

The southernmost records of Rebbachisauridae (Sauropoda: Diplodocoidea), from early Late Cretaceous deposits in central Patagonia

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ABSTRACT

We describe new and redescribe previously discovered sauropod dinosaur material from the Upper Cretaceous (middle Cenomanian–Turonian) Bajo Barreal Formation of south-central Chubut Province, central Patagonia, Argentina. The remains consist of associated and isolated axial skeletal elements recovered from three separate localities, and are herein assigned to the morphologically aberrant Rebbachisauridae clade. Several of the fossils exhibit osteological characters that were previously undocumented in rebbachisaurids, enhancing our understanding of the morphological diversity of this enigmatic sauropod group. In particular, the Bajo Barreal material demonstrates the occurrence within Rebbachisauridae of bifurcate neural spines in cervical vertebrae and well-developed, presumably pneumatic fossae in caudal vertebrae; among Diplodocoidea, these distinctive morphologies had previously been recognized only in flagellicaudatans. Furthermore, the Bajo Barreal fossils constitute the southernmost known occurrences of Diplodocoidea, adding to the globally sparse Late Cretaceous record of these sauropods and augmenting our knowledge of central Patagonian terrestrial vertebrate assemblages during this interval.

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1. Introduction

The fossil record of sauropod dinosaurs in the Cretaceous of South America is diverse and well represented. Although titanosaurs are by far the most common South American Cretaceous sauropods (Salgado and Bonaparte, 2007), remains of diplodocoids are also relatively abundant during the early and middle stages of the period (Novas, 2009). The South American diplodocoid record includes members of Rebbachisauridae (a poorly known lineage with bizarre craniodental specializations; see Sereno et al., 2007) and the short-necked, tall-spined Dicraeosauridae, as well as taxa of uncertain systematic position, such as *Zapalasaurus bonapartei* (Salgado et al., 2006a).

Bonaparte (1997) was the first to recognize Rebbachisauridae as a distinct sauropod clade; based on their analysis of *Limaysaurus* (= *Rebbachisaurus*) *tessonei*, Calvo and Salgado (1995) were the first to support cladistically the relationship between rebbachisaurids

and diplodocids. Most rebbachisaurids, including the first-reported member of the group, *Rebbachisaurus garasbae* (Lavocat, 1954), are known only from fragmentary or incompletely described fossils. Exceptions include another North African form, *Nigersaurus taqueti* (Sereno et al., 1999, 2007; Sereno and Wilson, 2005), and the Argentinean genus *Limaysaurus* (Calvo and Salgado, 1995; Calvo, 1999; Salgado et al., 2004), from the Early and middle Cretaceous, respectively. Although recently described specimens of these and other taxa have added substantial morphological and phylogenetic information to our understanding of Rebbachisauridae, the ingroup relationships of the clade have yet to be completely deciphered (Gallina and Apesteguía, 2005; Mannion, 2009;). Rebbachisauridae is typically recovered as the sister taxon of Flagellicaudata, the group that unites Diplodocidae and Dicraeosauridae (Harris and Dodson, 2004; Salgado and Bonaparte, 2007). Thus, although depending of the authors, rebbachisaurids are widely considered to be a basal lineage within Diplodocoidea (e.g., Wilson, 2002; Upchurch et al., 2004a).

Here we report on newly identified rebbachisaurid axial skeletal remains from sediments of the Upper Cretaceous (middle Cenomanian–Turonian) Bajo Barreal Formation exposed at three

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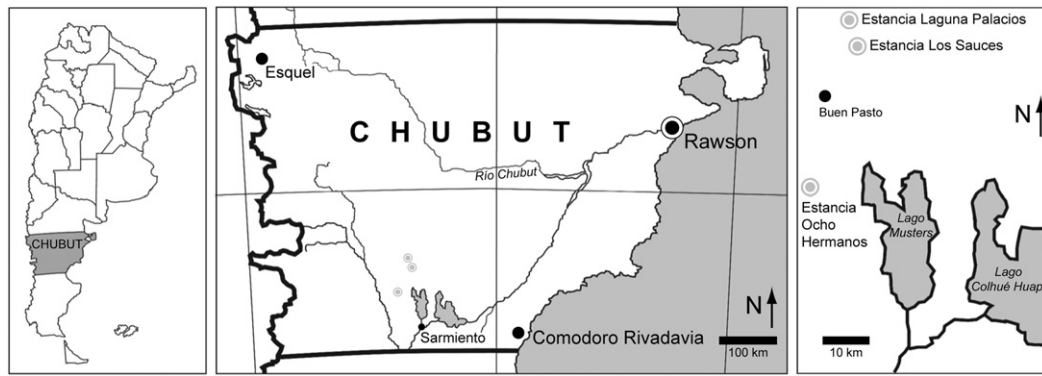


Fig. 1. Map of Chubut Province, in central Patagonia, Argentina, showing locations of sites where rebbachisaurid fossils described herein were discovered (the estancias Laguna Palacios, Los Sauces, and Ocho Hermanos).

localities in south-central Chubut Province, central Patagonia, Argentina (Fig. 1), and discuss the implications of this material for diplodocoid morphological diversity, evolution, and paleobiogeography. The fossils are significant in that they (1) add to the generally sparse global record of Cretaceous, especially Late Cretaceous, diplodocoids; (2) constitute the southernmost occurrences of Diplodocoidea worldwide; (3) exhibit osteological characters that have never previously been documented in Rebbachisauridae, some of which also occur in Flagellicaudata; and (4) establish the presence of rebbachisaurids in the Bajo Barreal Formation, which enlarges the known fossil fauna of this unit and therefore broadens our knowledge of the early Late Cretaceous continental vertebrate assemblages of central Patagonia.

Repository abbreviations. MIWG, Museum of Isle of Wight Geology; MMCH, Museo Municipal Ernesto Bachmann, Villa El Chocón; MPCA, Museo Provincial Carlos Ameghino, Cipolletti; MPS, Museo de Dinosaurios–Paleontología, Salas de los Infantes, Burgos; MOZ, Museo Profesor Dr. Juan A. Olsacher, Zapala; UFMA, Universidade Federal do Maranhão, São Luís; UNPSJB, Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia.

2. Geological setting

The south-central region of Chubut Province, Argentina exposes excellent outcrops of continental Cretaceous sedimentary sequences that were deposited in the San Jorge Basin. Cretaceous strata in the basin include (in ascending order) the D-129, Matasiete, Castillo, Bajo Barreal, and Laguna Palacios formations. The Bajo Barreal Formation, which transitionally overlies the Castillo Formation and underlies the Laguna Palacios Formation, is of particular paleontological and biostratigraphic interest due to the diversity and significance of its fossil vertebrate assemblage.

The Bajo Barreal Formation is presently differentiated into two stratigraphic members, the Lower Member and the Upper Member, both of which crop out extensively at sites in the vicinity of Lago Musters [e.g., the estancias (ranches) Laguna Palacios, Los Sauces, and Ocho Hermanos; Fig. 1]. Sediments of the Bajo Barreal Formation exposed at these localities were deposited during the early stages of the Late Cretaceous (middle Cenomanian–Turonian; Archangelsky et al., 1994; Bridge et al., 2000; Lamanna et al., 2002), and have yielded a diverse fauna that includes turtles, crocodyli-forms, pterosaurs, abelisauroid and tetanuran theropods, diplodocoid and titanosauriform sauropods, and the small-bodied ornithomimid *Notohypsilophodon comodorensis* (Lamanna et al., 2002, table 1; Ibiricu et al., 2010). Most of these fossil tetrapods come from the Lower Member. The rebbachisaurid material reported herein

was recovered from upper levels of the Lower Member exposed on the estancias Ocho Hermanos and Los Sauces, and lowermost strata of the Upper Member exposed on the Estancia Laguna Palacios (Fig. 2).

Outcrops of the Bajo Barreal Formation vary in thickness at different localities. At the Estancia Ocho Hermanos, this unit is approximately 255 m thick (Martínez et al., 1986; Rodríguez, 1993). At the Estancia Los Sauces, it is 180 m in thickness (Sciutto and Martínez, 1994), whereas at the nearby Estancia Laguna Palacios it is 166 m thick (Sciutto and Martínez, 1997). The Lower Member comprises fluviially deposited sediments. Its base consists primarily of mudstone with minor sandstone intercalations; sandstones

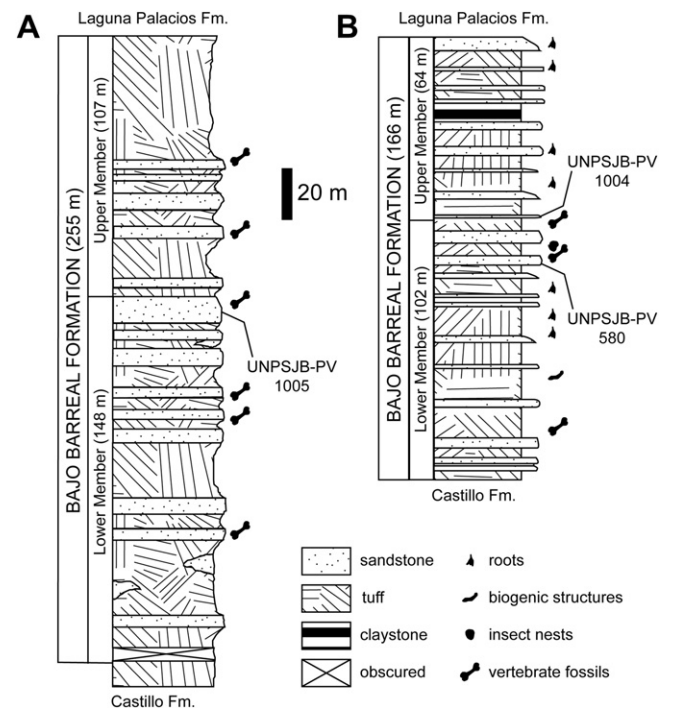


Fig. 2. Stratigraphy of the Upper Cretaceous Bajo Barreal Formation at selected localities that have yielded rebbachisaurid fossils. A, stratigraphic column at the Estancia Ocho Hermanos, the site that yielded the anterior or middle cervical vertebra UNPSJB-PV 1005 (modified from Martínez et al., 1986). B, stratigraphic column at the Estancia Laguna Palacios, the site that yielded the associated caudal sequence UNPSJB-PV 1004 (modified from Sciutto and Martínez, 1997). The approximate stratigraphic position of the anterior caudal vertebra UNPSJB-PV 580, from the neighboring Estancia Los Sauces, is also indicated.

increase in prevalence toward the top of the unit. The Upper Member consists of claystones and gray-brown mudstones that predominate over fluvial sandstones.

3. Systematic paleontology

Dinosauria Owen, 1842
 Saurischia Seeley, 1887
 Sauropodomorpha von Huene, 1932
 Sauropoda Marsh, 1878
 Diplodocoidea Upchurch, 1995
 Rebbachisauridae (Bonaparte, 1997) indet.

Material. UNPSJB-PV 1005, an isolated, nearly complete anterior or middle cervical vertebra; UNPSJB-PV 580, an isolated, nearly complete anterior caudal vertebra; and UNPSJB-PV 1004, an associated but fragmentary caudal series consisting of an anterior vertebra (UNPSJB-PV 1004/1) and neural arch (UNPSJB-PV 1004/2), a middle vertebra (UNPSJB-PV 1004/3) and neural arch (UNPSJB-PV 1004/4), and two anterior to middle haemal arches (UNPSJB-PV 1004/5 and UNPSJB-PV 1004/6). Although it is presently impossible to determine whether or not all the materials belong to a single taxon, they all exhibit morphological characteristics of Rebbachisauridae (see below).

Localities and horizons. Estancia Ocho Hermanos (UNPSJB-PV 1005), Estancia Los Sauces (UNPSJB-PV 580), and Estancia Laguna Palacios (UNPSJB-PV 1004), in the vicinity of Lago Musters, south-central Chubut Province, central Patagonia, Argentina (Fig. 1). Upper portion of the Lower Member (UNPSJB-PV 1005, UNPSJB-PV 580) and lowermost portion of the Upper Member (UNPSJB-PV 1004) of the Bajo Barreal Formation (Upper Cretaceous: middle Cenomanian–Turonian; Archangelsky et al., 1994; Bridge et al., 2000; Lamanna et al., 2002; Martínez et al., 2004; Fig. 2).

4. Description

Terminology. The nomenclature of vertebral fossae employed here is that of Britt (1993), with selected terms added or slightly modified from Harris (2006a) and Wilson et al. (2011); that of laminae is from Wilson (1999), with selected terms added from Calvo and Salgado (1995) and Gallina and Apesteguía (2005).

Anterior or middle cervical vertebra (UNPSJB-PV 1005; Fig. 3). Among the most anatomically informative of the remains described here is an isolated, well-preserved, nearly complete cervical vertebra (UNPSJB-PV 1005) that was recovered from the Estancia Ocho Hermanos in the early 1990s and briefly mentioned by Martínez (1998) and Lamanna et al. (2001). We interpret this specimen as pertaining to the anterior or middle portion of the neck. Unfortunately, the vertebra lacks its anterior half of the centrum, so the position of the cervical rib articulation that often serves as an indicator of general serial position cannot be determined. However, the overall morphology of the element, as well as comparisons with well-represented cervical sequences in other diplodocoid taxa, supports this positional assignment.

The vertebra preserves the posterior two-thirds of the low, elongate centrum and almost all of the neural arch, the latter missing only the anterior portion of its left side. The posterior articular surface of the centrum is strongly concave and subovate in contour, substantially wider transversely than tall dorsoventrally (Table 1). The ventral margin of the centrum extends further posteriorly than the dorsal; consequently, the posterior articular cotyle is approximately twice as deep ventrally (~28 mm) as it is dorsally (~14 mm). The central portion of the cotyle is floored by

a subcircular, flattened area approximately 21 mm in diameter. On both of its lateral surfaces, the centrum bears a well-defined, ovoid pneumatic fossa (“pleurocoel”) that extends for approximately half of the preserved centrum length. These fossae are posteriorly acute and anteriorly delimited by a thin, obliquely-oriented ridge (the “pleurocentral lamina” of Calvo and Salgado, 1995). The depths of the pneumatic fossae are unknown because they remain filled with matrix. Although the anterior half of the centrum is missing, sufficient space exists anterior to the pleurocentral lamina that there may have been a second pair of pneumatic fossae anterior to the one preserved. The ventral surface of the centrum is gently concave in lateral view, and possesses a prominent longitudinal keel that divides the surface into two flat, ventrolaterally facing planes.

Anteriorly, the ventrolateral extreme of the neural arch bears a low, anteroposteriorly elongate infradiapophyseal fossa (= centrodiaepophyseal fossa of Wilson et al., 2011) that is bordered ventrally by a thin, subhorizontal ridge and dorsally by the posterior centrodiaepophyseal lamina. The neural canal is subcircular and occupies most of the base of the neural arch. The centroprezygapophyseal lamina is transversely expanded dorsally, with a faint, triangular anterior peduncular fossa (the “cranial peduncular fossa” of Britt, 1993, “cranial infrazygapophyseal fossa” of Harris, 2006a and “centroprezygapophyseal fossa” of Wilson et al., 2011), occupying its dorsomedial end, immediately ventral to the intraprezygapophyseal lamina. On both lateral sides of the neural arch, prominent posterior centrodiaepophyseal and postzygodiaepophyseal laminae link the diapophysis with the posterodorsal margin of the centrum and the postzygapophysis, respectively, delimiting the subtriangular, deeply concave infrapostzygapophyseal fossa (centropostzygapophyseal fossa sensu Wilson et al., 2011), which bears several marked rugosities. Anterior centrodiaepophyseal and prezygodiaepophyseal laminae are observed on the better-preserved right side of the neural arch as well, and collectively define a deep infraprezygapophyseal fossa (centroprezygapophyseal fossa of Wilson et al., 2011). Immediately dorsal to the postzygodiaepophyseal lamina, the large, subtriangular parazygapophyseal fossa (spinodiaepophyseal fossa of Wilson et al., 2011) is bordered anteriorly by the spinoprezygapophyseal lamina and posteriorly by the spinopostzygapophyseal lamina. The anteroventral sector of this fossa is crossed by a slightly anterodorsally oriented lamina (the “accessory lamina” of Calvo and Salgado, 1995 and “accessory lamina 1” of Gallina and Apesteguía, 2005) that connects the postzygodiaepophyseal lamina and the posteroventral base of the prezygapophysis.

The preserved right prezygapophysis is directed anterodorsally; its ovoid articular facet is wide and dorsomedially oriented. The postzygapophyses are located posteroventral to the neural spine, and have flat, ventrolaterally facing articular facets that are, like the preserved prezygapophyseal facet, wide and ovoid. Dorsal to the postzygapophyseal facets, the rugose epipophyses project caudadorsally.

The subvertically (dorsally and slightly posteriorly) oriented neural spine is located dorsal to the posterior half of the centrum and is very tall, approximately twice the dorsoventral height of the centrum (such that the neural arch as a whole is more than three times taller than the centrum; Table 1). At its base, the anterior surface of the spine exhibits a low, sagittally positioned prespinal lamina. More dorsally, this lamina grades into a fainter ridge that ascends the right side of the anterior surface, intimating that the prespinal lamina may have been bifurcate. The posterior surface of the neural spine is occupied by a deep postspinal fossa (= spinopostzygapophyseal fossa) that is bounded laterally by the spinopostzygapophyseal and centropostzygapophyseal laminae.

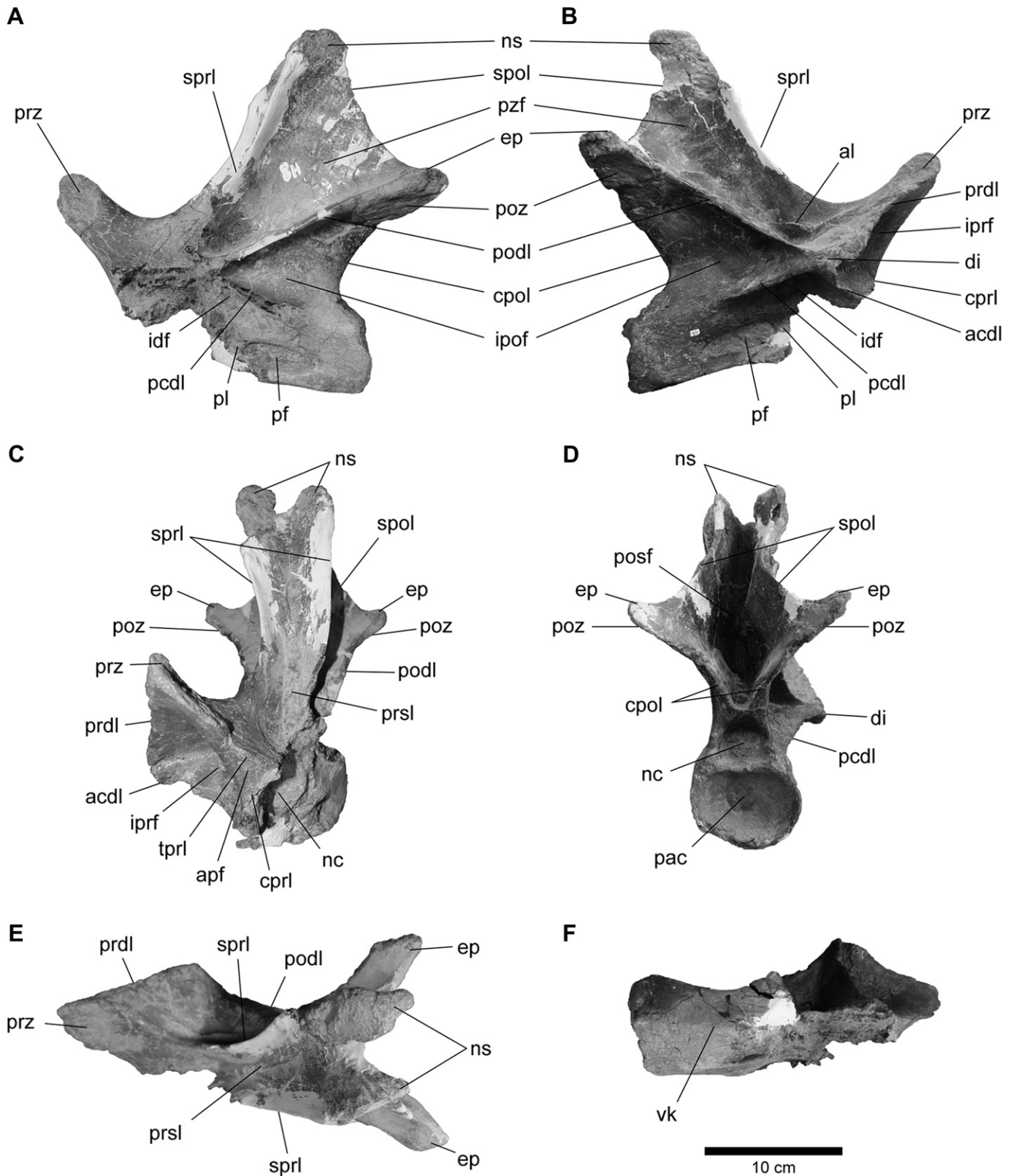


Fig. 3. Rebbachisaurid anterior or middle cervical vertebra from the Estancia Ocho Hermanos (UNPSJB-PV 1005). A, left lateral view. B, right lateral view. C, anterior view. D, posterior view. E, dorsal view. F, ventral view. Abbreviations: acdl, anterior centrodiapophyseal lamina; al, accessory lamina; apf, anterior peduncular fossa; cpol, centropostzygapophyseal lamina; cprl, centroprezygapophyseal lamina; di, diapophysis; ep, epipophysis; idf, infradiapophyseal fossa; ipof, infrapostzygapophyseal fossa; iprf, infraprezygapophyseal fossa; nc, neural canal; ns, neural spine; pac, posterior articular cotyle; pcdl, posterior centrodiapophyseal lamina; pf, pneumatic fossa (= "pleurocoel"); pl, pleurocentral lamina; podl, postzygodiapophyseal lamina; posf, postspinal fossa; poz, postzygapophysis; prdl, prezygodiapophyseal lamina; prsl, prespinal lamina; prz, prezygapophysis; pzf, parazygapophyseal fossa; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; tpri, intraprezygapophyseal lamina; vk, ventral keel. Scale bar represents 10 cm.

Table 1

Measurements (mm) of rebbachisaurid anterior or middle cervical vertebra from the Estancia Ocho Hermanos (UNPSJB-PV 1005). ^L, estimated; ^L, left; ^R, right.

Centrum anteroposterior length	187 [†]
Centrum transverse width, posterior	80
Centrum dorsoventral height, posterior	63
Neural arch transverse width (across lateral margins of postzygapophyses)	146
Neural arch dorsoventral height, posterior	201
Neural spine transverse width	70
Neural spine dorsoventral height (dorsal margin of postzygapophyses-neural spine apex)	120 ^L
Maximum anteroposterior length (prezygapophyses-postzygapophyses)	102 ^R
Maximum transverse width (across lateral margins of diapophyses)	173 [†]
Maximum dorsoventral height	264

This fossa contains a short but well-developed, vertical postspinal lamina that extends to its base. Uniquely among known rebbachisaurid cervical vertebrae, the neural spine is dorsally bifid, approximately 16 mm in depth, forming a pair of metapophyses. Though breakage may have slightly exaggerated its apparent depth, this bifurcation is clearly not a taphonomic artifact. This interpretation is further supported by the asymmetry of the prespinal lamina described above.

Anterior caudal vertebra (UNPSJB-PV 580; Fig. 4). This nearly complete diplodocoid caudal vertebra was initially described by *Sciutto and Martínez (1994)*, who assigned it to Diplodocidae. Later, *Novas (2009)*, suggested the inclusion of this caudal remain within Rebbachisauridae. Below, we redescribe the specimen from “Los Sauces” ranch and confirm its systematic affinities.

UNPSJB-PV 580 was very anteriorly situated in the tail of the sauropod to which it pertained, probably occupying the first or second position in the caudal sequence. Both articular surfaces of its anteroposteriorly compressed centrum are subcircular in contour and concave, the posterior surface slightly more so than the anterior. Each lateral surface bears a small but well-defined, presumably pneumatic fossa that is subdivided by a thin, well-developed, obliquely-oriented lamina. Ventrally, the centrum is anteroposteriorly concave in lateral view and devoid of sulci, ridges, and foramina.

The dorsolaterally directed left transverse process is wing-like and generally anteroposteriorly compressed. It consists of comparatively anteroposteriorly thick, dorsally- and ventrally-situated components (termed “bars” by *Gallina and Otero, 2009*) that are united by a thinner but continuous “web” of bone. The ventral component originates just dorsal to the lateral centrum foramen, whereas the dorsal component is nearly level with the dorsoventral plane of the prezygapophyses. The ventral component

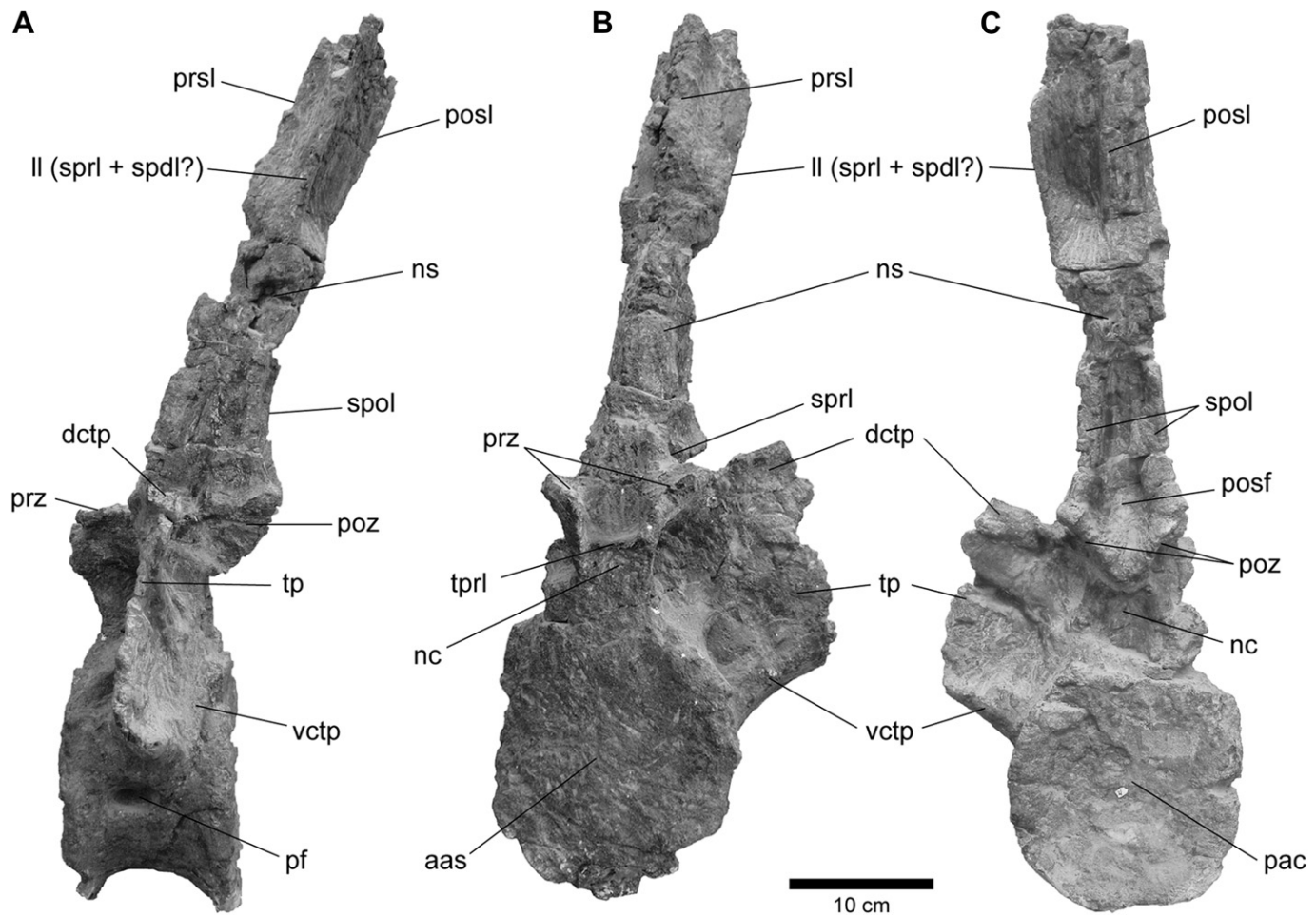


Fig. 4. Rebbachisaurid anterior caudal vertebra from the Estancia Los Sauces (UNPSJB-PV 580). A, left lateral view. B, anterior view. C, posterior view. Abbreviations: aas, anterior articular surface; dctp, dorsal component of transverse process; ll, lateral lamina; nc, neural canal; ns, neural spine; pac, posterior articular cotyle; pf, pneumatic fossa; posl, postspinal lamina; poz, postzygapophysis; prsl, prespinal lamina; prz, prezygapophysis; spd, spinodiapophyseal lamina; spol, spinopostzygapophyseal lamina; spri, spinoprezygapophyseal lamina; tp, transverse process; tpri, intraprezygapophyseal lamina; vctp, ventral component of transverse process. Scale bar represents 10 cm.

is noticeably more robust than the dorsal, both anteroposteriorly and dorsoventrally. The neural arch lies toward the anterior border of the centrum and the zygapophyses are small. The slightly anterodorsally projecting prezygapophyses are connected ventromedially by a pronounced intraprezygapophyseal lamina, and their articular facets face dorsomedially. The postzygapophyses lie slightly dorsal to the level of the prezygapophyses and are clearly visible in lateral view; their articular surfaces face ventrolaterally. The small neural canal opens immediately ventral to the level of the prezygapophyses, and is bounded dorsally by the intraprezygapophyseal lamina.

The neural spine is slightly more than twice the height of the centrum and is inclined posteriorly. The spine displays several fossae (e.g., spinoprezygapophyseal, spinodiapophyseal and spinopostzygapophyseal fossae of Wilson et al., 2011) that are bounded by well-developed prespinal, postspinal, spinoprezygapophyseal, and spinopostzygapophyseal laminae that are of similar thickness. Although damaged and slightly distorted by diagenesis, the neural spine exhibits a marked lateral lamina that is the result of the union of two laminae, the spinoprezygapophyseal and probably the spinodiapophyseal laminae.

Anterior caudal neural arch (UNPSJB-PV 1004/2; Fig. 5). The entirety of this complete neural arch, from “Laguna Palacios” ranch, is dorsoventrally shorter than the neural spine alone of UNPSJB-PV 580. This distinction suggests that, of the two vertebrae, UNPSJB-PV 1004/2 is the more posteriorly positioned (provided that, as appears to be the case, the sauropod individuals to which they pertained were comparable in size). The specimen resembles the corresponding region of UNPSJB-PV 580 in having small zygapophyses and in being embayed by marked fossae toward the base of the neural spine (i.e., spinoprezygapophyseal and spinopostzygapophyseal fossae). As in that vertebra, these fossae are framed by well-developed prespinal, spinoprezygapophyseal,

postspinal, and spinopostzygapophyseal laminae that are of similar thickness. Moreover, lateral laminae are present on the neural spine, and are again formed by the spinoprezygapophyseal and probably the spinodiapophyseal laminae. Indeed, the only substantial difference between the neural arches of UNPSJB-PV 580 and UNPSJB-PV 1004/2 is the lower height of the neural spine in the latter.

Anterior caudal vertebra (UNPSJB-PV 1004/1; Fig. 6). Based on morphological comparisons with UNPSJB-PV 1004/2 and UNPSJB-PV 580, we identify UNPSJB-PV 1004/1, from “Laguna Palacios” ranch, as an anterior caudal that occupied a position posterior to either of the former vertebrae. Although this vertebra has suffered some diagenetic deformation, most of its regions are nearly complete, with the exception of the transverse processes. The centrum is anteroposteriorly compressed, although less so than that of UNPSJB-PV 580, and has subcircular articular surfaces. The posterior surface is slightly concave, whereas the anterior is less so; these conditions may at least partly result from deformation. There is a single small, presumably pneumatic fossa on both lateral surfaces.

The neural arch lies dorsal to the anterior margin of the centrum, and the well defined, subcircular neural canal opens immediately ventral to the level of the zygapophyses. The anterodorsally projecting prezygapophyses are united by a short intraprezygapophyseal lamina that floors a marked fossa. Lateral to this fossa, on both sides, are two pronounced cavities.

The neural spine is slightly shorter than that of UNPSJB-PV 1004/2. The base of the spine possesses large anterolateral concavities that are bounded by spinoprezygapophyseal and prespinal laminae. On the posterior surface of the neural arch, a foramen is present just dorsal to the neural canal.

Middle caudal neural arch (UNPSJB-PV 1004/4; Fig. 7A). This essentially complete middle caudal neural arch from “Laguna

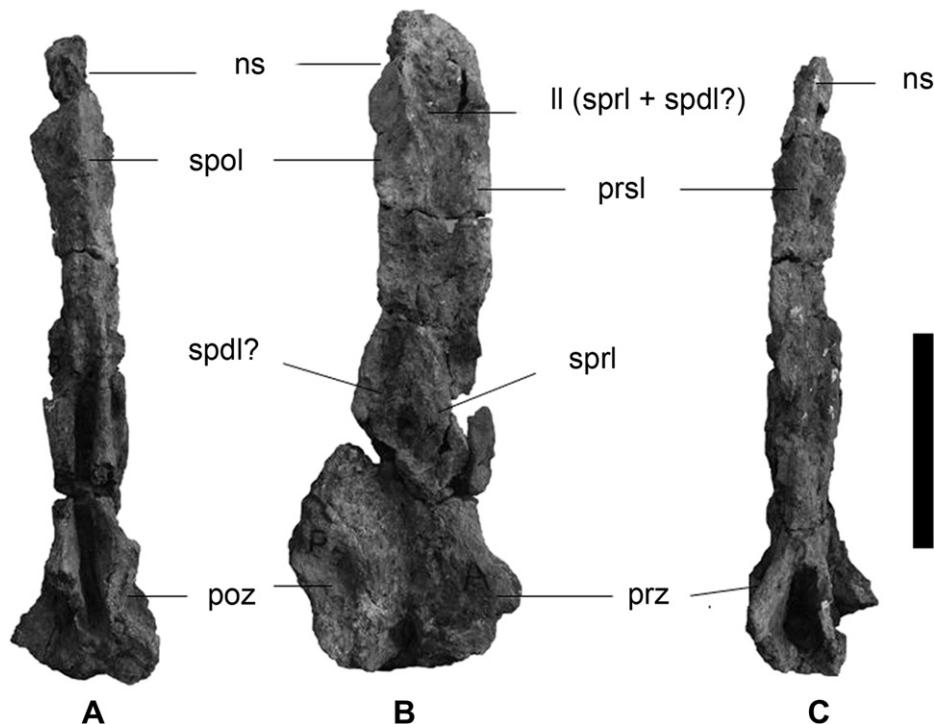


Fig. 5. Rebbachisaurid anterior caudal neural arch from the Estancia Laguna Palacios (UNPSJB-PV 1004/2). A, posterior view. B, right lateral view. C, anterior view. Abbreviations: ll, lateral lamina; ns, neural spine; poz, postzygapophysis; prsl, prespinal lamina; prz, prezygapophysis; spdl, spinodiapophyseal lamina; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina. Scale bar represents 10 cm.

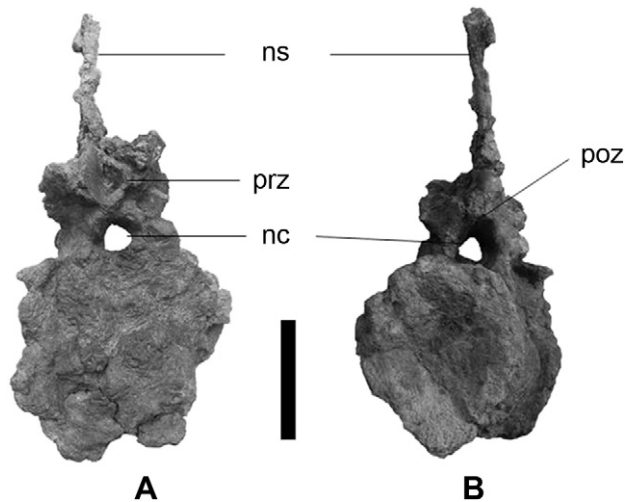


Fig. 6. Rebbachisaurid anterior nearly complete caudal vertebra from the Estancia Laguna Palacios (UNPSJB-PV 1004/1). A, anterior view. B, posterolateral view. Abbreviations: nc, neural canal; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis. Scale bar represents 10 cm.

Palacios" ranch, preserves the base, zygapophyses, and neural spine. The prezygapophyses are short and anteriorly directed and, as in the caudals described above, are united by an intraprezygapophyseal lamina. The postzygapophyses are slightly posterodorsally oriented and shorter than the prezygapophyses. The anteroposteriorly wide neural spine is directed posteriorly, and its posterodorsal apex only just surpasses the postzygapophyses posteriorly.

Middle caudal vertebra (UNPSJB-PV 1004/3; Fig. 7B and C). UNPSJB-PV 1004/3 ("Laguna Palacios" ranch) is a middle caudal vertebra that is moderately taphonomically distorted but preserves all major structures. Morphological comparisons with the other preserved caudal remains suggest that, relative to UNPSJB-PV 1004/4, UNPSJB-PV 1004/3 occupied a slightly more posterior position in the middle caudal sequence. Its centrum is slightly amphicoelous to amphiplatyan, possesses subcircular articular surfaces, and is moderately wider than tall. The lateral surfaces are flat dorsally, but become slightly concave ventrally, yielding a longitudinal ridge at the approximate dorsoventral midline of the centrum. Ventrally, the centrum exhibits a fairly pronounced groove, although diagenetic deformation may have exaggerated this feature.

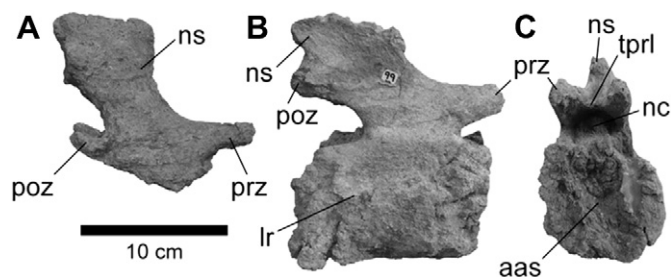


Fig. 7. Rebbachisaurid middle caudal vertebrae from the Estancia Laguna Palacios (UNPSJB-PV 1004). A, middle caudal neural arch (UNPSJB-PV 1004/4) in right lateral view. B, C, middle caudal vertebra (UNPSJB-PV 1004/3). B, right lateral view. C, anterior view. Abbreviations: aas, anterior articular surface; lr, longitudinal ridge; nc, neural canal; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; tpri, intraprezygapophyseal lamina. Scale bar represents 10 cm.

The neural arch arises from the anterior and middle parts of the centrum, though its base does not extend to the anterior edge. The short prezygapophyses barely surpass the anteroposterior plane of the anterior margin of the centrum. As observed in anterior view, the prezygapophyses are united by a thin intraprezygapophyseal lamina, dorsal to which is a fossa. The neural spine extends posterodorsally and its tip slightly surpasses the posterior edge of the centrum.

Haemal arches (UNPSJB-PV 1004/5, UNPSJB-PV 1004/6; Fig. 8). Two haemal arches from "Laguna Palacios" ranch, are preserved. Although both probably pertain to the anterior or middle part of the caudal sequence, UNPSJB-PV 1004/5 is probably from a more anterior position than UNPSJB-PV 1004/6. Both are characterized by an open haemal canal and the corresponding absence of a dorsal "crus". The haemal canal in UNPSJB-PV 1004/5 occupies approximately one-third of the total dorsoventral length of the element. Articular surfaces are well developed in this arch, and its blade is relatively long and laterally compressed ventral to the canal. In the more posteriorly situated haemal arch UNPSJB-PV 1004/6, the haemal canal occupies roughly 50% of the total length of the bone. This specimen also has well-developed articular surfaces and a laterally compressed blade, but the ventral portion of its blade projects posteriorly, rendering the element L-shaped in lateral view.

5. Comparisons

To ascertain the evolutionary affinities of the sauropod remains described herein within Diplodocoidea, and particularly within Rebbachisauridae, we compared the fossils to corresponding skeletal elements in a number of diplodocoid or putative diplodocoid taxa: the rebbachisaurids *Cathartesaura anaerobica* (Gallina and Apesteguía, 2005), *Limaysaurus* spp. (Calvo and Salgado, 1995; Calvo, 1999; Salgado et al., 2004), *Nigersaurus taqueti* (Serenó et al., 1999, 2007; Sereno and Wilson, 2005), *Rebbachisaurus garasbae* (Lavocat, 1954), and *Demandasaurus darwini* (Torcida Fernández-Baldor et al., 2001; Pereda Suberbiola et al., 2003; Torcida Fernández-Baldor et al., 2011); the dicraeosaurids *Aargasaurus cazaui* (Salgado and Bonaparte, 1991), *Brachytrachelopan mesai* (Rauhut et al., 2005), and *Dicraeosaurus* spp. (Janensch, 1929); the diplodocids *Apatosaurus* spp. (e.g., Riggs, 1903; Gilmore, 1936; Upchurch et al., 2004b), *Barosaurus lentus* (Lull, 1919; McIntosh, 2005), *Dinheirosaurus lourinhanensis* (Bonaparte and Mateus, 1999), *Diplodocus* spp. (e.g., Osborn, 1899; Hatcher,



Fig. 8. Rebbachisaurid haemal arches from the Estancia Laguna Palacios (UNPSJB-PV 1004) in anterior view. A, anterior or middle haemal arch (UNPSJB-PV 1004/6). B, anterior haemal arch (UNPSJB-PV 1004/5). Abbreviations: hc, haemal canal. Scale bar represents 10 cm.

1901; Gilmore, 1932), *Supersaurus vivianae* (Jensen, 1985; Lovelace et al., 2007), and *Tornieria africana* (Remes, 2006); the diplodocoids *Amazonsaurus maranhensis* (Carvalho et al., 2003), *Suuwassea emilieae* (Harris and Dodson, 2004; Harris, 2006a), and *Zapalasaurus bonapartei* (Salgado et al., 2006a); and the controversial neosauropod *Australodocus bohetii* (which was assigned to Diplodocidae by Remes, 2007, but removed to Macronaria by Whitlock, 2011).

The centrum of the anterior or middle cervical vertebra (UNPSJB-PV 1005) resembles those of rebbachisaurids, diplodocids, *Suuwassea*, *Zapalasaurus*, and *Australodocus* in having a well-developed, ovoid pneumatic fossa on both of its posterolateral surfaces. The position and morphology of this fossa are similar to those observed in rebbachisaurids (e.g., *Cathartesaura*, *Limaysaurus*, *Nigersaurus*) and some flagellicaudatans (e.g., *Apatosaurus*, *Suuwassea*). Derived diplodocids (e.g., *Barosaurus*, *Dinheirosaurus*, *Diplodocus*), however, exhibit a more complex pattern of posterolateral centrum pneumatization characterized by the presence of accessory cavities and laminae (Bonaparte and Mateus, 1999; McIntosh, 2005). Conversely, cervical centra of undisputed representatives of Dicraeosauridae lack well-defined posterolateral pneumatic fossae (Janensch, 1929; Salgado and Bonaparte, 1991; Rauhut et al., 2005). The estimated anteroposterior length of the centrum of UNPSJB-PV 1005 is approximately three times greater than its posterior dorsoventral height (Table 1). Thus, its proportions resemble those of other diplodocoids, with the exceptions of *Nigersaurus* (Sereno et al., 2007, fig. 3B) and diplodocids more derived than *Apatosaurus*, in which the middle cervical centra are four or more times longer than tall (Whitlock, 2011). Ventrally, the UNPSJB-PV 1005 centrum possesses a low, sagittal keel; such keels are uncommon in diplodocoid cervicals but have been reported in *Dinheirosaurus* (Bonaparte and Mateus, 1999, p. 17) and dicraeosaurids (e.g., *Brachytrachelopan*, *Dicraeosaurus*). Nevertheless, the ventral surfaces of most *Dicraeosaurus* cervicals exhibit deep fossae separated by the ventral keel (e.g., Harris, 2006a, text-fig. 2), whereas there are no such fossae in UNPSJB-PV 1005.

In the Bajo Barreal cervical, the centroprezygapophyseal lamina is dorsally expanded, but not divided as in diplodocids and reportedly in *Nigersaurus* and *Demandasaurus* (Sereno et al., 2007; Whitlock, 2011). The accessory lamina that connects the postzygodiapophyseal lamina and prezygapophysis is a distinctive feature that the Bajo Barreal cervical shares only with the limaysaurine rebbachisaurids *Cathartesaura* and *Limaysaurus*. Conversely, although these differences might be due to positional variation, UNPSJB-PV 1005 lacks the “suprapostzygapophyseal accessory lamina” that occurs in posterior cervicals of these limaysaurines (Calvo and Salgado, 1995, fig. 8B; Gallina and Apesteguía, 2005, fig. 2A) as well as the strut that connects the prezygodiapophyseal lamina and centrum in *Cathartesaura* (“accessory lamina 2” of Gallina and Apesteguía, 2005). Similarly, the Bajo Barreal vertebra does not possess the prezygapophyseal–epipophyseal lamina that is prominent in the fifth cervical of *Nigersaurus* (Sereno et al., 2007, fig. 3B) and that probably also occurs in *Zapalasaurus* (Salgado et al., 2006a, fig. 4C, “podl (sz)”; Whitlock, 2011). The neural spine of UNPSJB-PV 1005 is divided by a shallow but well-defined notch comparable to that in the sixth cervical of *Suuwassea* (Harris, 2006a, text-fig. 7A, C). This dorsally bifurcate neural spine is unique among non-flagellicaudatan diplodocoids.

The posterior surface of the centrum of the very anteriorly positioned caudal vertebra UNPSJB-PV 580 is slightly more concave than the anterior, as in anterior caudals of *Limaysaurus* sp. (Salgado et al., 2004). Anterior caudal centra of other rebbachisaurids exhibit similar morphologies: those of *Limaysaurus tessonei* are described as platycoelous (Calvo and Salgado, 1995), while the centrum of

the single known anterior caudal of *Cathartesaura* is amphiplatyan (Gallina and Apesteguía, 2005). The centra of the anteriormost known caudals of the Spanish rebbachisaurid MPS-RV II (= *Demandasaurus*) have flat anterior and slightly concave posterior surfaces (Pereda Suberbiola et al., 2003), whereas the centrum of the recently described anterior caudal (MIWG 5384, Mannion et al., 2011), is amphicoelous. All known caudals of *Zapalasaurus* are amphicoelous (Salgado et al., 2006a). In contrast, flagellicaudatans have weakly procoelous anteriormost caudal vertebrae (Salgado et al., 2004); moreover, in some diplodocids (e.g., *Diplodocus carnegii*; Hatcher, 1901), procoely extends posteriorly through much of the anterior caudal series. The well-developed, presumably pneumatic fossae (“pleurocoels”) in the centrum are a striking character of the Bajo Barreal caudal. Within Diplodocoidea, such structures are well documented only in diplodocids more derived than *Apatosaurus* (Whitlock, 2011). Interestingly, however, comparable, though much more dorsally-positioned, foramina occur in a possible rebbachisaurid anterior caudal centrum from the Cenomanian of Brazil (UFMA 1.10.283; Medeiros and Schultz, 2004, p. 276, figs. 2D, 3).

The ventral surface of the UNPSJB-PV 580 centrum is flat and essentially featureless, thereby differing from the condition in anterior caudals of most other diplodocoids, which exhibit either a series of irregularly-placed nutrient foramina (*Suuwassea*), one or more longitudinal grooves or sulci (*Limaysaurus tessonei*, *Demandasaurus*, *Barosaurus*, *Diplodocus*, *Tornieria*), a sagittal keel (*Apatosaurus*, *Supersaurus*), or a combination of the first two morphologies (*Dicraeosaurus hansemanni*) in this region (see Harris, 2006a; Remes, 2006; Lovelace et al., 2007).

The general morphology of the wing-like transverse process of UNPSJB-PV 580 is comparable to those of most diplodocoids, although the presence of thickened dorsal and ventral components, where the ventral component is more robust than the dorsal, differs from the condition in all flagellicaudatans except *Apatosaurus*. In the Bajo Barreal form, as in most diplodocoids, the dorsal and ventral components of transverse processes are connected by an anteroposteriorly thinner but continuous bony “web”. In this regard, UNPSJB-PV 580 contrasts with *Limaysaurus tessonei* (Calvo and Salgado, 1995) and some *Apatosaurus* specimens (Gilmore, 1936), in which the anterior caudal transverse processes are perforated by large fenestrae. *Cathartesaura* possesses wing-like transverse processes similar to that of UNPSJB-PV 580 (Gallina and Apesteguía, 2005; Gallina and Otero, 2009), but the two forms differ in the development of the ventral component, which is seemingly more pronounced in the former. Moreover, in *Cathartesaura*, the ventral component is more strongly arched dorsally, while the dorsal component is comparatively shorter mediolaterally than in the caudal vertebra of the Bajo Barreal specimen. The transverse process of UNPSJB-PV 580 is directed strongly dorsolaterally, as in *Cathartesaura*, *Demandasaurus*, *Dicraeosaurus*, *Limaysaurus*, and *Zapalasaurus*, and in contrast to the more laterally oriented processes of diplodocids. The prezygapophyses are noticeably less anterodorsally elongate than in the anterior caudals of *Nigersaurus*, *Dicraeosaurus*, diplodocids, *Amazonsaurus* (Carvalho et al., 2003, fig. 8C, D, F), and *Zapalasaurus*, though in some cases (e.g., *Nigersaurus*, *Amazonsaurus*, *Zapalasaurus*) this difference could conceivably be due to positional rather than taxonomic variation.

The neural spine of the Bajo Barreal vertebra resembles those of diplodocoids in general and rebbachisaurids in particular. It is approximately twice as tall dorsoventrally as the centrum. Similarly elevated anteriormost caudal neural spines occur in *Limaysaurus tessonei* (Calvo and Salgado, 1995) and *Dicraeosaurus hansemanni*; neural spines of *Cathartesaura* and *Dicraeosaurus sattleri* are proportionally even taller, while those of diplodocids are invariably

shorter (approximately 1.5 times the height of the centrum, except in *Supersaurus* where they are lower; Lovelace et al., 2007, fig. 6). The UNPSJB-PV 580 neural spine is transversely expanded toward its dorsal apex, being broader than anteroposteriorly long, as in virtually all diplodocoids for which anterior caudal neural spines are preserved. The spine of the Bajo Barreal caudal is transversely constricted at its mid-length; as such, its contour in anteroposterior view appears intermediate between the “petal-shaped”, gradually dorsally expanded neural spines of *Nigersaurus*, MPS-RV II, *Dicraeosaurus*, *Amazonsaurus*, and some specimens of *Limaysaurus tessonei* (Calvo and Salgado, 1995, fig. 10A; but see Calvo, 1999, fig. 3) and the more rectangular spines of diplodocids. UNPSJB-PV 580 lacks the very abrupt dorsal transverse expansion seen in *Supersaurus* (Lovelace et al., 2007) and anteriormost caudals of some *Apatosaurus* specimens (e.g., Gilmore, 1936, pl. 33, fig. 1A, C). In lateral view, the neural spine of the Bajo Barreal vertebra is straight, as in figured anterior caudals of *Limaysaurus tessonei*, *Nigersaurus*, most flagellicaudatans, and *Amazonsaurus*, rather than noticeably curved anteriorly toward its dorsal extreme as in *Cathartesaura*, MPS-RV II, *Dicraeosaurus hansemanni* (Janensch, 1929, pl. 3), and *Zapalasaurus* (Salgado et al., 2006a, fig. 5.4). The spinoprezygapophyseal lamina appears to extend onto the lateral aspect of the neural spine, as is common in Diplodocoidea, and, although imperfect preservation renders this difficult to confirm, probably merges with the spinodiapophyseal lamina to form the lateral lamina. In contrast, in anterior caudals of most other diplodocoids, the lateral lamina is comprised of the conjoined spinoprezygapophyseal and spinopostzygapophyseal laminae (Wilson, 1999; Whitlock, 2011); exceptions include *Nigersaurus* (Serenó et al., 2007, fig. 3D), *Dicraeosaurus* (Janensch, 1929), *Amazonsaurus* (Carvalho et al., 2003), *Zapalasaurus* (Salgado et al., 2006a, p. 702), and possibly *Demandasaurus* (Pereda Suberbiola et al., 2003; Torcida Fernández-Baldor et al., 2011). The lateral laminae of UNPSJB-PV 580 lack the prominent, triangular lateral projections present in the nigersaurine rebbachisaurids *Nigersaurus* (Serenó et al., 2007, fig. 3D) and *Demandasaurus* (Pereda Suberbiola et al., 2003, fig. 2B, C, E), and that also reportedly occur in *Zapalasaurus* (Whitlock, 2011). Unlike the condition in *Nigersaurus* and *Demandasaurus* (Serenó et al., 2007; Whitlock, 2011), there is no substantial depression between the lateral and postspinal laminae (i.e., the posterior edge of the postspinal lamina is not markedly expanded transversely as in at least the Spanish form; see Pereda Suberbiola et al., 2003, fig. 2E). Although the dorsalmost tip of the neural spine is imperfectly preserved, there is no indication of the bifurcation observed in *Diplodocus* (Osborn, 1899; Hatcher, 1901). The anterior caudals of UNPSJB-PV 1004 differ only slightly from UNPSJB-PV 580, and in aspects consistent with their slightly more posterior position in the caudal sequence (e.g., lower neural spine height); these similarities mean that the same comparative criteria outlined above apply to these vertebrae as well.

The centrum of the middle caudal vertebra UNPSJB-PV 1004/3 is either amphiplatyan or shallowly amphicoelous; diagenetic deformation renders the precise condition of its articular surfaces difficult to determine. Regardless, diplodocoid middle caudal centra typically exhibit one of these two morphologies. Relative to its dorsoventral height, the centrum is proportionately intermediate in anteroposterior length between the elongate middle caudals of *Zapalasaurus* (Salgado et al., 2006a, fig. 5) and the derived diplodocoids *Barosaurus*, *Diplodocus*, and *Tornieria*, and the unusually short centra of *Amazonsaurus* (Carvalho et al., 2003, figs. 10A, 11A), resembling most other diplodocoids in this regard. As in many diplodocoids (e.g., *Apatosaurus*, *Dicraeosaurus*, *Suuwassee*), the articular surfaces are roughly circular in anteroposterior view, differing from the subtriangular, ventrally broad profiles of *Cathartesaura* (Gallina and Apesteguía, 2005, p. 156), *Limaysaurus* spp.

(Calvo and Salgado, 1995; Salgado et al., 2004, fig. 4E, I), *Amazonsaurus* (Carvalho et al., 2003, fig. 11B), and especially UFMA 1.10.015, 1.10.168, 1.10.188, and 1.10.806, a collection of probable rebbachisaurid caudal centra from northeastern Brazil (Medeiros and Schultz, 2004, fig. 3.1–4). The lateral surfaces of the centrum are not uniformly concave as reported in *Cathartesaura*, *Limaysaurus tessonei*, and *Amazonsaurus*. Instead, these surfaces possess a single, low, anteroposteriorly oriented ridge similar to that in some comparably positioned caudals of *Limaysaurus* sp. (Pv-6729-MOZ; Salgado et al., 2004), MPS-RV II (Pereda Suberbiola et al., 2003), *Apatosaurus* (e.g., Upchurch et al., 2004b), *Dicraeosaurus*, and *Suuwassee* (Harris, 2006a). The ventral surface of UNPSJB-PV 1004/3 is slightly concave, unlike the condition in *Cathartesaura* and *Amazonsaurus*, where this surface is described as flat, and that in derived diplodocids (i.e., *Barosaurus*, *Diplodocus*, *Tornieria*), the middle caudals of which are characterized by a deep ventral groove. In this vertebra, as well as in the middle caudal neural arch UNPSJB-PV 1004/4, the zygapophyses are short and the neural spine is posterodorsally inclined. These conditions are common in diplodocoids, with a few exceptions (e.g., *Diplodocus*, where the prezygapophyses extend well past the anterior margin of the centrum and the neural spine is vertical; Osborn, 1899, fig. 13; Gilmore, 1932, fig. 3).

The haemal arches (UNPSJB-PV 1004/5–6) are characterized by the absence of the dorsal “crus”, as in rebbachisaurids and macronarian sauropods, but not the anterior haemal arches of flagellicaudatans. The anteriormost of the two preserved haemal arches, UNPSJB-PV 1004/5, possesses a relatively long, straight, laterally compressed shaft similar to those of *Amazonsaurus* (Carvalho et al., 2003, fig. 14). UNPSJB-PV 1004/6, which, based on comparisons with the haemal arch series of other diplodocoids (e.g., *Apatosaurus*; Riggs, 1903, fig. 18; Upchurch et al., 2004b, pl. 9), was probably positioned in the middle part of the caudal series, exhibits a moderate L-shape similar to that reported for *Limaysaurus tessonei* (Carvalho et al., 2003, p. 708). This Bajo Barreal haemal arch resembles that illustrated in *Demandasaurus* (MPS-RV II; Torcida Fernández-Baldor et al., 2001, fig. 3), which was purported to pertain to the anterior region of the tail of this Spanish rebbachisaurid (Pereda Suberbiola et al., 2003).

6. Discussion

6.1. Systematic assessment

The fossils described herein display multiple derived characters that support their inclusion in Rebbachisauridae. Cervical vertebra UNPSJB-PV 1005 possesses a low longitudinal keel on its ventral surface. In his recent analysis of diplodocoid phylogeny, Whitlock (2011, appendix 4) proposed this character as an independently-acquired synapomorphy of both Dicraeosauridae and the unnamed clade within Rebbachisauridae that unites the subclades Limaysaurinae and Nigersaurinae. Furthermore, within Diplodocoidea, the accessory lamina that connects the postzygodiapophyseal lamina and prezygapophysis in UNPSJB-PV 1005 is otherwise known only in *Cathartesaura anaerobica* and *Limaysaurus tessonei* (Calvo and Salgado, 1995; Gallina and Apesteguía, 2005), and has accordingly been proposed as a synapomorphy of Limaysaurinae (Whitlock, 2011). Consequently, the Bajo Barreal cervical may be confidently referred to Rebbachisauridae, and within that clade, possibly to Limaysaurinae.

The anterior caudal vertebra UNPSJB-PV 580 and the anterior caudals of UNPSJB-PV 1004 also exhibit a number of the synapomorphies of clades within Diplodocoidea proposed by Whitlock (2011). Transverse expansion of the neural spine and extension of the spinoprezygapophyseal lamina onto the lateral aspect of the neural spine are potentially diagnostic of the clade comprising

Amazonsaurus maranhensis and more derived diplodocoids, while wing-like transverse processes and elevated neural spines are synapomorphies of Rebbachisauridae + Flagellicaudata (= Diplodocimorpha of Taylor and Naish, 2005). The dorsolaterally directed transverse processes of UNPSJB-PV 580 are synapomorphic of both *Amargasaurus cazau* + more derived dicraeosaurids and Limaysaurinae + Nigersaurinae. Amphicoelous anterior caudal centra with the posterior articular surface more concave than the anterior is a feature shared only by UNPSJB-PV 580, UNPSJB-PV 1004 (specifically, UNPSJB-PV 1004/1), and the limaysaurine rebbachisaurid *Limaysaurus* spp. (Salgado et al., 2004). Salgado et al. (2004, p. 906) considered this articular surface morphology autapomorphic of the latter genus, but its presence in UNPSJB-PV 580 and UNPSJB-PV 1004/1, which are clearly distinct from anterior caudals of *Limaysaurus* in other regards (e.g., pneumatic fossae in the centra of both Bajo Barreal vertebrae, transverse processes not fenestrate and neural spine transversely constricted at midlength in UNPSJB-PV 580), demonstrates that this character is instead a synapomorphy of Rebbachisauridae or a subclade within, perhaps Limaysaurinae. Regardless of the precise level within Rebbachisauridae to which this morphology is diagnostic, its presence in UNPSJB-PV 580 and UNPSJB-PV 1004 indicates that both are referable to this clade. Within Rebbachisauridae, the specimens may pertain to Limaysaurinae, but this is less certain. Additional evidence that at least UNPSJB-PV 580 may be referable to this Patagonian rebbachisaurid subclade occurs in the precise combination of characters manifest in its transverse processes. Within Diplodocoidea, winglike transverse processes comprised by dorso-laterally oriented, dorsally and ventrally positioned osseous bars connected by a continuous bony web, with the ventral bar significantly more robust than the dorsal, are otherwise known only in the limaysaurine *Cathartesaura* (Gallina and Apesteguía, 2005; Gallina and Otero, 2009). In summary, all of the fossils described herein are clearly referable to Rebbachisauridae, and within that clade, possibly to Limaysaurinae, but we cannot definitively assign the specimens to the latter group given the data currently at hand.

6.2. Significance for rebbachisaurid morphology and evolution

The Bajo Barreal material, specifically anterior-middle cervical vertebra UNPSJB-PV 1005 and anterior caudal vertebrae UNPSJB-PV 580 and UNPSJB-PV 1004/1, exhibits morphological features that are unknown in other definitive rebbachisaurids, namely the forked neural spine in UNPSJB-PV 1005 and the presumably pneumatic fossae in the centra of UNPSJB-PV 1004/1 and UNPSJB-PV 580, which are divided by a thin, obliquely oriented, well-marked lamina in the latter. Intriguingly, within Diplodocoidea, bifid cervical neural spines are otherwise known only in flagellicaudatans, and caudal pneumatic fossae only in derived diplodocids (*Barosaurus lentus*, *Diplodocus* spp., *Supersaurus vivianae*, and *Tornieria africana*).

Bifurcate cervical neural spines appear to have evolved independently several times within Sauropoda (Wilson and Sereno, 1998; Tsuihiji, 2004). Indeed, Flagellicaudata and some of its subclades are the only presently recognized sauropod groups for which forked neural spines are considered synapomorphic (Wilson, 2005; Whitlock, 2011). Specifically, according to Whitlock (2011, appendix 4), bifid posterior cervical neural spines are a synapomorphy of Flagellicaudata, whereas bifid anterior cervical spines were convergently acquired by both Diplodocidae and the dicraeosaurid subclade comprising *Amargasaurus*, *Brachytrachelopan mesai*, and *Dicraeosaurus* spp. UNPSJB-PV 1005 indicates that bifurcate neural spines occur in the anterior or middle cervical series of at least one rebbachisaurid taxon as well. It is presently unclear whether this morphology constitutes a retention of a plesiomorphic state that arose in a more basal diplodocoid clade (e.g.,

Rebbachisauridae + Flagellicaudata of Whitlock, 2011) and was lost in other known rebbachisaurids, or whether the condition evolved convergently in the Bajo Barreal form and flagellicaudatans.

UNPSJB-PV 1005 displays a number of additional morphological features, probably related to anatomical function and soft tissue attachment that resemble those in cervical vertebrae of other rebbachisaurids. Definitive diplodocid and dicraeosaurid cervicals possess an assortment of depressions and non-communicating fossae on the surfaces of the neural arch (Wedel and Sanders, 2002; Schwarz and Fritsch, 2006; Schwarz et al., 2007). These structures have been proposed as excavations created by pneumatic diverticula (Wedel and Sanders, 2002), attachment sites for hyposomatic musculature (Bonaparte, 1999; Gallina and Apesteguía, 2005), or fossae that functioned primarily in weight reduction (McIntosh, 2005; Schwarz and Fritsch, 2006). On the other hand, as in the Bajo Barreal vertebra, cervicals of *Suuwassea emilieae* and rebbachisaurids (e.g., *Cathartesaura*, *Limaysaurus*) have less complex systems of neural arch fossae. The UNPSJB-PV 1005 neural arch also exhibits several probable muscle insertion sites, possibly for the M. cervicalis ascendens and M. flexor colli lateralis (Wedel and Sanders, 2002; Salgado et al., 2006b). The notch between the metapophyses of the neural spine may have housed the ligamentum supraspinale and median epaxial musculature (Wedel and Sanders, 2002; Tsuihiji, 2004).

As with the bifid neural spine of UNPSJB-PV 1005, the pneumatic fossae in the centra of anterior caudal vertebrae UNPSJB-PV 580 and UNPSJB-PV 1004/1 may represent either a plesiomorphic retention of a basal diplodocoid condition or homoplasy between one or more Bajo Barreal rebbachisaurid taxa and derived members of Diplodocidae. We favor the latter possibility because, assuming that current understanding of the higher-level structure of diplodocid phylogeny (e.g., Calvo and Salgado, 1995; Wilson, 2002; Upchurch et al., 2004a; Rauhut et al., 2005; Taylor and Naish, 2005; Harris, 2006b; Whitlock, 2011) is basically correct, the former would require multiple independent losses of caudal pneumatic fossae within Diplodocoidea.

Wilson (2002) cited the presence of wing-like transverse processes in the anterior caudals as a synapomorphy of the clade comprising Diplodocidae and Dicraeosauridae, now known as Flagellicaudata. Nevertheless, the transverse processes of UNPSJB-PV 580 are also wing-like in morphology, as are those of another rebbachisaurid, *Cathartesaura* (Gallina and Apesteguía, 2005; Gallina and Otero, 2009). Conversely, the rebbachisaurid *Limaysaurus* has repeatedly been reported to lack wing-like transverse processes (Calvo and Salgado, 1995; Calvo, 1999; Salgado et al., 2004; Gallina and Otero, 2009). The fact that UNPSJB-PV 580, *Cathartesaura*, and flagellicaudatans all show this type of transverse processes supports the hypothesis (proposed by a number of workers, e.g., Calvo and Salgado, 1995; Whitlock, 2011) that this condition is a synapomorphy of a diplodocoid clade more inclusive than Flagellicaudata (e.g., Rebbachisauridae + Flagellicaudata). As originally argued by Calvo and Salgado (1995), wing-like transverse processes may subsequently have been lost in *Limaysaurus*.

The neural spines of the anterior caudals UNPSJB-PV 580 and UNPSJB-PV 1004/2 are characterized by the presence of a robust lateral lamina that is formed from the union of two laminae, the spinoprezygapophyseal and probably the spinodiapophyseal laminae. This morphology is highly comparable, if not identical, to that in *Amazonsaurus* (Gallina and Apesteguía, 2005; contrarily, Carvalho et al., 2003, argued that the lateral lamina of the Brazilian taxon was composed of the spinoprezygapophyseal and postzygodiapophyseal laminae). This suggests that this morphology constitutes a synapomorphy of a clade within Diplodocoidea (perhaps *Amazonsaurus* + more derived diplodocoids of Whitlock, 2011), rather than an autapomorphy of *Amazonsaurus* as was provisionally interpreted by Carvalho et al. (2003, p. 707).

6.3. Paleobiogeographic implications

Representatives of Rebbachisauridae are currently known only from the Early and middle Cretaceous, and predominantly from the Gondwanan landmasses. The clade includes the Argentinean taxa *Cathartesaura* (Gallina and Apesteguía, 2005), *Limaysaurus* (Calvo and Salgado, 1995; Calvo, 1999; Salgado et al., 2004), *Nopcsaspondylus alarconensis* (Nopcsa, 1902; Apesteguía, 2007), and *Rayosaurus agrioensis* (Bonaparte, 1996; Carballido et al., 2010), and other, unnamed northern Patagonian forms (e.g., MMCH-Pv 49; Apesteguía et al., 2010), as well as the North African *Nigersaurus taqueti* (Serenio et al., 1999, 2007; Serenio and Wilson, 2005) and *Rebbachisaurus garasbae* (Lavocat, 1954). Moreover, several recent discoveries from the Lower Cretaceous of Europe (Dalla Vecchia, 1998; Naish and Martill, 2001; Torcida Fernández-Baldor et al., 2001; Pereda Suberbiola et al., 2003; Mannion, 2009; Mannion et al., 2011) have extended the distribution of this sauropod group to the Northern Hemisphere. Additional, putative rebbachisaurids are known from Brazil (*Amazonsaurus*; Carvalho et al., 2003, and generically indeterminate material; Medeiros and Schultz, 2004; Castro et al., 2007), Patagonia (*Zapalasaurus bonapartei*; Salgado et al., 2006a, and indeterminate material; Apesteguía, 2007), and sub-Saharan Africa (*Algoasaurus bauri*; Broom, 1904; Canudo and Salgado, 2003, and indeterminate material; O'Connor et al., 2006).

The Cretaceous distribution of Rebbachisauridae is best explained both phylogenetically and paleobiogeographically by the extension of its ghost lineage into the Middle or Late Jurassic (Carvalho et al., 2003; Pereda Suberbiola et al., 2003; Serenio et al., 2007; Whitlock, 2011), when dispersal between Laurasia and Gondwana was more feasible for large-bodied terrestrial vertebrates such as sauropods. If rebbachisaurids did indeed originate and attain a global distribution in the Jurassic, then the observed absence of definitive representatives of the clade in Gondwana during the earliest stages of the Cretaceous (i.e., Berriasian–Barremian) and in Laurasia during the mid Cretaceous (i.e., in post-Barremian strata) may be the result of regional extinction, taxonomic misidentification, the incompleteness of the fossil record, or some combination of these factors (Canudo and Salgado, 2003; Carvalho et al., 2003; Canudo et al., 2009). The discovery of additional rebbachisaurid fossils, as well as further phylogenetic and paleobiogeographic analyses involving these sauropods, may eventually provide firm support for one of these alternatives.

The fossils described herein add to our knowledge of the paleobiogeography of Rebbachisauridae in that they constitute the southernmost known records of the clade and of Diplodocoidea as a whole. Prior to the recognition of rebbachisaurid remains from the Bajo Barreal Formation of the estancias Laguna Palacios, Los Sauces, and Ocho Hermanos in southern Chubut Province, the southernmost definitive record of the clade (and of Diplodocoidea in general) was that of the *Cathartesaura* holotype (MPCA-232), from the “La Buitrera” locality of Río Negro Province some 600 km to the north (Gallina and Apesteguía, 2005). Consequently, UNPSJB-PV 580, 1004, and 1005 extend the distribution of rebbachisaurids to central Patagonia. In so doing, these specimens enhance our understanding of the mid Cretaceous continental vertebrate assemblages of southern South America.

6.4. Middle Cretaceous sauropod turnover

Several authors (e.g., Lamanna et al., 2001; Leanza et al., 2004; Salgado et al., 2004, 2006a; Coria and Salgado, 2005; Calvo et al., 2006) have called attention to the important role that diplodocoid sauropods played in Patagonian paleoecosystems during the Early and mid Cretaceous. Rebbachisauridae appears to be the only diplodocoid clade to have survived into the Late Cretaceous, possibly as late as the Coniacian (Gallina and

Apesteguía, 2005). Coincident with and following the apparent extinction of rebbachisaurids (and by extension, Diplodocoidea as a whole) during the early Late Cretaceous, titanosaurian sauropods underwent an extensive radiation (Salgado et al., 2004; Coria and Salgado, 2005; Gallina and Apesteguía, 2005; Apesteguía, 2007). The occurrence of basal titanosaurians in Patagonia during the Early and mid Cretaceous indicates that these sauropods coexisted with diplodocoids, although the two clades may have occupied distinct ecological niches (Salgado et al., 2004; Coria and Salgado, 2005; Remes, 2007). In addition to the sauropod fossils described herein, middle Cenomanian–Turonian strata of the Bajo Barreal Formation in the San Jorge Basin have yielded abundant titanosaurian material (e.g., isolated elements and partial to nearly complete skeletons of the basal titanosaurian *Epachthosaurus sciuttoi*; Powell, 1990, 2003; Martínez et al., 2004; Casal and Ibiricu, 2010; LMI, pers. obs.). With the documentation of rebbachisaurid remains in these sediments, the coexistence of diplodocoids and basal titanosaurians in the early Late Cretaceous of central Patagonia is confirmed. In contrast, the only sauropod material thus far recovered from latest Cretaceous sediments in the region (Campanian–?Maastrichtian deposits exposed near Lago Colhué Huapi and currently assigned to the Upper Member of the Bajo Barreal Formation) pertains to derived titanosaurians (e.g., the holotypic articulated caudal sequence of *Aeolosaurus colhuehuapensis*; Lamanna et al., 2001, 2003; Luna et al., 2003; Casal et al., 2007; Ibiricu et al., 2010).

There is as yet insufficient evidence to infer the cause(s) of the extinction of diplodocoids in general and of rebbachisaurids in particular. Conceivably, this extinction may have been influenced by paleoenvironmental and floral changes that occurred during the early Late Cretaceous (Coria and Salgado, 2005). Perhaps titanosaurians were able to adapt to these changes, but rebbachisaurids were not, allowing the former to exploit new resources and outcompete the latter.

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