Fig. 6). The shape and position of the lateral fossa of the second caudal is remarkably similar to the blind fossa present in the second caudal vertebra of some specimens of *Giraffatitan* (MB.R. 2921.2; Wedel and Taylor, 2013). In contrast, the second caudal centrum of *Brachiosaurus* lacks such blind fossae (Taylor, 2009; FMNH P 25107). The presence of blind lateral fossae on anterior caudal vertebrae was noted by Tidwell et al. (1999) for

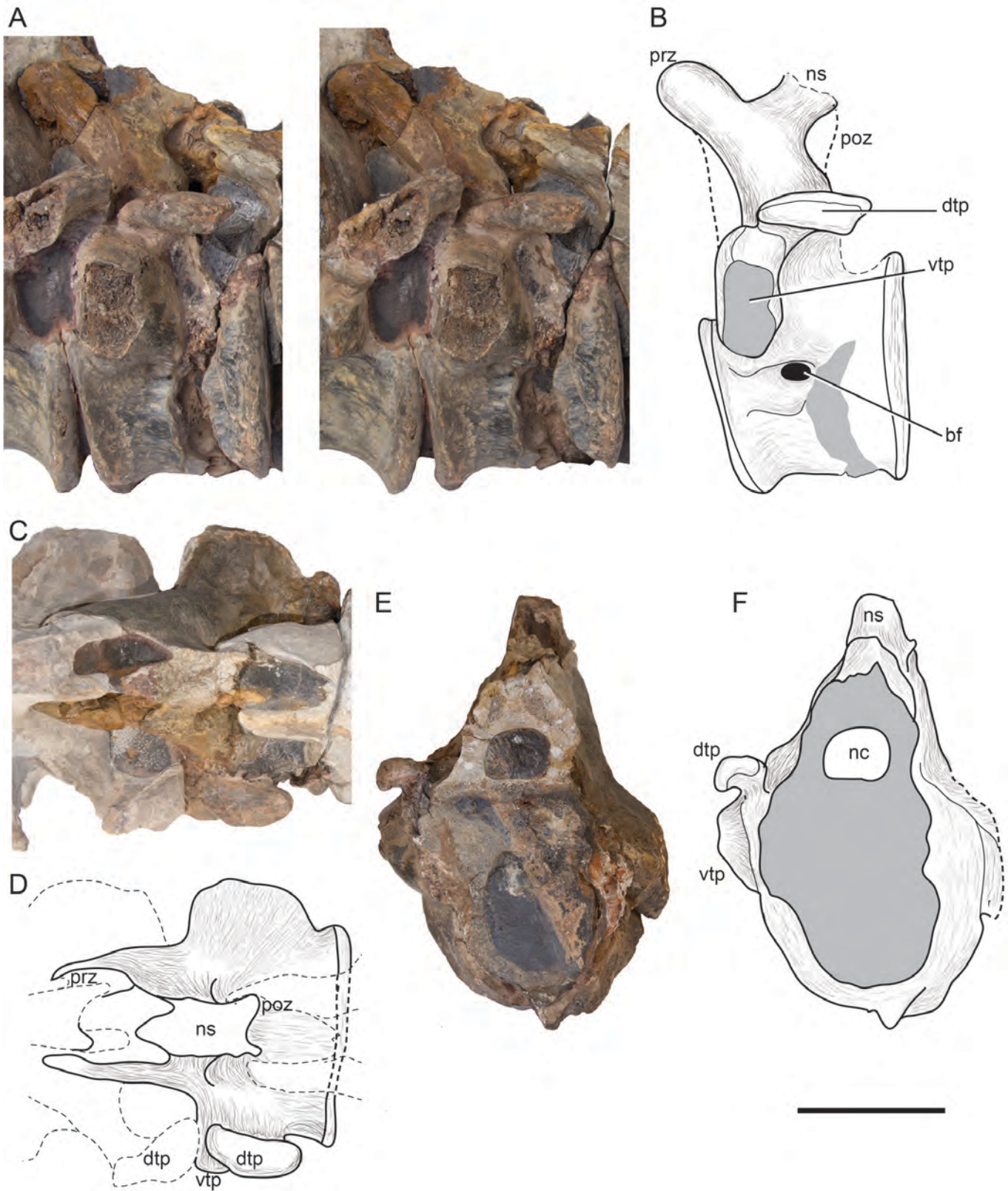


FIGURE 5. *Padillasaurus leivaensis*, JACVM 0001, second caudal vertebra in **A, B**, left lateral view; **B–D**, dorsal view; **E, F**, posterior view. **Abbreviations:** bf, blind fossa; dtp, dorsal segment of the transverse process; nc, neural canal; ns, neural spine; poz, postzygapophyses; prz, prezygapophyses; vtp, ventral segment of the transverse process. Scale bar equals 100 mm.

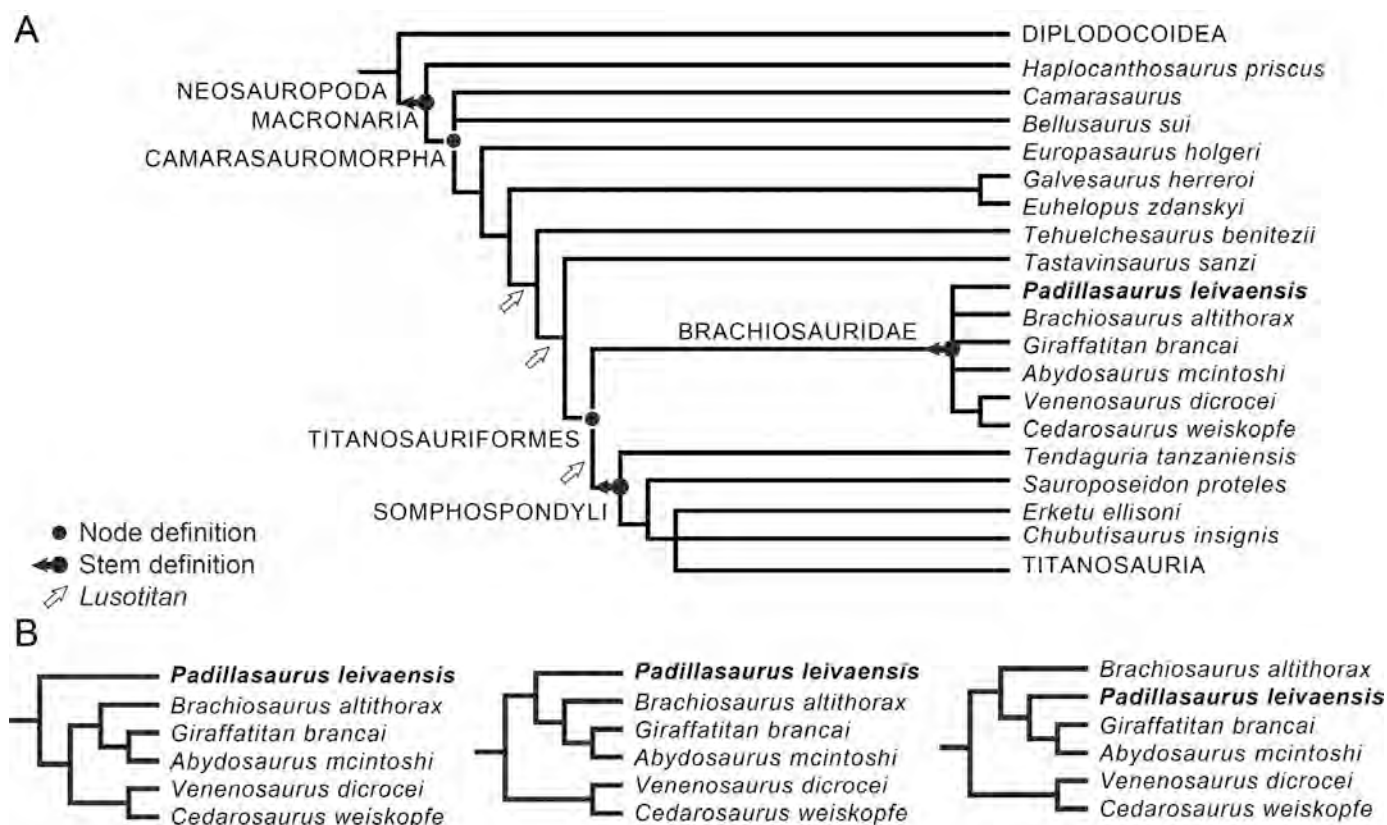


FIGURE 6. Phylogenetic relationships of *Padillasaurus leivaensis* within basal Camarasauromorpha, showing **A**, the strict consensus tree of the 10 most parsimonious trees of 1075 steps; **B** different positions that *Padillasaurus* can occupy within Brachiosauridae.

Cedarosaurus and subsequently by Tidwell et al. (2001) for *Venenosaurus*. In *Abydosaurus*, blind fossae are present on anterior caudal vertebrae (D'Emic, 2012), although they are not as deep as those of *Venenosaurus* (Chure et al., 2010). Based on this character distribution, D'Emic (2012) recently recovered the presence of blind fossae in caudal vertebrae as a brachiosaurid synapomorphy. Due to the discontinuous presence of this character within the caudal series, it cannot be confirmed if it was present in *Brachiosaurus*, because its holotype only preserves the two anterior-most caudal vertebrae. The morphology of the relatively small and more sporadically present blind fossae of *Padillasaurus* more closely resembles the condition of some specimens of *Giraffatitan* (see Wedel and Taylor, 2013), than the larger and more continually present fossae of *Venenosaurus* and *Cedarosaurus* (Tidwell et al., 1999; Tidwell et al., 2001).

As for the first caudal vertebra, the preserved transverse processes of the second, third, and fifth caudals are mediolaterally short and divided into ventral and dorsal branches (Fig. 6C), both unique characters of *Padillasaurus*. In the other caudal vertebrae, the transverse processes are broken and this condition cannot be evaluated. The division of the transverse process is most strongly developed in the second caudal vertebra (Fig. 5). Whereas in the third and fifth caudal vertebrae the division of the transverse process is marked by a gently developed step, in the second caudal vertebra there is a prominent and deep recess dividing the distal end of the transverse process (Fig. 5A, C). The ventral branch of the transverse process, or hypertrophied ventral bulge, is much larger than the dorsal branch. The dorsal branch is posterodorsally directed, but not as dorsally deflected as in the first caudal. In posterior view (Fig. 5C), the deep step formed between the ventral and dorsal

branches of the transverse process resembles the foramen described for *Lusotitan* (Mannion et al., 2013:fig. 5), but in *Padillasaurus* this is clearly open laterally, not closed as interpreted in *Lusotitan*.

The neural arches of all preserved caudal vertebrae are anteriorly positioned, with the anterior edge located at the same level as the anterior articular surface of the centrum. Although not completely preserved, the bases of the neural spines are posteriorly positioned with respect to the anterior articular surface of the centrum. A similar condition is widespread among camarasauromorph dinosaurs (e.g., *Europasaurus*, *Giraffatitan*, *Malguesaurus*; Carballido and Sander, 2014) but differs from the more anteriorly positioned neural spine of *Tastavinsaurus* (Royo-Torres, 2009:figs. 4.51, 4.62) and the brachiosaurids *Cedarosaurus* (Tidwell et al., 1999:fig. 3) and *Venenosaurus* (Tidwell et al., 2001:fig. 11.4). The anterior position of the neural spine seems to be related to the more vertical or anterior direction of the neural spine of these taxa. In contrast, the neural spines of *Padillasaurus* are posterodorsally oriented, as is evident from the preserved section of the neural spine of the second caudal. This condition resembles that of most camarasauromorphs (e.g., *Giraffatitan*, '*Paluxysaurus*,' *Europasaurus*; Janensch, 1950; Rose, 2007; Carballido and Sander, 2014).

DISCUSSION

Phylogenetic Relationships of *Padillasaurus*

The specimen JACVM 0001 bears unique characters allowing the recognition of a new sauropod species, *Padillasaurus leivaensis*, which shares derived characters with titanosauriform

sauropods, and, in particular, with brachiosaurids. In order to test the phylogenetic position of *Padillasaurus*, a phylogenetic analysis was conducted through the inclusion of the new taxon in a modified version of the matrix recently used by Carballido et al. (2012) and Carballido and Sander (2014). The complete list of modifications is detailed in Supplementary Data 1 and mainly includes the incorporation of the camarasauromorphs *Abydosaurus* and *Lusotitan*, minor changes in character definitions, and the inclusion of seven new characters and 22 characters from the data set recently published by D'Emic (2012). The terminal taxon '*Paluxysaurus*' and its scorings were revised following the synonymy of this taxon with *Sauroposeidon* as recently proposed by D'Emic (2013). The data set includes the taxon *Sauroposeidon*, and its character scorings were based on the available published information (Rose, 2007; Wedel et al., 2000a, 2000b; D'Emic and Foreman, 2012). The final data matrix was composed of 370 characters and 72 taxa. Characters 12, 58, 95, 96, 106, 108, 115, 116, 120, 145, 152, 163, 213, 216, 232, 233, 234, 252, 256, 299, and 301 were treated as ordered.

The phylogenetic analysis was conducted through an equally weighted parsimony analysis using TNT 1.1 (Goloboff et al., 2008a, 2008b). The heuristic tree search was performed starting from 1000 replicates of Wagner trees (with random addition sequence of taxa) followed by tree bisection-reconstruction (TBR) branch swapping (saving 10 trees per replicate). This procedure recovered 50 most parsimonious trees (MPTs) of 1075 steps, which were found in 231 of the 1000 replicates. An additional round of branch swapping was performed among the saved trees but failed to find additional MPTs. The strict consensus tree (see Supplementary Data 1) has some minor differences with respect to that of Carballido and Sander (2014). Most of these differences involve taxa that were identified by that previous analysis as unstable and therefore related to the low nodal support obtained among camarasauromorphs (Carballido and Sander, 2014). One of these changes is the recovery of *Sauroposeidon* as a basal somphospondylan, in a similar position to that recovered for this taxon by D'Emic (2012) and outside Brachiosauridae (as recovered for its junior synonym '*Paluxysaurus*' by Carballido and Sander, 2014:fig. 29). *Lusotitan* was recovered in three different positions among camarasauromorphs: as sister taxon of *Tastavinsaurus* and more derived camarasauromorphs; as the sister taxon of Titanosauriformes; and as a basal Somphospondyli. This result is more congruent with the LCDM (*Lusotitan* continuous + discrete matrix) analysis performed by Mannion et al. (2013) in which this taxon was recovered as the sister taxon to Titanosauriformes.

All the MPTs recovered *Padillasaurus* as a brachiosaurid sauropod, forming part of an unresolved polytomy in the strict consensus tree with *Abydosaurus*, *Giraffatitan*, *Brachiosaurus*, and the clade formed by *Venenosaurus* and *Cedarosaurus* (Fig. 6A). This polytomy is caused by the alternative positions that *Padillasaurus* takes within Brachiosauridae (Fig. 6B). In the MPTs, *Padillasaurus* is placed in alternative positions among the basal branches of Brachiosauridae, ranging from the very base of the clade up to a position as the sister taxon to *Abydosaurus* + *Giraffatitan* (Fig. 6B). Based on the results of the IterPCR method (Pol and Escapa, 2009), the alternative positions that *Padillasaurus* occupies among the MPTs are due to the lack of information (incompleteness) of this taxon rather than to character conflict. It must be noted that due to the incompleteness of the material, the inclusion of *Padillasaurus* in Brachiosauridae is not robustly supported, and only one extra step is required to place *Padillasaurus* among basal camarasauromorphs more derived than *Tehuelchesaurus* and basal to *Sauroposeidon*. If *Padillasaurus* is forced to occupy even more basal (basal macronarian or non-neosauropod) or derived (among titanosaurs) positions, two or more extra steps are required, providing support for its affinities among basal camarasauromorphs. Nonetheless, given the

available information, the position of *Padillasaurus* within Brachiosauridae is the most parsimonious interpretation and is supported by the presence of derived features shared with this clade (see below).

In the present analysis, as in Carballido and Sander (2014), *Europasaurus* is placed as a basal camarasauromorph (outside Brachiosauridae), a position that is supported by the presence of several plesiomorphic characters and the absence of brachiosaurid apomorphies (see Carballido and Sander, 2014; Marpmann et al., 2014).

Brachiosauridae is here supported by one unambiguous synapomorphy for all trees: presence of a blind lateral fossa in anterior caudal vertebrae (character 359). Additionally, two extra synapomorphies are recovered for some trees: (1) ratio of humerus length to femur length greater than 0.9 (character 252; in some trees due to absence of information in *Padillasaurus*); and (2) distal end of metatarsal IV dorsomedially oriented (character 370; in some trees due to absence of information in *Padillasaurus*). Among these characters, the presence of blind fossae in *Padillasaurus* supports its inclusion among brachiosaurids (Fig. 6B). It is important to note that although pneumatic axial characters were described for other titanosauriforms (e.g., Cerda et al., 2012; Wedel and Taylor, 2013), the presence of blind fossae has so far only been reported for brachiosaurid titanosauriforms.

Venenosaurus and *Cedarosaurus* are recovered as sister taxa, in agreement with the recent analysis published by D'Emic (2012). The exclusion of *Padillasaurus* from the *Venenosaurus* + *Cedarosaurus* clade is supported by the lack of anteriorly oriented neural spines in caudal vertebrae (an unambiguous synapomorphy of this clade; character 213). *Padillasaurus* has the plesiomorphic state for this character, because the neural spines of caudal vertebrae are posterodorsally oriented.

In the present analysis, *Brachiosaurus*, *Giraffatitan*, and *Abydosaurus* are recovered as a monophyletic assemblage in all MPTs (with the possible inclusion of *Padillasaurus*; see Fig. 6B). The phylogenetic position of these taxa varies among recently published analyses (e.g., D'Emic, 2012; Mannion et al., 2013; Carballido and Sander, 2014; Fig. 6B). Part of these differences may reflect the inclusion or exclusion of cranial information for *Brachiosaurus altithorax* (see Supplementary Data 1), as well as differences in character and taxon sampling among these studies. In our analysis, the clade formed by *Brachiosaurus*, *Giraffatitan*, and *Abydosaurus* is supported by a single unambiguous synapomorphy: femur head perpendicular to the femur shaft (character 304), a reversal to the plesiomorphic condition present in basal neosauropods and outgroups. A single synapomorphic character supports the monophyly of *Abydosaurus* and *Giraffatitan*: the width of the parietal surface that separates the supratemporal fenestrae is less than the long axis of the supratemporal fenestra (character 42). This character was recently recovered as synapomorphic for Brachiosauridae (including *Europasaurus*) by D'Emic (2012). Nevertheless, in *Europasaurus*, the long axis of the supratemporal fenestrae is subequal to the parietal width, as in most non-diplodocoids and non-titanosaur sauropods (see Marpmann et al., 2015).

The Paleogeographic Distribution of Brachiosauridae

Although the first undisputed brachiosaurid records are from the Late Jurassic (*Giraffatitan*, *Brachiosaurus*), the origin of this clade has generally been regarded as extending back to the Middle Jurassic, before the beginning of the fragmentation of Pangea (e.g., Wilson and Sereno, 1998; Day et al., 2002; D'Emic, 2012; Mannion et al., 2013). This interpretation is mainly based on the broad distribution of Brachiosauridae during the Late Jurassic (see Mannion et al., 2013). Late Jurassic unequivocal brachiosaurid taxa are known from North America (*Brachiosaurus* Riggs,

1903) and Africa (*Giraffatitan* [Janensch, 1914]). In addition to these well-known taxa, other more fragmentary Late Jurassic sauropod remains from Europe are currently considered as brachiosaurids, increasing the diversity and distribution of the clade during this time. One of these records is the 'French *Bothriospondylus*' from the Oxfordian of France (Lapparent, 1943), which was recently identified as a brachiosaurid (Mannion et al., 2013), and which represents the oldest record of this group. A second possible brachiosaurid from the Late Jurassic of Europe is *Lusotitan atalaiensis* from the Kimmeridgian of Portugal (Antunes and Mateus, 2003), which was placed within brachiosaurids in the LCDM analyses carried out by Mannion et al. (2013), but outside this clade in the present analysis (see above). Finally, a possible brachiosaurid has also been reported from the Late Jurassic of South America. Rauhut (2006) described fragmentary sauropod materials from the Cañadón Calcáreo Formation of Patagonia (Oxfordian–Kimmeridgian) and referred it to Brachiosauridae, although there is no current agreement on the brachiosaurid affinities of these remains (D'Emic, 2012; Mannion et al., 2013). Despite the uncertainties regarding the affinities of some of the more fragmentary material, it is clear from the fossil record that undisputed brachiosaurid remains were present during the Late Jurassic in both the northern (North America, Europe) and southern (Africa) hemispheres.

Despite the widespread distribution of brachiosaurids during the Late Jurassic, they have a much more restricted distribution during the Early Cretaceous. Up to now, Cretaceous brachiosaurids were exclusively known from the Aptian–Albian of North America (*Venenosaurus*, *Cedarosaurus*, and *Abydosaurus*; Tidwell et al., 1999, 2001; Chure et al., 2010). This Early Cretaceous distribution has been interpreted as a product of local extinctions in Europe, Africa, and South America (Wilson and Sereno, 1998; D'Emic, 2012). Mannion et al. (2013), however, recently noted that this absence could also be caused by a bias in the poor Early Cretaceous sauropod fossil record, and noted the presence of two isolated teeth from the Early Cretaceous of Lebanon (Buffetaut et al., 2006) that have posteriorly twisted crowns as in the brachiosaurids *Giraffatitan* and *Abydosaurus* (Chure et al., 2010; D'Emic, 2012).

The Early Cretaceous is indeed a period of low sauropod diversity worldwide, especially for the earliest Cretaceous and in comparison with the high diversity recorded in the Late Jurassic (Mannion et al., 2011). Whether or not this decrease is the product of truly low diversity following an extinction event at the Jurassic/Cretaceous boundary or is mainly controlled by sampling biases is unclear at the moment (Mannion et al., 2011). New records and a more complete knowledge of the Early Cretaceous sauropod faunas will be critical to thoroughly test these alternative explanations (including the extent of the local extinctions of brachiosaurids after the Late Jurassic).

The brachiosaurid affinities of *Padillasaurus leivaensis* from the Early Cretaceous (Barremian) of Colombia (recovered here in all most parsimonious hypotheses, although with low character support) are relevant to these questions, because they suggest that this clade survived in northwestern Gondwana after the Jurassic/Cretaceous boundary. Furthermore, considering also the putative brachiosaurid teeth from Lebanon (Buffetaut et al., 2006; Mannion et al., 2013), it is possible that brachiosaurids actually survived into the Cretaceous at low latitudes in all of northern Gondwana. During the Early Cretaceous, Colombia was located close to the equator in northwestern Gondwana (Scotese, 2001) and Lebanon was part of the Afro-Arabian plate in northeastern Gondwana (Buffetaut et al., 2006; Ksepka and Norell, 2010; Mannion et al., 2013).

In more general terms, this new information, coupled with the recent discovery of a diplodocid from the Early Cretaceous of southern South America (Gallina et al., 2014), suggests that part of the high sauropod diversity recorded during the Late Jurassic

survived the Jurassic/Cretaceous extinction event recognized by Raup and Sepkoski (1986). The rarity of these sauropod records in the Early Cretaceous may reflect a decrease in diversity and abundance of these lineages in combination with an overall poorer fossil record (especially in Gondwana).

CONCLUSIONS

The vertebral remains described here allow the recognition of *Padillasaurus leivaensis*, a new titanosauriform taxon from the Early Cretaceous of Colombia. This record provides the first informative dinosaurian record for the Early Cretaceous of northern South America, which was previously limited to a single sauropod vertebra of uncertain affinities. The comparative and phylogenetic analyses performed place the new taxon within Brachiosauridae in all most parsimonious hypotheses, although the character support for its position is weak given the incompleteness of some skeletal regions that would be phylogenetically informative (e.g., humerus, femur, metatarsus).

The brachiosaurid affinities of *Padillasaurus* are relevant for understanding the biogeographic history of this group given that this clade of titanosauriform sauropods is broadly distributed during the Late Jurassic but has a markedly restricted distribution during the Early Cretaceous. In particular, these remains provide support for considering the apparent absence of brachiosaurids outside North America during the Early Cretaceous to be due to a deficient fossil record rather than due to local extinctions (at least in northern Gondwana).

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