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Katepensaurus goicoecheai, gen. et sp. nov., a Late Cretaceous rebbachisaurid (Sauropoda, Diplodocoidea) from central Patagonia, Argentina

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ARTICLE

KATEPENSAURUS GOICOECHEAI, GEN. ET SP. NOV., A LATE CRETACEOUS REBBACHISAURID (SAUROPODA, DIPLODOCOIDEA) FROM CENTRAL PATAGONIA, ARGENTINA

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ABSTRACT—We describe *Katepensaurus goicoecheai*, gen. et sp. nov., a diplodocoid sauropod dinosaur from the Bajo Barreal Formation (Upper Cretaceous: Cenomanian–Turonian) of south-central Chubut Province, central Patagonia, Argentina. The holotypic specimen is a closely associated partial axial skeleton that includes cervical, dorsal, and caudal vertebrae. The dorsal vertebrae of *Katepensaurus* exhibit the following distinctive characters that we interpret as autapomorphies: (1) internal lamina divides lateral pneumatic fossa of centrum; (2) vertical ridges or crests present on lateral surface of vertebra, overlying neurocentral junction; (3) pair of laminae in parapophyseal centrodiapophyseal fossa; (4) transverse processes perforated by elliptical fenestrae; and (5) well-defined, rounded fossae on lateral aspect of postzygapophyses. Based on the results of previous phylogenetic analyses, we regard the new taxon as a member of Rebbachisauridae; more specifically, it may pertain to Limaysaurinae, a rebbachisaurid subclade that, to date, is definitively known only from southern South America. As currently understood, the rebbachisaurid fossil record suggests that the clade achieved its greatest taxonomic diversity within a few million years of its extinction during the early Late Cretaceous.

INTRODUCTION

Cretaceous strata in southernmost South America preserve a rich and important record of sauropod dinosaurs (e.g., Lydekker, 1893; Huene, 1929; Bonaparte and Gasparini, 1979; Bonaparte, 1996; Powell, 2003; Martínez et al., 2004; Salgado and Bonaparte, 2007; Novas, 2009; Mannion and Otero, 2012). Although this record mainly comprises titanosauriform sauropods, diplodocoids have also been discovered with increasing frequency, mainly in 'middle' Cretaceous sediments (Calvo and Salgado, 1995; Gallina and Apesteguía, 2005; Carballido et al., 2010, 2012; Haluza et al., 2012; Ibiricu et al., 2012; Salgado et al., 2012). At present, the most substantial Cretaceous sauropod records from southernmost South America come from the Neuquén and San Jorge basins of Argentine Patagonia (Salgado and Bonaparte, 2007; Novas, 2009).

In terms of vertebrate fossils, the Upper Cretaceous Bajo Barreal Formation of the San Jorge Basin in central Patagonia constitutes one of the most important South American Cretaceous units (e.g., Lamanna et al., 2002; Martínez et al., 2004; Casal and Ibiricu, 2010; Ibiricu et al., 2011, 2012; Mannion and Otero, 2012). The vertebrate assemblage of this formation presently includes representatives of Testudines, Crocodylomorpha, Pterosauria, and Dinosauria (Ibiricu et al., 2012). Many of the taxa recorded, particularly several of the dinosaurs, are regarded as primitive representatives of their respective clades, and are therefore significant for understanding the evolutionary histories of these groups (Martínez et al., 2004; Martínez and Novas, 2006; Ibiricu et al., 2011).

Here we describe a new rebbachisaurid diplodocoid taxon based on an associated partial skeleton recovered from an exposure of the Bajo Barreal Formation on the Estancia Laguna Palacios in south-central Chubut Province, Argentina (Fig. 1). The new taxon contributes information regarding the morphology and paleobiogeography of this enigmatic sauropod group. Although the rebbachisaurid fossil record has increased considerably in recent years, most members of the clade are still represented only by fragmentary material, with the exceptions of the comparatively well-preserved taxa *Comahuesaurus* (Salgado et al., 2004; Carballido et al., 2012), *Demandasaurus* (Torcida Fernández-Baldor et al., 2011), *Limaysaurus* (Calvo and Salgado, 1995), and *Nigersaurus* (Sereno et al., 1999, 2007; Sereno and Wilson, 2005). Rebbachisaurids are known predominantly from Gondwana; nevertheless, recent discoveries have broadened the distribution of the group to include Europe as well (Dalla Vecchia, 1998, 1999, 2005; Pereda Suberbiola et al., 2003; Mannion, 2009; Mannion et al., 2011; Torcida Fernández-Baldor et al., 2011; see Table 1). The known stratigraphic range of these diplodocoids extends from the Lower Cretaceous (upper Hauterivian–lower Barremian) to the lower part of the Upper Cretaceous (Cenomanian–Turonian). Rebbachisaurids remain unknown from the Late Cretaceous of Laurasia; conversely, they were a significant component of Gondwanan paleoecosystems during the early part of this epoch.

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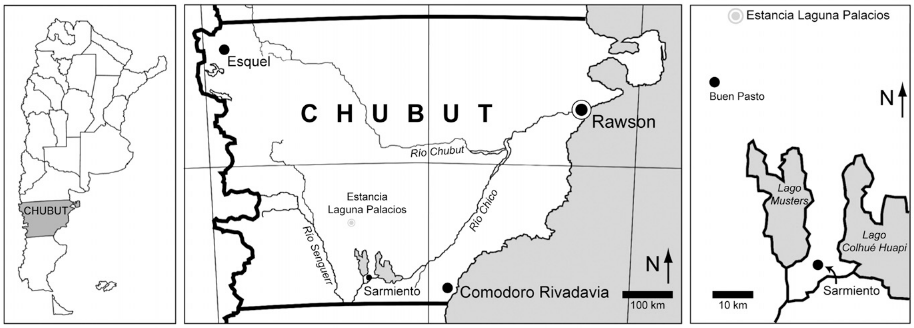

FIGURE 1. Map of Chubut Province, central Patagonia, Argentina, showing location of the Estancia Laguna Palacios, the type locality of *Katepensaurus goicoecheai*, gen. et sp. nov. (modified from Ibiricu et al., 2012).

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The relationship of sauropods now recognized as rebbachisaurids to other diplodocoids was first hypothesized by Calvo and Salgado (1995). Subsequently, Bonaparte (1997) coined the name Rebbachisauridae for these bizarre dinosaurs, although he did not propose a formal definition for the clade. Upchurch et al. (2004a) provided the first formal definition of Rebbachisauridae (a stem-based taxon defined as Diplodocoidea more closely related to *Rebbachisaurus* than to *Diplodocus*), which has been followed by other authors (e.g., Apesteguía et al., 2010). Rebbachisaurid ingroup relationships have yet to be conclusively established. Nevertheless, recent morphological and phylogenetic analyses suggest that several South American rebbachisaurids (e.g., *Cathartesaura*, *Limaysaurus*) constitute a monophyletic group, Limaysaurinae, whereas at least some Afro-European rebbachisaurids (e.g., *Demandasaurus*, *Nigersaurus*) pertain to the subclade Nigersaurinae (Carballido et al., 2010, 2012; Mannion et al., 2011, 2012; Torcida Fernández-Baldor et al., 2011; Whitlock, 2011; Ibiricu et al., 2012).

TABLE 1. Named taxa of Rebbachisauridae and generically unidentified rebbachisaurid specimens (represented by the abbreviations of institutions in which they are housed), including tentatively referred materials (modified from Mannion, 2009).

Taxon/Institutional abbreviation	Age	Country
Histriasaurus boscarollii	EK (late Hau–early Barr)	CR
MACN	EK (Barr)	AR
MIWG	EK (Barr)	EN
Demandasaurus darwini	EK (late Barr–early Apt)	SP
Zapalasaurus bonapartei	EK (late Barr–early Apt)	AR
Amazonsaurus maranhensis	EK (Apt–Alb)	BR
Comahuesaurus windhauseni	EK (Apt–Alb)	AR
Nigersaurus taqueti	EK (Apt–Alb)	NI
cf. *Zapalasaurus*	EK (Apt–Alb)	AR
CCC	EK (Alb)	BR
Nopcsaspondylus alarconensis	LK (Cen)	AR
Rayososaurus agrioensis	LK (Cen)	AR
Rebbachisaurus garasbae	LK (Cen)	MO
Cathartesaura anaerobica	LK (Cen–Tur)	AR
Katepensaurus goicoecheai	LK (Cen–Tur)	AR
Limaysaurus tessonei	LK (Cen–Tur)	AR
MMCH	LK (Cen–Tur)	AR
UNPSJB	LK (Cen–Tur)	AR

Ages of *Cathartesaura*, *Limaysaurus tessonei*, *Nopcsaspondylus*, and MMCH material after Garrido (2010); those of *Rayososaurus* and *Rebbachisaurus* after Carballido et al. (2010) and Cavin et al. (2010), respectively. **Abbreviations**: **Alb**, Albian; **Apt**, Aptian; **AR**, Argentina; **Barr**, Barremian; **BR**, Brazil; **Cen**, Cenomanian; **CR**, Croatia; **EK**, Early Cretaceous; **EN**, England; **Haut**, Hauterivian; **LK**, Late Cretaceous; **MO**, Morocco; **NI**, Niger; **SP**, Spain; **Tur**, Turonian. For institutional abbreviations, see text.

Institutional Abbreviations—CCC, Casa de Cultura do Município de Coroatá, Coroatá, Brazil; **CM**, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; **MACN**, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; **MIWG**, Dinosaur Isle (Museum of Isle of Wight Geology), Sandown, U.K.; **MMCH**, Museo Municipal Ernesto Bachmann, Villa El Chocón, Argentina; **UNPSJB-PV**, Universidad Nacional de la Patagonia San Juan Bosco Laboratorio de Paleovertebrados, Comodoro Rivadavia, Argentina; **UWGM**, University of Wyoming Geological Museum, Laramie, Wyoming, U.S.A.

Anatomical Abbreviations—ac, anterior articular condyle; **acdl**, anterior centrodiapophyseal lamina; **acpl**, anterior centroparapophyseal lamina; **apcr**, anterior process of cervical rib; **as**, anterior surface; **cdf**, centrodiapophyseal fossa; **cpol**, centropostzygapophyseal lamina; **cprf**, centroprezygapophyseal fossa; **cprl**, centroprezygapophyseal lamina; **cr**, cervical rib; **dp**, diapophysis; **dpacdfl**, dorsal parapophyseal centrodiapophyseal fossa lamina; **ipfl**, internal pneumatic fossa lamina; **ipozl**, infrapostzygapophyseal lamina; **lat. spol**, lateral spinopostzygapophyseal lamina; **ldpf**, laterodiapophyseal fenestra; **ll**, lateral lamina; **lpof**, lateral postzygapophyseal fossa; **med. spol**, medial spinopostzygapophyseal lamina; **nc**, neural canal; **ns**, neural spine; **pacdf**, parapophyseal centrodiapophyseal fossa; **pacprf**, parapophyseal centroprezygapophyseal fossa; **pc**, posterior articular cotyle; **pcdl**, posterior centrodiapophyseal lamina; **pf**, pneumatic fossa; **pocdf**, postzygapophyseal centrodiapophyseal fossa; **podl**, postzygodiapophyseal lamina; **posl**, postspinal lamina; **poz**, postzygapophysis; **ppcr**, posterior process of cervical rib; **prcdf**, prezygapophyseal centrodiapophyseal fossa; **prcdfl**, prezygapophyseal centrodiapophyseal fossa lamina; **prdl**, prezygodiapophyseal lamina; **prsdf**, prezygapophyseal spinodiapophyseal fossa; **prsl**, prespinal lamina; **prz**, prezygapophysis; **ps**, posterior surface; **sdf**, spinodiapophyseal fossa; **spdl**, spinodiapophyseal lamina; **spof**, spinopostzygapophyseal fossa; **spol**, spinopostzygapophyseal lamina; **spol-f**, spinopostzygapophyseal lamina fossa; **sprf**, spinoprezygapophyseal fossa; **sprl**, spinoprezygapophyseal lamina; **tlp**, triangular lateral process; **tp**, transverse process; **tprl**, intraprezygapophyseal lamina; **vk**, ventral keel; **vpacdfl**, ventral parapophyseal centrodiapophyseal fossa lamina; **vr**, vertical ridges.

SYSTEMATIC PALEONTOLOGY

SAURISCHIA Seeley, 1887
SAUROPODOMORPHA Huene, 1932

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SAUROPODA Marsh, 1878
DIPLODOCOIDEA Marsh, 1884 (sensu Upchurch, 1995)
REBBACHISAURIDAE Bonaparte, 1997
KATEPENSAURUS GOICOECHEAI, gen. et sp. nov.
(Figs. 3–11)

Diagnosis—*Katepensaurus goicoecheai* possesses the following characters in the middle to posterior dorsal vertebrae that are here interpreted as autapomorphies: (1) internal lamina divides lateral pneumatic fossa of centrum; (2) vertical ridges or crests present on lateral surface of vertebra, overlying neurocentral junction; (3) pair of laminae in parapophyseal centrodiapophyseal fossa; (4) transverse processes perforated by elliptical fenestrae (that decrease in size posteriorly through the dorsal vertebral series and occupy approximately two-thirds of the mediolateral width of the processes); and (5) well-defined, rounded fossae on lateral aspect of postzygapophyses.

Etymology—Generic name from Tehuelche (the indigenous people of central Patagonia) word ‘katepenk’ (‘hole’), in reference to one of the most distinctive features of the new taxon, the fenestrae in the dorsal vertebral transverse processes; and Greek ‘saurus’ (‘lizard’). Species in honor of Mr. Alejandro Goicoecheai, owner of the Estancia Laguna Palacios where the specimen was found, who has allowed the UNPSJB team and their collaborators to conduct field research there for nearly two decades.

Holotype—UNPSJB-PV 1007, an associated partial skeleton consisting of three anterior to middle cervical vertebrae (UNPSJB-PV 1007/1, 1007/2, and 1007/3), three middle to posterior dorsal vertebrae (UNPSJB-PV 1007/4, 1007/5, and 1007/6), two anterior caudal vertebrae (UNPSJB-PV 1007/7 and 1007/8), and two indeterminate elements (UNPSJB-PV 1007/9 and 1007/10).

Locality and Horizon—‘2005 Quarry’ (44°54′23.82″S, 69°22′43.67″W), Estancia Laguna Palacios, south-central Chubut Province, central Patagonia, Argentina (Fig. 1). Upper part of the Lower Member of the Bajo Barreal Formation (Upper Cretaceous; Fig. 2), Chubut Group. The age of the Lower Member of the Bajo Barreal Formation is widely regarded as Cenomanian–Turonian (e.g., Archangelsky et al., 1994; Bridge et al., 2000; Lamanna et al., 2002; Ibiricu et al., 2012). UNPSJB-PV 1007 was recovered from the base of a 1.25-m-thick, fining-upward fluvial deposit of lenticular geometry and erosive base. The specimen comes from a coarse green sandstone with numerous mudstone clasts in the matrix. Other vertebrate fossils recovered from the ‘2005 Quarry’ include the partial skeletons of a turtle (M.C.L., pers. observ.) and an abelisaurid theropod dinosaur (Lamanna et al., 2011, 2012), as well as several isolated theropod teeth.

DESCRIPTION AND COMPARISONS

Terminology

The nomenclature of vertebral fossae employed here is that of Wilson et al. (2011); that of laminae is taken from Wilson (1999, 2012), with selected terms added from Calvo and Salgado (1995) and Gallina and Apesteguía (2005).

Cervical Vertebrae

The holotypic partial skeleton of *Katepensaurus goicoecheai* includes three fairly well-preserved cervical vertebrae (UNPSJB-PV 1007/1, 1007/2, and 1007/3; Figs. 3–5; Table 2). In UNPSJB-PV 1007/1 (Fig. 3), the posterior part of the centrum and the dorsal portion of the neural arch are missing, whereas in UNPSJB-PV1007/2 (Fig. 4) only a thin longitudinal section of the centrum, the ventral part of the neural arch, and a cervical rib are preserved, all on the right side of the element. Based on comparisons with well-represented cervical sequences of other diplodocoids (e.g., *Nigersaurus*; see Wilson et al., 2011), these two *Katepensaurus* bones are regarded as anterior cervical vertebrae. Except

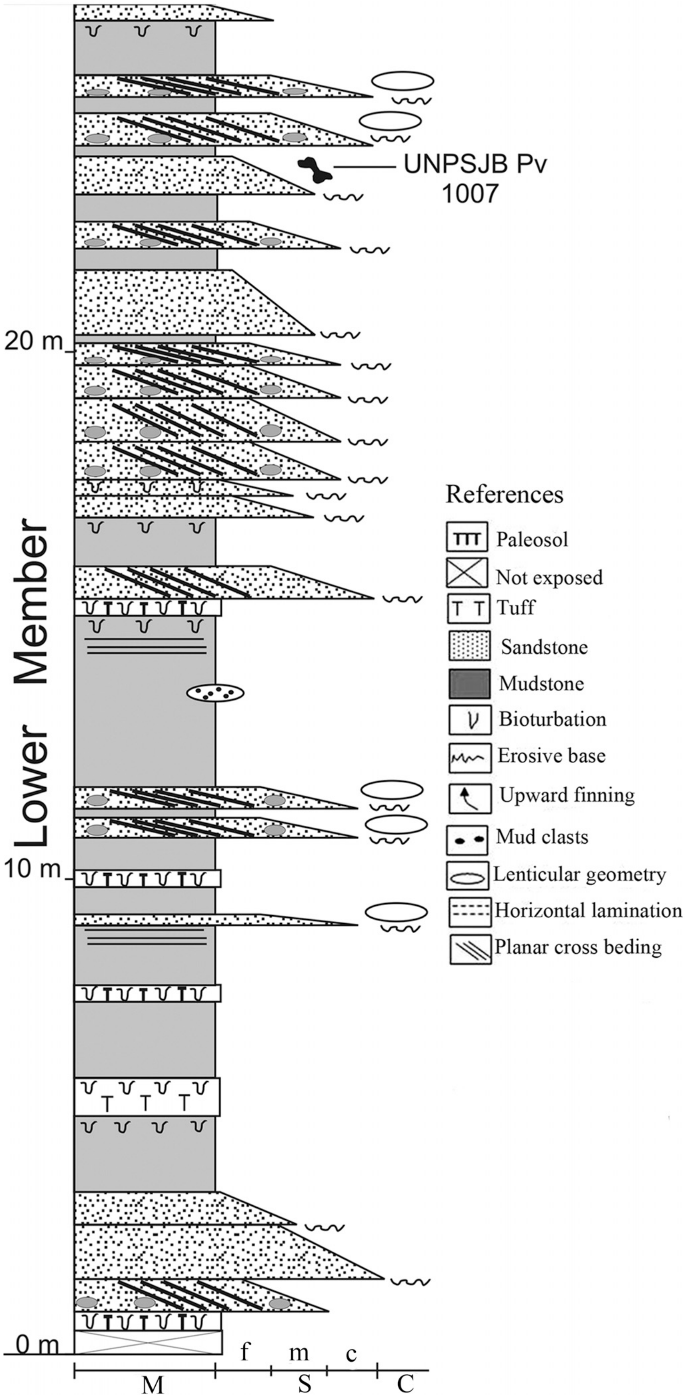

FIGURE 2. Stratigraphic section of the Upper Cretaceous (Cenomanian–Turonian) Lower Member of the Bajo Barreal Formation as exposed on the Estancia Laguna Palacios, the type locality of *Katepensaurus goicoecheai*, gen. et sp. nov. **Abbreviations**: **C**, conglomerate; **c**, coarse-grained; **f**, fine-grained; **M**, mudstone; **m**, medium-grained; **S**, sandstone.

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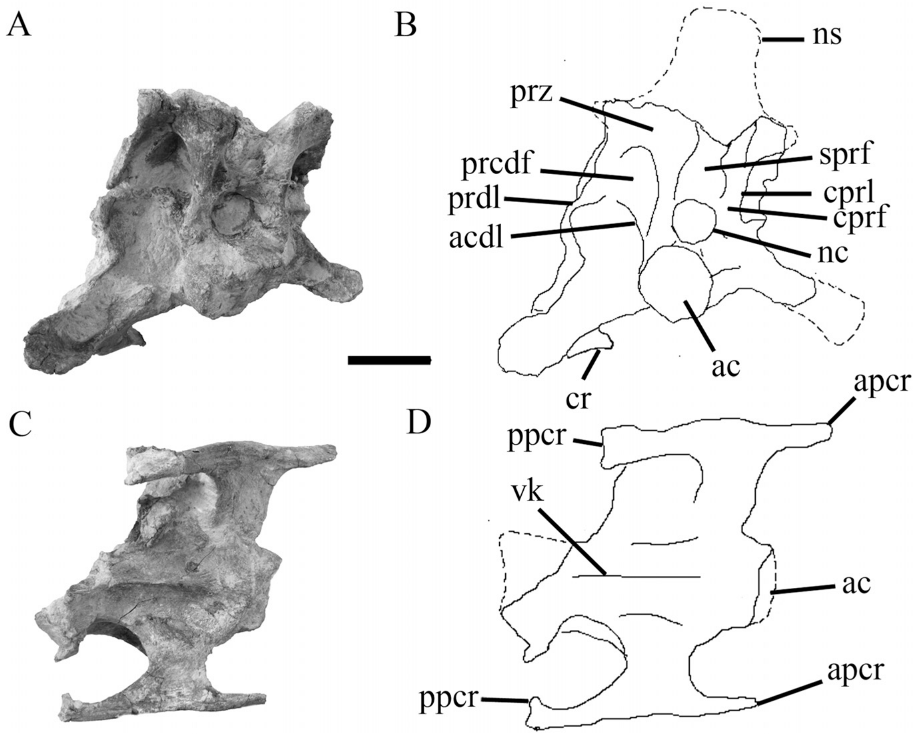

FIGURE 3. Photographs (**A**, **C**) and interpretive drawings (**B**, **D**) of anterior cervical vertebra (UNPSJB-PV 1007/1) of *Katepensaurus goicoecheai*, gen. et sp. nov., in anterior (**A**, **B**) and ventral (**C**, **D**) views. For abbreviations, see text. Scale bar equals 10 cm.

for the dorsal end of the neural spine, the third preserved cervical vertebra (UNPSJB-PV 1007/3; Fig. 5) is nearly complete and belongs to the middle part of the series.

Due to damage and deformation, the morphology of the anterior articular surface of the centrum of UNPSJB-PV 1007/1 (Fig. 3) is difficult to determine, but it appears to be gently convex and slightly taller than wide. Therefore, although the posterior articular surface is missing, the preserved portion of this cervical vertebra suggests that its centrum was opisthocoelous. The left lateral surface of the centrum bears two well-defined, ovate pneumatic fossae ('pleurocoels') that collectively occupy approximately three-fourths of its preserved length. These fossae are divided by a robust, obliquely oriented septum (the 'pleurocentral lamina' of Calvo and Salgado [1995] and Gallina and Apesteguía [2005]). The position and overall morphology of the lateral pneumatic fossae and septum of UNPSJB-PV 1007/1 resemble the conditions in other rebbachisaurids (e.g., *Cathartesaura* [Gallina and Apesteguía, 2005], *Limaysaurus* [Calvo and Salgado, 1995], *Nigersaurus* [Sereno et al., 1999, 2007; Wilson et al., 2011]), some diplodocids (e.g., *Apatosaurus*; Riggs, 1903; Gilmore, 1936; Upchurch et al., 2004b), and *Suuwassea* (Harris and Dodson, 2004; Harris, 2006) (although in some of these taxa, the serial position of known cervical vertebrae does not exactly correspond to that of UNPSJB-PV 1007/1). Conversely, derived diplodocids such as *Barosaurus* (Lull, 1919; McIntosh, 2005), *Dinheirosaurus* (Bonaparte and Mateus, 1999; Mannion et al., 2012), and *Diplodocus* (e.g., Osborn, 1899; Hatcher, 1901; Gilmore, 1932) exhibit complex lateral centrum pneumatization in the form of

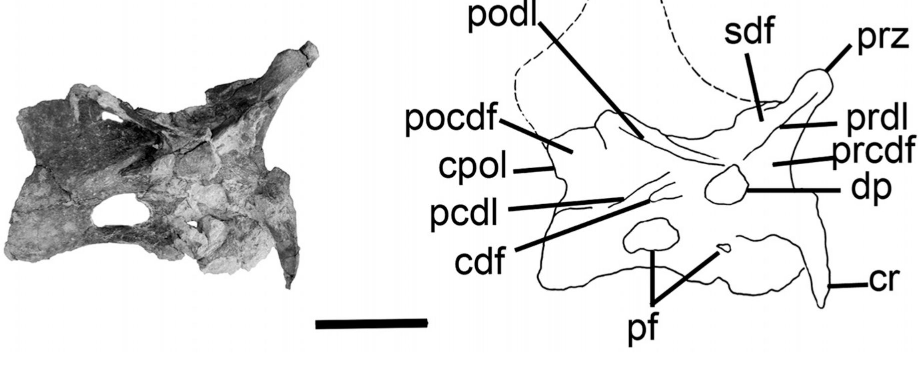

FIGURE 4. Photograph (**A**) and interpretive drawing (**B**) of anterior cervical vertebra (UNPSJB-PV 1007/2) of *Katepensaurus goicoecheai*, gen. et sp. nov., in right lateral view. For abbreviations, see text. Scale bar equals 10 cm.

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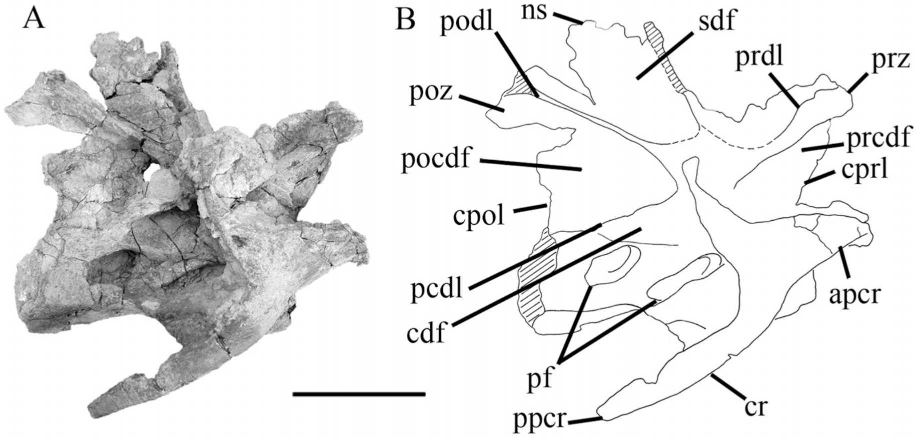

FIGURE 5. Photograph (**A**) and interpretive drawing (**B**) of middle cervical vertebra (UNPSJB-PV 1007/3) of *Katepensaurus goicoecheai*, gen. et sp. nov., in right lateral view. For abbreviations, see text. Scale bar equals 10 cm.

accessory cavities and laminae (Bonaparte and Mateus, 1999; McIntosh, 2005). In addition, cervical centra of dicraeosaurids lack well-defined lateral pneumatic fossae (Janensch, 1929; Salgado and Bonaparte, 1991; Rauhut et al., 2005).

The ventral surface of UNPSJB-PV 1007/1 is gently concave in lateral view, and possesses a prominent longitudinal keel that divides this surface into two strongly concave, ventrolaterally facing planes. Such a sagittal keel has been reported in selected rebbachisaurids (*Demandasaurus* [Torcida Fernández-Baldor et al., 2011]; cf. *Zapalasaurus* [Salgado et al., 2012], an unnamed taxon from the Late Cretaceous of Villa El Chocón, Argentina [MMCH-Pv-49; Haluza et al., 2012], and an isolated anterior to middle cervical vertebra from the Bajo Barreal Formation [UNPSJB-PV 1005; Ibiricu et al., 2012]), the diplodocids *Dinheirosaurus* (Bonaparte and Mateus, 1999; Mannion et al., 2012) and *Supersaurus* (Lovelace et al., 2007), and dicraeosaurids (e.g., *Brachytrachelopan* [Rauhut et al., 2005], *Dicraeosaurus* [Janensch, 1929]; see Whitlock, 2011). Nevertheless, the ventral surfaces of most *Dicraeosaurus* cervical vertebrae exhibit deep fossae separated by the ventral keel (Harris, 2006; Ibiricu et al., 2012), a condition that differs from that of *Katepensaurus*.

The neural canal of UNPSJB-PV 1007/1 is well marked and ovate in outline. The prezygapophyses are relatively long and their facets are wide, ovate in contour, and slightly dorsomedially oriented. The complex of neural arch laminae that can be observed in anterior view includes the two robust, undivided, beam-like centroprezygapophyseal laminae, the thin but marked spinoprezygapophyseal laminae, and the prezygodiapophyseal laminae (Fig. 3A, B). Moreover, although it is distorted, the right side of UNPSJB-PV 1007/1 also preserves the anterior centrodiapophyseal lamina. Neural arch fossae exposed in anterior view include the large and very deep prezygapophyseal centrodiapophyseal fossa, the small centroprezygapophyseal fossa, and the shallow spinoprezygapophyseal fossa, which bears a rudimentary prespinal lamina. Two additional neural arch fossae can also be discerned in this vertebra: the small, ovate postzygapophyseal centrodiapophyseal fossa and the spinodiapophyseal fossa. The system of fossae in the anterior cervical vertebrae of *Nigersaurus* (Sereno et al., 1999, 2007; see also Wilson et al., 2011; Wilson, 2012) appears to be more pronounced than that of *Katepensaurus*. In addition, the dorsally expanded but undivided centroprezygapophyseal lamina in the new Bajo Barreal form differs from the divided condition present in diplodocids and *Nigersaurus* (Whitlock, 2011; Ibiricu et al., 2012). Thus, neither the neural arch laminae nor the fossae of the anterior cervical vertebrae of *Nigersaurus* closely resemble the conditions in UNPSJB-PV 1007/1. In these regards, the overall morphology of the *Katepensaurus* vertebra is more comparable to that of the only known cervical of *Zapalasaurus* (Salgado et al., 2006). Unfortunately, most parts of the lateral surfaces of the neural arch are not preserved, nor is the neural spine.

The incomplete cervical ribs of UNPSJB-PV 1007/1 are fused to the vertebra. Each possesses a well-developed anterior process (‘spine’ sensu Sereno et al., 2007) that is dorsoventrally taller than the remainder of the rib. A strongly developed anterior process also occurs in some species of *Apatosaurus*, such as *A. ajax* (see Upchurch et al., 2004b) and *A. excelsus* (UWGM 15556 [= CM 563]; Gilmore, 1936; *A. parvus* per Upchurch et al. [2004b]), as well as in *Diplodocus* (Hatcher, 1901), *Limaysaurus* (Calvo and Salgado, 1995), *Nigersaurus*, and *Demandasaurus*;

TABLE 2. Measurements (cm) of vertebrae of *Katepensaurus goicoecheai*, gen. et sp. nov. (UNPSJB-PV 1007).

Vertebra	Number	tlc	twas	dvhas	twps	dvhps	nah
Anterior cervical	UNPSJB-PV 1007/1	19.6*	6.5*	5.4*	**	**	10.2*
Middle cervical	UNPSJB-PV 1007/3	19.3*	5.5*	5.1*	7.2*	6.1*	15.8*
Middle-posterior dorsal	UNPSJB-PV 1007/4	17.5	10.4*	13.8*	10.7	13.8	46.5*
Middle-posterior dorsal	UNPSJB-PV 1007/5	11.6*	10.7*	9.8*	13.4	13.6	44.5*
Anterior caudal	UNPSJB-PV 1007/7	10.6*	10.8*	7.1*	**	**	23.5*
Anterior caudal	UNPSJB-PV 1007/8	**	**	**	**	**	23.8

Abbreviations: *, element incomplete, measurement as preserved; **, no measurement provided due to very incomplete preservation; **dvhas**, dorsoventral height, anterior articular surface; **dvhps**, dorsoventral height, posterior articular surface; **nah,** neural arch height; **tlc**, total lateral length, centrum; **twas**, transverse width, anterior articular surface; **twps**, transverse width, posterior articular surface.

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nevertheless, the latter taxon differs from the Bajo Barreal sauropod in having pneumatic cavities in its cervical ribs. In UNPSJB-PV 1007/1, the angle between the capitulum and tuberculum is approximately 90°.

In UNPSJB-PV 1007/2 (Fig. 4), only part of the right side of the vertebra is preserved, including the centrum, the base of the neural arch, and the prezygapophysis. Two ovoid lateral pneumatic fossae can be observed in the centrum, the more anterior of them still filled with matrix. The anterodorsally directed right prezygapophysis is elongate and robust. Neural arch laminae include the anterior centrodiapophyseal, prezygodiapophyseal, centropostzygapophyseal, postzygodiapophyseal, and posterior centrodiapophyseal laminae. These laminae are strongly developed, particularly the last two. Ventrolaterally, near the anterior margin of the centrum, most of the right cervical rib is present, although it has been taphonomically displaced from its position in life.

The morphology of the third preserved cervical vertebra of the *Katepensaurus* holotype, UNPSJB-PV 1007/3 (Fig. 5), is generally comparable to that of the other two cervicals, the main distinctions being related to their differing positions in the neck. Although UNPSJB-PV 1007/3 has suffered some diagenetic deformation, especially on its left side, several salient features can be observed. The lateral surface of the centrum is excavated by well-developed, ovoid pneumatic fossae that are divided by the pleurocentral lamina. Ventrally, the centrum exhibits a sagittal keel that is more pronounced than in UNPSJB-PV 1007/1. The complex of neural arch laminae and fossae includes a thin but well-marked posterior centrodiapophyseal lamina and a horizontal (i.e., anteroposteriorly oriented) lamina located directly dorsal to the pneumatic fossae. Collectively, these two laminae enclose a deep, subtriangular centrodiapophyseal fossa. The broad postzygapophyseal centrodiapophyseal fossa is surrounded by the prominent postzygodiapophyseal, posterior centrodiapophyseal, and centropostzygapophyseal laminae. As best observed in lateral view, the wide prezygapophyseal centrodiapophyseal fossa is placed ventral to the prezygodiapophyseal lamina. The prezygapophyses are long and anterodorsally projected, whereas the preserved portion of the postzygapophysis is oval in outline. The cervical rib is fused to the vertebra, though rotated anteriorly, and exhibits a well-developed anterior process. The angle between the capitulum and tuberculum is less than 90°. The general morphology of UNPSJB-PV 1007/3 is closely comparable to that seen in the cervical vertebrae of other Patagonian rebbachisaurids (e.g., *Cathartesaura*, *Limaysaurus*, MMCH-Pv-49). In several features, this *Katepensaurus* vertebra also resembles those of *Demandasaurus* and *Nigersaurus*; in these two Early Cretaceous rebbachisaurids, however, the pattern of lateral cervical vertebral pneumatization is more complex due to the presence of subdivided fossae.

Dorsal Vertebrae

Three dorsal vertebrae of *Katepensaurus* were recovered (UNPSJB-PV 1007/4, 1007/5, and 1007/6; Figs. 6–8; Table 2), but only two of these (UNPSJB-PV 1007/5 [Figs. 6, 8] and 1007/4 [Fig. 7]) will be described in detail herein, because the remaining vertebra (UNPSJB-PV 1007/6) is poorly preserved. UNPSJB-PV 1007/4, 1007/5, and 1007/6 are identified as middle to posterior dorsal vertebrae that probably form a continuous sequence. This interpretation is based on morphological features (the position of parapophyses, the degree of opisthocoely, and the height of the neural arches in relation to that of the centra; see Table 2) as well as on comparisons with well-represented dorsal vertebral sequences of other diplodocoids.

The centra of these middle to posterior dorsal vertebrae are slightly opisthocoelous, a character that is shared with a few other diplodocoids, such as *Amazonsaurus* (Carvalho et al., 2003; Whitlock, 2011 [although it is not certain that the opisthocoelous

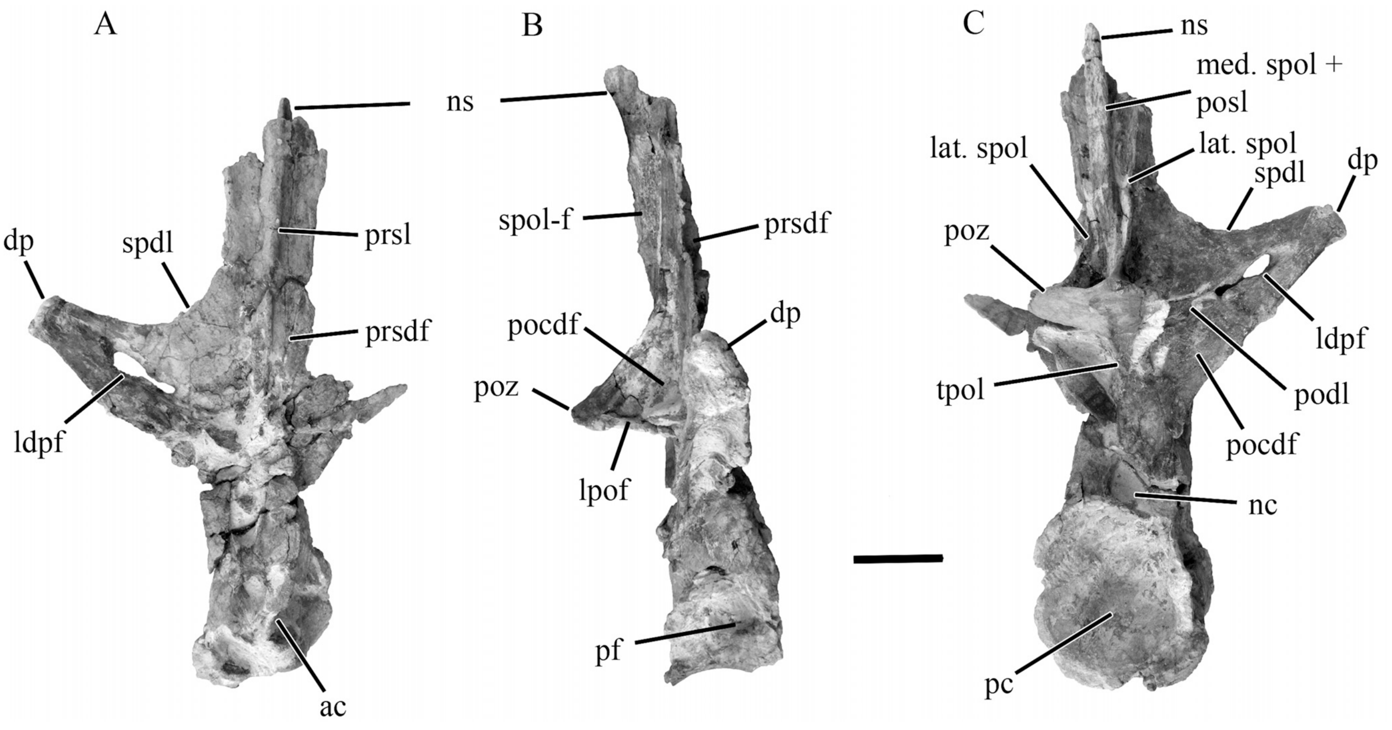

FIGURE 6. Middle or posterior dorsal vertebra (UNPSJB-PV 1007/5) of *Katepensaurus goicoecheai*, gen. et sp. nov., in anterior (**A**), right lateral (**B**), and posterior (**C**) views. For abbreviations, see text. Scale bar equals 10 cm.

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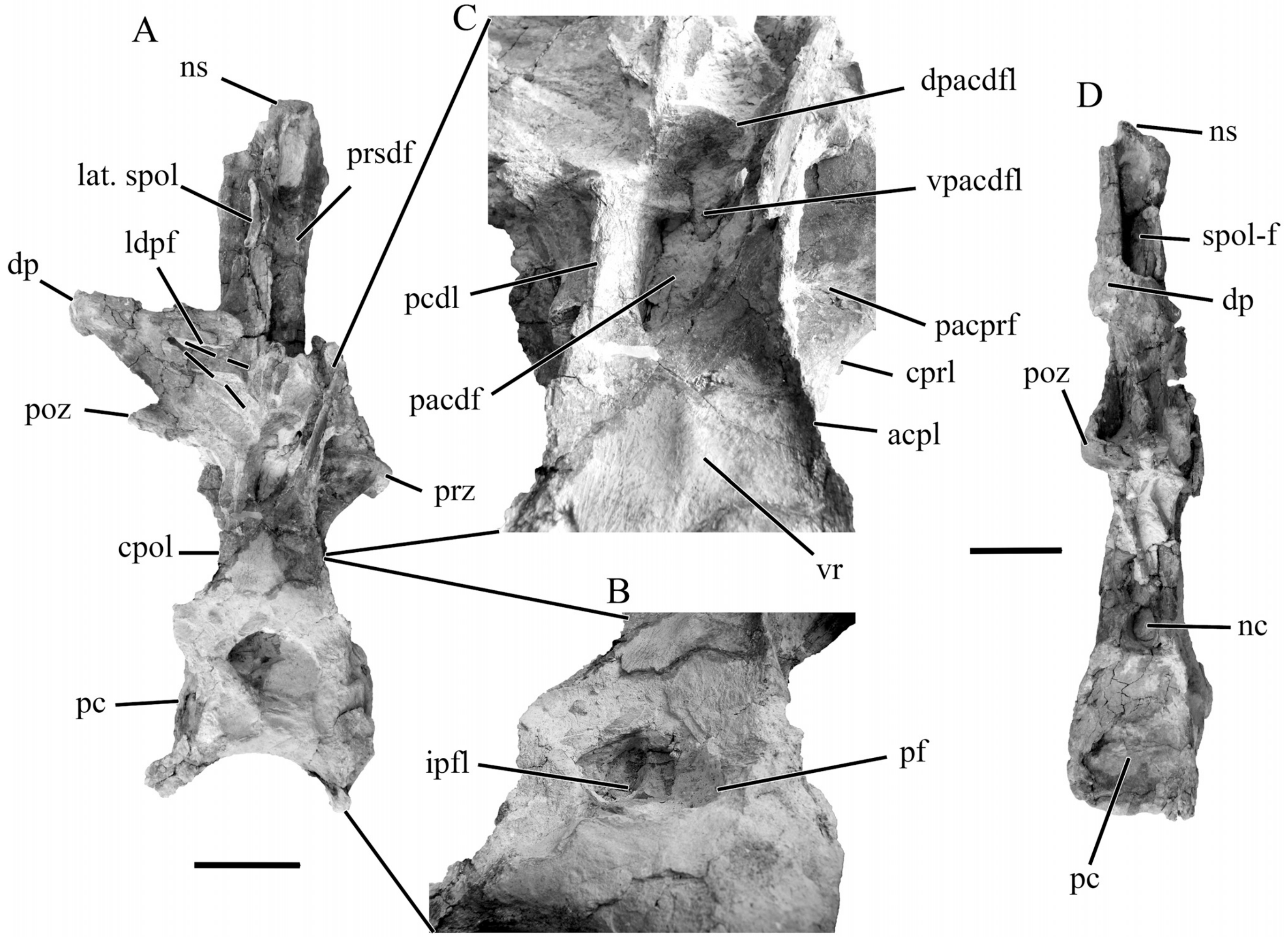

FIGURE 7. Middle or posterior dorsal vertebra (UNPSJB-PV 1007/4) of *Katepensaurus goicoecheai*, gen. et sp. nov. Entire vertebra (**A**), detail of pneumatic fossa of centrum **(B)**, and detail of ventral part of neural arch (**C**) in right lateral view. **D**, entire vertebra in posterior view. For abbreviations, see text. Scale bars in **A** and **D** equal 10 cm.

dorsal vertebrae of this Brazilian taxon actually pertain to the middle or posterior part of the column; see Mannion et al., 2012]), *Demandasaurus* (Torcida Fernández-Baldor et al., 2011), and MMCH-Pv-49 (Haluza et al., 2012). In contrast, in *Comahuesaurus* (Salgado et al., 2004; Carballido et al., 2012), *Limaysaurus* (Calvo and Salgado, 1995), *Nigersaurus* (Sereno et al., 1999, 2007), and *Rebbachisaurus* (Lavocat, 1954; Bonaparte, 1999), as well as in most diplodocids (i.e., *Apatosaurus* [Riggs, 1903; Gilmore, 1936; Upchurch et al., 2004b], *Barosaurus* [Lull, 1919; McIntosh 2005], *Dinheirosaurus* [Bonaparte and Mateus, 1999; Mannion et al., 2012], *Diplodocus* [Osborn, 1899; Hatcher, 1901; Gilmore, 1932]) and dicraeosaurids (e.g., *Amargasaurus* [Salgado and Bonaparte, 1991], *Brachytrachelopan* [Rauhut et al., 2005], *Dicraeosaurus* [Janensch, 1929]), the middle-posterior dorsal centra are amphiplatyan to slightly amphicoelous. The dorsal centra of *Katepensaurus* are anteroposteriorly compressed, with strongly anteroposteriorly concave ventral surfaces, as in most other diplodocoids (e.g., *Amargasaurus*, *Apatosaurus*, *Barosaurus*, *Comahuesaurus*, *Demandasaurus*, *Dicraeosaurus*, *Dinheirosaurus*, *Diplodocus*, *Limaysaurus*, *Nigersaurus*, *Rebbachisaurus*) with rare exceptions (e.g., *Amazonsaurus*, which has comparatively low, elongate centra [Carvalho et al., 2003], and *Brachytrachelopan*, in which the posterior dorsal centra appear ventrally flat [Rauhut et al., 2005]). Middle-posterior dorsal centra of *Demandasaurus* are reported to have a broad, shallow ventral groove (Torcida Fernández-Baldor et al., 2011) that is absent in *Katepensaurus*.

In *Katepensaurus*, the lateral sides of the dorsal centra are invaded by well-defined, ovate pneumatic fossae that extend anteroposteriorly for approximately half of the length of the centra. These large fossae are deep and internally partitioned by a thin, dorsoventrally oriented lamina (Fig. 7B). In general shape and size, the dorsal vertebral pneumatic fossae of *Katepensaurus* are similar to those of many other non-dicraeosaurid diplodocoids (e.g., *Amazonsaurus*, *Apatosaurus*, *Barosaurus*, *Comahuesaurus*, *Demandasaurus*, *Dinheirosaurus*, *Diplodocus*, *Histriasaurus* [Dalla Vecchia, 1999], *Limaysaurus*, *Nigersaurus*, *Nopcsaspondylus* [Nopcsa, 1902; Apesteguía, 2007], *Rebbachisaurus*, MMCH-Pv-49). However, although divided pneumatic fossae are present in dorsal centra of the diplodocids *Dinheirosaurus* and *Supersaurus* (see Mannion et al., 2012), *Katepensaurus* is the only

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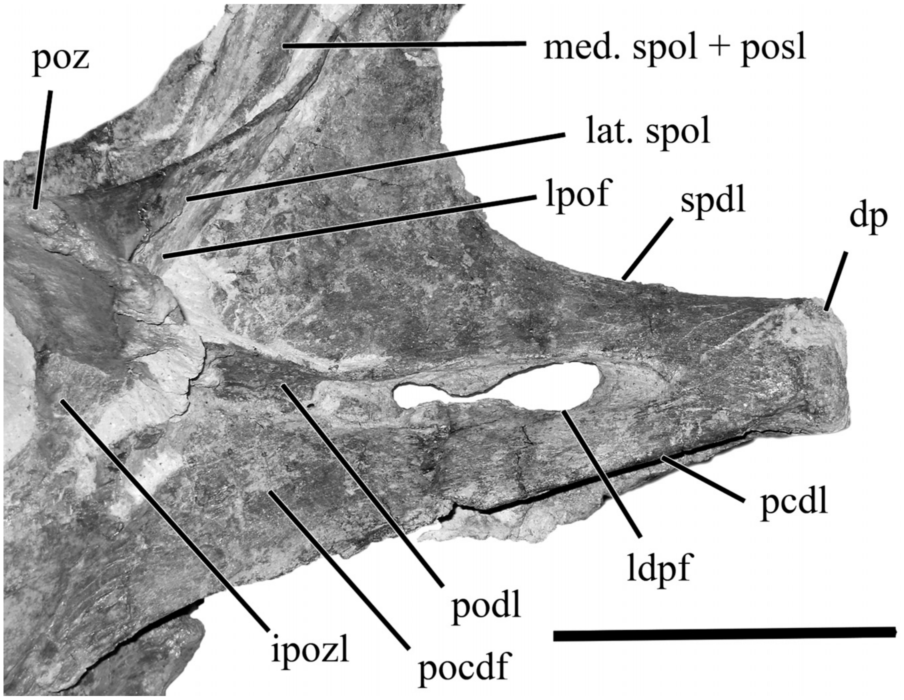

FIGURE 8. Middle or posterior dorsal vertebra (UNPSJB-PV 1007/4) of *Katepensaurus goicoecheai*, gen. et sp. nov. Detail of laterodiapophyseal fenestra and modified postzygodiapophyseal lamina in right posterolateral view. For abbreviations, see text. Scale bar equals 10 cm.

rebbachisaurid in which this morphology has been documented. Furthermore, marked, vertically oriented ridges are present on the lateral surfaces of the Bajo Barreal vertebrae, on the base of the neural arch just dorsal to the neurocentral junction (Fig. 7C); such structures are not observed in other diplodocoids. The oval neural canal of each *Katepensaurus* dorsal vertebra is proportionally large, and its dorsal margin is acute. The neural arches are oriented vertically with respect to the centra and occupy almost their entire length.

One of the most characteristic features of rebbachisaurid dorsal vertebrae is the extreme height of the neural arches, particularly the neural spines. Indeed, in several members of the clade (e.g., *Limaysaurus*, *Nopcsaspondylus*, MMCH-Pv-49), the dorsoventral height of the posterior dorsal neural spines is between three and four times the anteroposterior lengths of their respective centra (Apesteguía et al., 2010; Haluza et al., 2012). Furthermore, in posterior dorsal vertebrae of *Rebbachisaurus*, the height of the neural spine relative to centrum length is even greater (see Bonaparte, 1999; Wilson, 2002). Although the neural spines of all known *Katepensaurus* dorsal vertebrae are incomplete, they appear to have been at least three times taller than their centra are long (see Figs. 6, 7; Table 2).

The transverse processes of UNPSJB-PV 1007/5 are dorsolaterally projected, as in the middle to posterior dorsal vertebrae of many diplodocoids, with the exception of most diplodocids. Consequently, in *Katepensaurus*, the diapophyses are positioned at a much more dorsal level than the zygapophyses. Unfortunately, the transverse processes of UNPSJB-PV 1007/4 and 1007/6 have been taphonomically displaced and distorted. In the former specimen, however, they appear to have been less dorsally oriented than in UNPSJB-PV 1007/5, which may indicate that UNPSJB-PV 1007/4 occupied a slightly more anterior position in the dorsal vertebral column. Each transverse process is pierced by a well-defined fenestra, here termed the laterodiapophyseal fenestra. Although, at first glance, these fenestrae might appear to be taphonomic artifacts, they almost certainly are not, as evidenced by their smooth, undamaged margins as well as their occurrence in all three known dorsal vertebrae of *Katepensaurus* (see Figs. 6–8). The laterodiapophyseal fenestrae are united with the postzygapophyses medially and with the diapophyses laterally by a thin but clearly observed postzygodiapophyseal lamina; in other words, the postzygodiapophyseal laminae are 'interrupted' by these fenestrae. The laterodiapophyseal fenestrae and their consequent modifications to the postzygodiapophyseal laminae constitute a complex of morphologies that have not been documented in other representatives of Rebbachisauridae.

In addition to the postzygodiapophyseal lamina, several other laminae are present on the ventral parts of the dorsal vertebral neural arches of *Katepensaurus*. Laterally, the centroprezygapophyseal laminae and posterior centroparapophyseal laminae delimit the deep parapophyseal centroprezygapophyseal fossa. The lateral surfaces of the neural arches also display additional oval and similarly deep cavities: the postzygapophyseal centrodiapophyseal fossa and the more elongate parapophyseal centrodiapophyseal fossa. The latter fossa is subdivided by two laminae, here termed the dorsal parapophyseal centrodiapophyseal fossa lamina and the ventral parapophyseal centrodiapophyseal fossa lamina. The ventral parapophyseal centrodiapophyseal fossa lamina is anterodorsally oriented and placed approximately in the middle of the parapophyseal centrodiapophyseal fossa, whereas the shorter, horizontal, and less robust dorsal parapophyseal centrodiapophyseal fossa lamina is located near the dorsal edge of this fossa. Generally, the laminae and fossae of the ventral part of the neural arch in *Katepensaurus* are comparable to those seen in other rebbachisaurids (e.g., *Histriasaurus*) as well as flagellicaudatans such as *Apatosaurus*. However, the additional laminae within the parapophyseal centrodiapophyseal fossa have not been documented in other diplodocoids.

The middle-posterior dorsal vertebrae of *Katepensaurus* lack hyposphene-hypantrum articulations, as in a number of other

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rebbachisaurids, with the following exceptions: *Histriasaurus* (see Dalla Vecchia, 1998); MACN PV N35, a probable basal rebbachisaurid ('rebbachisauroid' sensu Apesteguía, 2007) middle-posterior dorsal neural arch from the Early Cretaceous La Amarga Formation of northern Patagonia; *Comahuesaurus*, *Demandasaurus*, and *Nigersaurus*, which possess a 'laminar hyposphene' according to Torcida Fernández-Baldor et al. (2011) and Carballido et al. (2012); and possibly CCC 017, an isolated, probably rebbachisaurid posterior dorsal neural arch from the Early Cretaceous of Brazil (Castro et al., 2007; Whitlock, 2011). Derived titanosaurians also lack hyposphene-hypantrum articulations (Salgado et al., 1997). Nearly all other sauropods, in contrast, possess this articular complex (Apesteguía, 2005; Apesteguía et al., 2010).

In dorsal vertebrae of *Katepensaurus*, the prezygapophyses are proportionally smaller than the postzygapophyses. In vertebra UNPSJB-PV 1007/4, the prezygapophyses exhibit well-marked facets that are united to form a continuous articular surface. A prominent lamina or ridge extends ventrally from the transverse midpoint of the unified prezygapophyses. Two well-developed centroprezygapophyseal laminae are also present and surrounded by fossae. The postzygapophyses mirror the morphology of the prezygapophyses in exhibiting united facets that are subcircular in outline. Ventrally, the coalesced postzygapophyses intersect a short infrapostzygapophyseal lamina or ridge, probably the same as the laminar hyposphene described in *Comahuesaurus* (Salgado et al., 2004; Carballido et al., 2012) and *Demandasaurus* (Torcida Fernández-Baldor et al., 2011). Both the intraprezygapophyseal and intrapostzygapophyseal laminae are present. Also, the new Bajo Barreal sauropod possesses well-defined, rounded fossae on the lateral surfaces of the postzygapophyses.

In *Katepensaurus*, the general morphology of the zygapophyses and related structures (i.e., the associated complex of laminae and fossae) most closely resembles those of *Limaysaurus*, *Nopcsaspondylus* (Nopcsa, 1902), *Rebbachisaurus*, and especially the unnamed rebbachisaurid MMCH-Pv-49 (Apesteguía et al., 2010; Haluza et al., 2012). Conversely, *Haplocanthosaurus* (Hatcher, 1903), dicraeosaurids (e.g., *Dicraeosaurus*), diplodocids (e.g., *Barosaurus*, *Diplodocus*), and several other rebbachisaurids (e.g., *Comahuesaurus*, *Demandasaurus*, *Histriasaurus*, MACN PV N35) have hyposphene-hypantrum articulations and divided zygapophyseal facets.

The dorsal vertebral neural spines of the new central Patagonian sauropod are approximately twice as tall dorsoventrally as the centra, and pneumatized (i.e., deep and well-marked fossae or cavities are present). Given that the spines are dorsally incomplete, they would have been even taller in life. The neural spines bear well-developed pre- and postspinal laminae, with the former being more robust than the latter. The prespinal laminae are gently arched anteriorly and do not reach the base of the neural arch. The pre- and postspinal laminae of the Bajo Barreal dorsal vertebrae resemble those of other diplodocoids in general and rebbachisaurids in particular. These laminae are situated within deep, bilateral fossae, the prezygapophyseal spinodiapophyseal fossa and the spinopostzygapophyseal lamina fossa, respectively. These fossae exhibit flat bases or 'fossa floors,' unlike those observed in other rebbachisaurids (e.g., MMCH-Pv-49) that are slightly concave. Lateral to the postspinal lamina there are two well-marked spinopostzygapophyseal laminae that course dorsolaterally–ventromedially. These laminae, here identified as the lateral spinopostzygapophyseal laminae, surpass the dorsoventral plane of the dorsal margins of the transverse processes and extend to the broken dorsal edge of the neural spine (see, for example, UNPSJB-PV 1007/5; Fig. 6). Conversely, in most other rebbachisaurids (with the exceptions of *Comahuesaurus*, *Histriasaurus*, *Rebbachisaurus*, and possibly MMCH-Pv-49; see Apesteguía et al., 2010; Carballido et al., 2012; Haluza et al., 2012; Wilson, 2012), the lateral spinopostzygapophyseal laminae are apparently not present, or at least are strongly reduced. In these rebbachisaurids (e.g., *Limaysaurus*, *Nopcsaspondylus*, MACN PV N35), this condition results in there being a single, continuous fossa on the posterolateral surface of the neural arch that is bounded medially by the conjoined medial spinopostzygapophyseal and postspinal laminae, dorsally by the spinodiapophyseal lamina, and ventrolaterally by the postzygodiapophyseal lamina. In dorsal vertebrae of *Katepensaurus*, *Histriasaurus*, *Rebbachisaurus*, and possibly *Comahuesaurus* and MMCH-Pv-49, the presence of the lateral spinopostzygapophyseal lamina divides this fossa in two, into mediolaterally narrow dorsomedial and wider ventrolateral portions.

Caudal Vertebrae

Two sauropod caudal vertebrae were recovered from the *Katepensaurus* type locality (UNPSJB-PV 1007/7, 1007/8; Figs. 9–11; Table 2). The more complete of the two, UNPSJB-PV 1007/7 (Figs. 9, 11), preserves much of its right side, including the transverse process and part of the centrum. Only the neural arch is preserved in UNPSJB-PV 1007/8 (Fig. 10). Based on features present in the neural arches of these specimens, as well as on comparisons with well-preserved diplodocoid caudal sequences (e.g., that of *Limaysaurus*; Calvo and Salgado, 1995), we assign these vertebrae to the anterior, but not the anterior-most, part of the tail.

A well-defined, oval neural canal is evident in UNPSJB-PV 1007/7. The wing-like right transverse process is directed dorsolaterally, as in several non-diplodocid diplodocoids such as *Cathartesaura*, *Comahuesaurus*, *Demandasaurus*, *Dicraeosaurus*, *Limaysaurus*, *Nigersaurus*, *Zapalasaurus*, and MIWG 5384, an isolated rebbachisaurid anterior caudal vertebra from the Early Cretaceous of England (Mannion et al., 2011). Ventrally, the process arises from the dorsal portion of the centrum; dorsally, it contacts the neural arch at a position nearly level with the dorsoventral plane of the prezygapophyses. The anterior surface of the process is excavated by a relatively large prezygapophyseal centrodiapophyseal fossa, resembling, at least generally, the anterior caudal transverse processes of several other diplodocoids (e.g., *Apatosaurus ajax*, *A. louisae*, *Barosaurus*, *Comahuesaurus*, *Demandasaurus* [Torcida Fernández-Baldor et al., 2011], *Diplodocus*, *Supersaurus*, MIWG 5384 [Mannion et al., 2011]) in this regard. Nevertheless, the transverse process of UNPSJB-PV 1007/7 remains thick and robust throughout its extent (i.e., although the process is, in general, anteroposteriorly compressed, no part of it consists of a thin bony 'lamina' or 'web'). By contrast, in the single known anterior caudal vertebra of *Cathartesaura*, the transverse process consists of anteroposteriorly thickened dorsal and ventral components (termed 'bars' by several authors: e.g., Calvo and Salgado, 1995; Gallina and Otero, 2009) that are united throughout their length by a much thinner 'web' of bone. Moreover, in the anterior-most two to three caudal vertebrae of *Apatosaurus excelsus* (UWGM 15556: Gilmore, 1936; *A. parvus* per Upchurch et al., 2004b) and *Limaysaurus* (Calvo and Salgado, 1995), the 'bars' remain separate until their lateral ends (i.e., the 'web' is reduced or absent); as such, the transverse processes of these vertebrae contain fenestrae.

The dorsal edge of the anterior caudal transverse process of *Katepensaurus* is formed by a well-developed lamina, here interpreted as the prezygodiapophyseal lamina following Wilson (1999) and Torcida Fernández-Baldor et al. (2011), which courses approximately mediolaterally, delineating the dorsal margin of the prezygapophyseal centrodiapophyseal fossa. Near its lateral end, the prezygodiapophyseal lamina is intersected by a second, steeply dorsolaterally–ventromedially oriented lamina, here termed the

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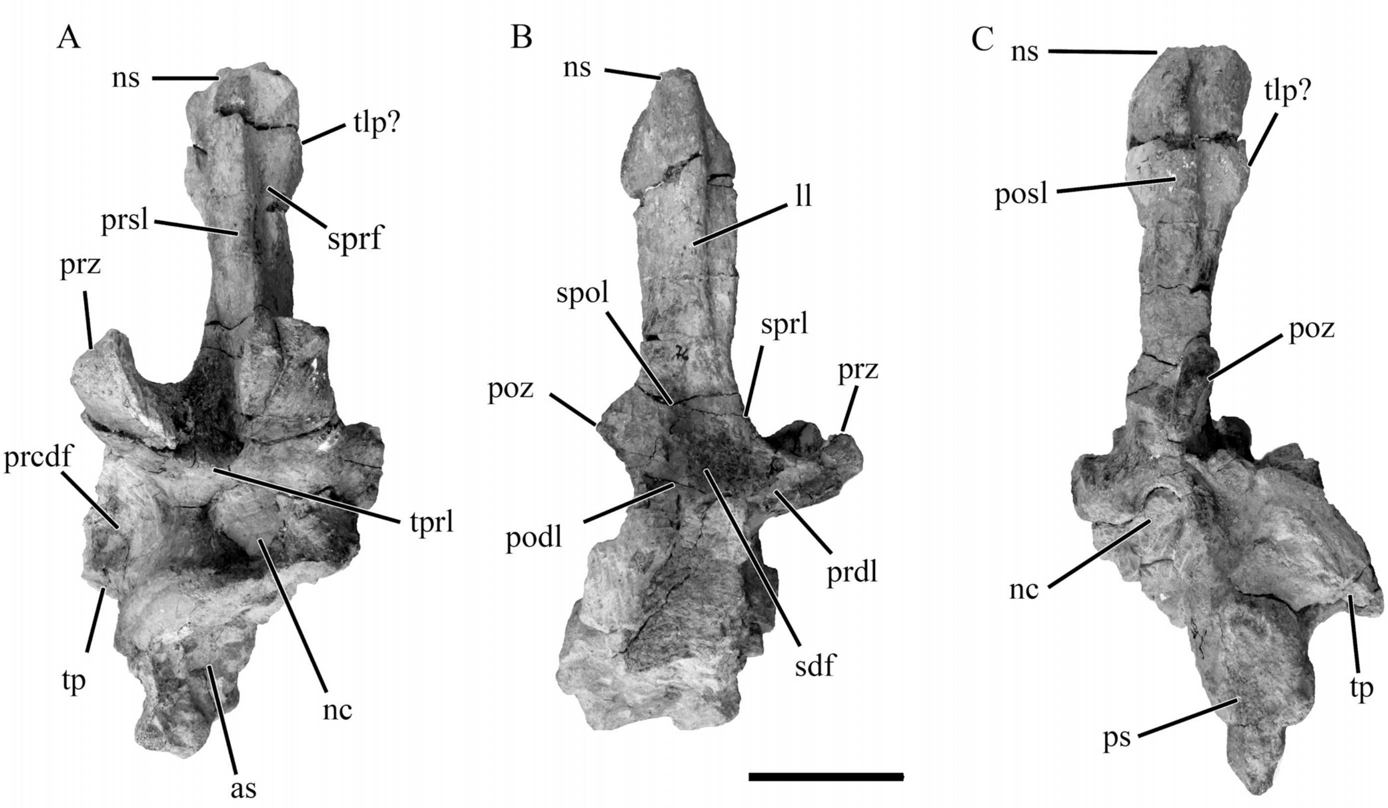

FIGURE 9. Anterior caudal vertebra (UNPSJB-PV 1007/7) of *Katepensaurus goicoecheai*, gen. et sp. nov., in anterior (**A**), right lateral (**B**), and posterior (**C**) views. For abbreviations, see text. Scale bar equals 10 cm.

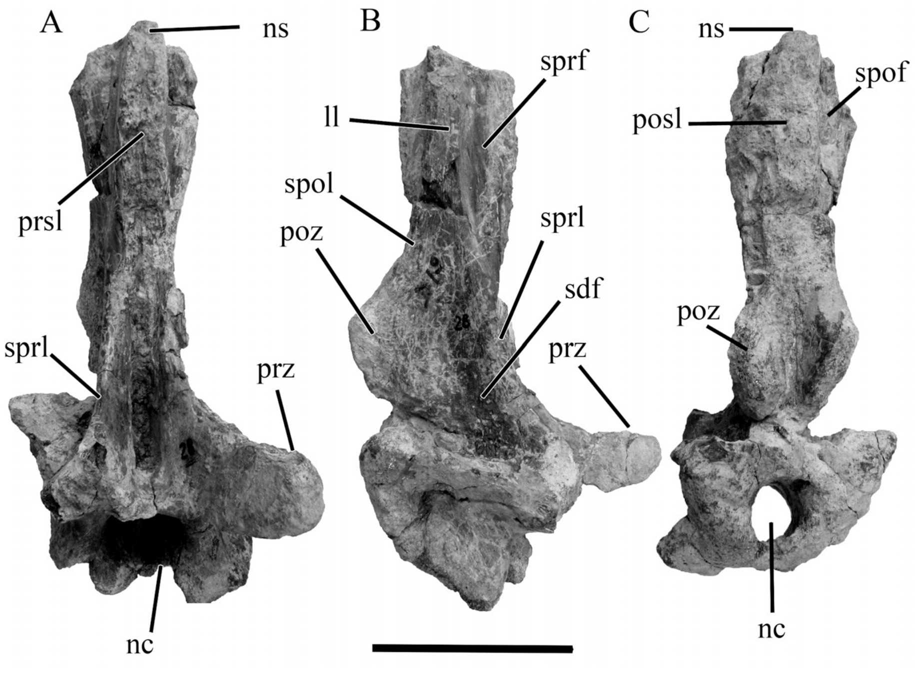

FIGURE 10. Anterior caudal vertebra (UNPSJB-PV 1007/8) of *Katepensaurus goicoecheai*, gen. et sp. nov., in anterior (**A**), right lateral (**B**), and posterior (**C**) views. For abbreviations, see text. Scale bar equals 10 cm.

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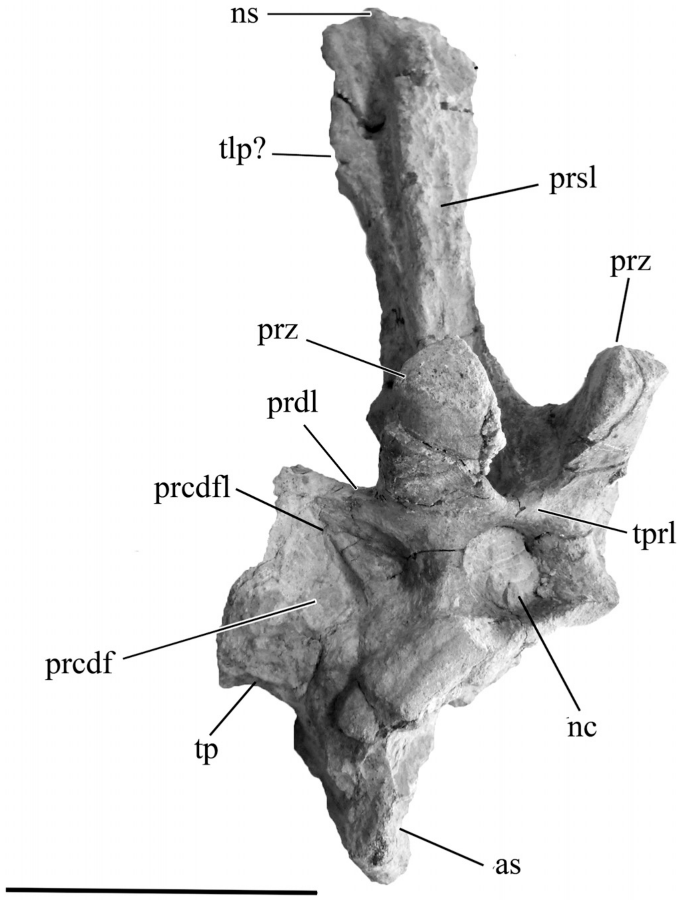

FIGURE 11. Anterior caudal vertebra (UNPSJB-PV 1007/7) of *Katepensaurus goicoecheai*, gen. et sp. nov., in right anterolateral view, showing prezygapophyseal centrodiapophyseal fossa lamina of transverse process. For abbreviations, see text. Scale bar equals 10 cm.

prezygapophyseal centrodiapophyseal fossa lamina, that arises from the dorsolateral margin of the centrum and isolates the dorsomedial corner of the prezygapophyseal centrodiapophyseal fossa from the remainder of this fossa (Fig. 11). Comparable laminae occur on the anterior surfaces of the transverse processes of MIWG 5384, although in this English rebbachisaurid vertebra these laminae originate from the ventral margins of the prezygodiapophyseal lamina and angle ventrolaterally, reaching the lateral edges of the transverse processes (Mannion et al., 2011). Similar laminae are also present in anterior caudal vertebrae of *Demandasaurus*; nevertheless, the position and extent of these laminae differ from those seen in *Katepensaurus* (see Torcida Fernández-Baldor et al., 2011).

The prezygapophyses of UNPSJB-PV 1007/7 are robust, anteriorly elongate, anterodorsally directed, and united by a short intraprezygapophyseal lamina, as in *Amazonsaurus*, *Dicraeosaurus*, diplodocids, *Nigersaurus*, and *Zapalasaurus*. Moreover, their ovoid facets are dorsomedially oriented, a feature that is also present in the aforementioned diplodocoids. The postzygapophyses are slightly posterodorsally projected and shorter than the prezygapophyses, as in many other diplodocoids (e.g., *Amazonsaurus*, *Apatosaurus*, *Dicraeosaurus*, *Diplodocus*, *Nigersaurus*, *Tornieria* [Remes, 2006], and *Zapalasaurus*, among others).

Unfortunately, the centrum of UNPSJB-PV 1007/7 is not complete; therefore, its height relative to that of the neural spine cannot be ascertained. In lateral view, the spine is essentially straight, as in anterior caudal vertebrae of *Amazonsaurus*, *Limaysaurus*, *Nigersaurus*, and most flagellicaudatans, rather than noticeably curved anteriorly towards its dorsal extreme as in *Cathartesaura*, *Dicraeosaurus hansemanni*, and some caudal vertebrae of *Demandasaurus* (Pereda Suberbiola et al., 2003) and *Zapalasaurus* (Salgado et al., 2006). The neural spine of *Katepensaurus* is transversely expanded toward its dorsal apex, being broader than anteroposteriorly long, as in virtually all other diplodocoids for which anterior caudal vertebrae are known. When observed in anterior or posterior view (Fig. 9A, C) it exhibits the 'petal shape' characteristic of other rebbachisaurids and *Dicraeosaurus*. The neural spine of the Bajo Barreal vertebra appears to exhibit 'triangular lateral processes' (sensu Mannion et al. [2011] and Whitlock [2011]) comparable to those seen in *Demandasaurus*, *Nigersaurus*, and MIWG 5384 (see Figs. 9, 11); nevertheless, in *Katepensaurus*, these processes are less prominent than in those Afro-European rebbachisaurids. According to Mannion et al. (2011) and Whitlock (2011), the anterior caudal vertebrae of *Zapalasaurus* also possess incipient 'triangular lateral processes.' Although the tip of the neural spine is imperfectly preserved, there is no indication of the deep bifurcation present in *Diplodocus* (Osborn, 1899; Hatcher, 1901).

The anterior surface of the neural spine of UNPSJB-PV 1007/7 is excavated by a spinoprezygapophyseal fossa that is particularly deep toward its ventral end and that bears a well-developed prespinal lamina. This lamina is transversely broader in its dorsal portion, a morphology that is shared with several other diplodocoids (e.g., *Apatosaurus*, *Barosaurus*, *Cathartesaura*, *Demandasaurus*, *Diplodocus*, *Limaysaurus*, *Nigersaurus*, MIWG 5384). A relatively well-developed postspinal lamina is present on the posterior surface of the neural spine; unfortunately, however, the complex of fossae in this area cannot be reliably interpreted due to diagenetic deformation of the vertebra. A well-marked but not very deep spinodiapophyseal fossa is observed on both lateral sides of the neural arch, and is surrounded by the spinoprezygapophyseal, prezygodiapophyseal, spinopostzygapophyseal, and postzygodiapophyseal laminae. A robust lateral lamina, formed by the fusion of the spinoprezygapophyseal and spinopostzygapophyseal laminae, is present on the lateral aspect of the neural spine. The morphology and composition of the lateral lamina appears to vary considerably between different rebbachisaurid taxa (Gallina and Apesteguía, 2005; Mannion et al., 2011; Ibiricu et al., 2012). For example, that seen in MIWG 5384, where the lateral lamina is composed entirely of the spinodiapophyseal lamina, differs from those of *Limaysaurus* and *Nigersaurus*, where the lateral lamina consists of the fused spinoprezygapophyseal and spinopostzygapophyseal laminae. In *Cathartesaura*, the lateral lamina is said to arise from the junction of the spinoprezygapophyseal, spinopostzygapophyseal, and spinodiapophyseal laminae (Gallina and Apesteguía, 2005), whereas in *Demandasaurus* it "seems to originate halfway up the neural spine" according to Mannion et al. (2011:778).

The remaining caudal vertebral element of the *Katepensaurus* holotype is a well-preserved neural arch (UNPSJB-PV 1007/8), the morphology of which does not differ appreciably from that of UNPSJB-PV 1007/7. Although all major features described for the neural arch of UNPSJB-PV 1007/7 are also present in UNPSJB-PV 1007/8, the latter is smaller in size. Therefore, UNPSJB-PV 1007/8 probably corresponds to an anterior caudal vertebra, but one that is posteriorly located in the sequence in relation to UNPSJB-PV 1007/7. The zygapophyses are smaller in UNPSJB-PV 1007/8 than in UNPSJB-PV 1007/7, as is the complex of laminae (i.e., prespinal, postspinal, and lateral [= conjoined

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spinoprezygapophyseal and spinopostzygapophyseal] laminae) and fossae (spinoprezygapophyseal and spinopostzygapophyseal fossae), with the exception of the spinodiapophyseal fossa.

DISCUSSION

Phylogenetic Affinities

To assess the phylogenetic position of *Katepensaurus goicoecheai*, we evaluated, in UNPSJB-PV 1007, the condition of synapomorphic characters of Diplodocoidea and clades within that have been proposed by previous authors. Following Whitlock (2011:appendix 4), *Katepensaurus* is considered a diplodocoid because the spinoprezygapophyseal laminae in its dorsal vertebrae are fused to form a single prespinal lamina, and the anteroposterior length of its cervical ribs is subequal to that of their corresponding centra. Furthermore, the new taxon shares the following synapomorphies of the anterior caudal neural arches with the clade formed by *Amazonsaurus* + more derived diplodocoids (Whitlock, 2011): (1) neural spines 'petal-shaped' in anterior/posterior view; (2) neural spines transversely broad; and (3) spinoprezygapophyseal lamina extends onto lateral aspect of neural spine. The Bajo Barreal sauropod also exhibits middle dorsal vertebrae with neural spines that are at least twice as tall dorsoventrally as their respective centra are anteroposteriorly long; according to Whitlock (2011), this morphology is a synapomorphy of the clade formed by *Amphicoelias* + more derived diplodocoids.

In *Katepensaurus*, the neural spines of the middle-posterior dorsal vertebrae are dorsoventrally taller than their respective neural arch pedicels, and the anterior caudal transverse processes are wing-like, conditions that Whitlock (2011) considered synapomorphic of the clade Rebbachisauridae + Flagellicaudata (which, following Calvo and Salgado [1995] and Taylor and Naish [2005], might reasonably be termed Diplodocimorpha). Moreover, the new Patagonian diplodocoid displays a combination of characters in its middle-posterior dorsal vertebrae that confirms its referral to Rebbachisauridae: (1) transverse processes inclined steeply dorsally (Rauhut et al., 2005; Whitlock, 2011); (2) spinopostzygapophyseal laminae divided near postzygapophyses (Whitlock, 2011); and (3) neural spines 'petal-shaped' in anterior/posterior view (Wilson, 2002). Additionally, Apesteguía et al. (2010) argued that large, flat spaces (here interpreted as shallow fossae) between the prespinal lamina and diapophyses on the anterior surfaces of the posterior dorsal neural arches are characteristic of rebbachisaurids; such fossae are evident in *Katepensaurus*. (Because these fossae are formed primarily by the spinodiapophyseal lamina, which is 'festooned' away from the neural spine and diapophysis, we interpret the condition described by Apesteguía et al. [2010] as equivalent to the derived state of Whitlock's [2011] character 104.)

Katepensaurus also possesses a number of morphologies that, according to Whitlock (2011), are diagnostic of clades within Rebbachisauridae. Namely, the new Bajo Barreal taxon has middle-posterior dorsal vertebrae in which the neural arch pedicels are dorsoventrally taller than their corresponding centra and hyposphene-hypantrum articulations are lacking, conditions that were considered to be synapomorphies of *Rebbachisaurus* + more derived rebbachisaurids (although the latter character state was regarded as a synapomorphy of Rebbachisauridae by Wilson [2002] and Apesteguía et al. [2010]). *Katepensaurus* also displays anterior-middle cervical vertebrae with a longitudinal ridge on the ventral surface of the centrum, no paired pneumatic fossae on the ventral centrum face, and no external pneumatization of the dorsal surface of the parapophysis, as well as anterior caudal vertebrae with dorsally directed transverse processes. Whitlock (2011) postulated these four characters as diagnostic of the rebbachisaurid subclade Limaysaurinae + Nigersaurinae. The new central Patagonian sauropod also has anterior caudal neural spines with spinoprezygapophyseal lamina–spinopostzygapophyseal lamina contact, a hypothesized synapomorphy of Limaysaurinae (Whitlock, 2011). Interestingly, however, *Katepensaurus* also shares selected morphologies with rebbachisaurid taxa that are frequently regarded as belonging to Nigersaurinae. For instance, the anterior caudal vertebra UNPSJB-PV 1007/7 possesses a lamina in the prezygapophyseal centrodiapophyseal fossa, as in *Demandasaurus* and the isolated caudal vertebra MIWG 5384 (Mannion et al., 2011). Furthermore, the neural spine of this *Katepensaurus* vertebra shows what appear to be 'triangular lateral processes'; such processes are well developed in *Demandasaurus*, *Nigersaurus*, and MIWG 5384, and incipiently present in *Zapalasaurus* (Mannion et al., 2011; Whitlock, 2011). In sum, based on the apomorphic character states it possesses, we regard *Katepensaurus* as a member of Rebbachisauridae and provisionally as part of the subclade Limaysaurinae. Nevertheless, the significance of the features that the new taxon shares with nigersaurines should be explored in future analyses of rebbachisaurid interrelationships.

Significance of *Katepensaurus* for Rebbachisaurid Morphology and Evolution

Several osteological characters of *Katepensaurus* are deserving of further comment. As mentioned above (Description and Comparisons), the middle-posterior dorsal vertebrae of this central Patagonian diplodocoid exhibit peculiar zygapophyseal articulations, the morphology of which is comparable to that of several other Gondwanan Late Cretaceous rebbachisaurids, including *Limaysaurus*, *Nopcsaspondylus*, *Rebbachisaurus*, and MMCH-Pv-49 (Apesteguía et al., 2010; Haluza et al., 2012). The condition of this articular complex (including the zygapophyses and their associated laminae) might therefore represent one or more presently unrecognized synapomorphies of a particular rebbachisaurid subclade (e.g., *Rebbachisaurus* + more derived rebbachisaurids of Whitlock [2011]). Additionally, the posterior surfaces of the dorsal vertebral neural spines of *Katepensaurus* exhibit laminae that are here interpreted as lateral spinopostzygapophyseal laminae. Although such laminae are widespread within Eusauropoda (Wilson, 1999), they appear to be lacking, or at least strongly reduced, in most other rebbachisaurids, with the exceptions of *Comahuesaurus*, *Histriasaurus*, *Rebbachisaurus*, and possibly MMCH-Pv-49 (see Bonaparte, 1999; Apesteguía et al., 2010; Carballido et al., 2012; Haluza et al., 2012; Wilson, 2012). Consequently, the reduction or loss of the lateral spinopostzygapophyseal lamina in dorsal vertebrae may eventually be shown to constitute a synapomorphy of a clade within Rebbachisauridae.

Wilson (2002) viewed the presence of wing-like anterior caudal transverse processes as a synapomorphy of Diplodocidae + Dicraeosauridae (= Flagellicaudata; Harris and Dodson, 2004). Nevertheless, such transverse processes also occur in *Cathartesaura* (Gallina and Apesteguía, 2005; Gallina and Otero, 2009), *Demandasaurus* (Torcida Fernández-Baldor et al., 2011), *Katepensaurus*, and the isolated rebbachisaurid caudal vertebra UNPSJB-PV 580 (Ibiricu et al., 2012). Consequently, the anatomy of *Katepensaurus* reinforces the hypothesis, originally postulated by Calvo and Salgado (1995) and supported by several subsequent authors (e.g., Whitlock, 2011; Whitlock et al., 2011; Ibiricu et al., 2012), that the occurrence of wing-like anterior caudal transverse processes is synapomorphic of a diplodocoid clade more inclusive than Flagellicaudata (e.g., Rebbachisauridae + Flagellicaudata).

Finally, among the proposed autapomorphies of the recently named Spanish Early Cretaceous rebbachisaurid *Demandasaurus* are large, deep cavities (here identified as prezygapophyseal centrodiapophyseal fossae following Wilson et al. [2011]) that are

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subdivided by laminae in the anterior caudal transverse processes (Torcida Fernández-Baldor et al., 2011). A closely similar morphology is evident in MIWG 5384, an isolated rebbachisaurid anterior caudal vertebra from approximately coeval deposits in England (Mannion et al., 2011). The preserved anterior caudal transverse process of *Katepensaurus* does not exhibit a deep cavity, but does possess a lamina (here termed the prezygapophyseal centrodiapophyseal fossa lamina) similar to those present in the two European forms (see Fig. 11). Consequently, although evidence for close affinities between *Katepensaurus* and these European taxa is otherwise weak, the presence of comparable caudal vertebral laminae in these three rebbachisaurids could conceivably represent a diagnostic character state of a clade composed of these forms. Alternatively, this condition might constitute a synapomorphy of a more inclusive rebbachisaurid clade that would have subsequently been lost in selected taxa within the group (e.g., *Cathartesaura*, *Limaysaurus*). Future phylogenetic analyses of Rebbachisauridae may shed light on these possibilities.

‘Middle’ Cretaceous Rebbachisaurid Diversity

Recently, Ibiricu et al. (2012) described a collection of associated (UNPSJB-PV 1004) and isolated (UNPSJB-PV 580, UNPSJB-PV 1005) rebbachisaurid axial skeletal elements that were recovered from exposures of the Bajo Barreal Formation at the Laguna Palacios, Los Sauces, and Ocho Hermanos localities (respectively) in south-central Chubut Province (Argentina). Given the close geographic and stratigraphic coincidence of these fossils with the *Katepensaurus* holotype (UNPSJB-PV 1007), it is conceivable that some or all of them could pertain to the new taxon. One of these elements, an isolated anterior to middle cervical vertebra (UNPSJB-PV 1005), overlaps at least approximately with the *Katepensaurus* cervicals described herein. The morphologies of the lateral pneumatic fossae of the centrum and the neural arch laminae and fossae of UNPSJB-PV 1005 differ in some details from the equivalent structures in the cervical vertebrae of UNPSJB-PV 1007 (e.g., the laminae are more pronounced and the fossae are deeper in the former vertebra). Nevertheless, the sagittally positioned ventral keel, a feature not reported in many rebbachisaurids, occurs in both specimens. Unfortunately, none of the cervical neural spines of UNPSJB-PV 1007 are completely preserved; therefore, the presence or absence of the dorsally bifid condition of UNPSJB-PV 1005 (a morphology that, among rebbachisaurids, is presently unique to this vertebra) cannot be evaluated in the *Katepensaurus* holotype. Consequently, at present, the evidence is insufficient to determine whether or not UNPSJB-PV 1005 is referable to *Katepensaurus*. We continue to regard the former specimen as Rebbachisauridae indet.

Ibiricu et al. (2012) also redescribed UNPSJB-PV 580, a well-preserved rebbachisaurid anterior-most caudal vertebra that was originally described by Sciutto and Martínez (1994). Although the two known caudal vertebrae of *Katepensaurus* (UNPSJB-PV 1007/7 and 1007/8) are also anterior caudals, they do not directly overlap in position with UNPSJB-PV 580. However, several unusual features of the latter are also present in the *Katepensaurus* caudal vertebrae, including a neural spine that is tall, transversely expanded toward its dorsal apex, petal-shaped in anterior and posterior views, straight in lateral view, and that possesses a well-developed lateral lamina. Nevertheless, UNPSJB-PV 1007/7 and 1007/8 also differ from UNPSJB-PV 580 in multiple regards, including lower neural spines and longer zygapophyses in the former two vertebrae. Furthermore, unlike the condition in UNPSJB-PV 580, the transverse process of UNPSJB-PV 1007/7 does not exhibit well-defined, anteroposteriorly thick dorsal and ventral ‘bars’ that are connected by a much thinner bony ‘web.’ These discrepancies between UNPSJB-PV 580 and the two *Katepensaurus* caudals may be due exclusively to the differing positions of these vertebrae in the tail (see, for example, *Demandasaurus*, in which the morphology of different anterior caudal vertebrae varies substantially; Torcida Fernández-Baldor et al., 2011); however, they may also be due to taxonomic distinction. At present, it is not possible to confidently support either of these alternatives. Finally, the fragmentary caudal series UNPSJB-PV 1004 is too poorly preserved to allow for meaningful comparisons with *Katepensaurus*. As with UNPSJB-PV 1005, we regard UNPSJB-PV 580 and UNPSJB-PV 1004 as Rebbachisauridae indet. There is, at present, no concrete evidence for more than one rebbachisaurid taxon in the Bajo Barreal Formation.

Based on its possession of a proposed synapomorphy of the clade (anterior caudal neural spines with spinoprezygapophyseal lamina–spinopostzygapophyseal lamina contact; Whitlock, 2011), *Katepensaurus* is regarded as a possible member of Limaysaurinae. Provided that the systematics of this rebbachisaurid subclade have been adequately assessed, it would appear that these sauropods were diverse in the ‘middle’ Cretaceous (Aptian–Turonian) of southernmost South America, especially toward the end of that temporal span (Table 1). At least three limaysaurine or putative limaysaurine genera (*Cathartesaura*, *Limaysaurus*, and *Katepensaurus*) are known from the early Late Cretaceous (Cenomanian–Turonian) of Patagonia; this number would increase to four or even five if, as seems likely, the fragmentary *Rayososaurus* and the generically unidentified rebbachisaurid MMCH-Pv-49 are also part of this clade (Apesteguía et al., 2010; Carballido et al., 2010; Haluza et al., 2012). Furthermore, two additional genera of Rebbachisauridae, albeit of less certain lower-level relationships, are known from the Cenomanian: *Nopcsaspondylus* from northern Patagonia and *Rebbachisaurus* from Morocco (Table 1). It therefore appears that at least six rebbachisaurid genera were in existence in parts of western Gondwana (Patagonia and North Africa) during the Cenomanian–Turonian. No fossils of the clade have, as yet, been discovered in more recent deposits. It thus seems that Rebbachisauridae may have achieved its greatest taxonomic diversity within a few million years of its extinction.

CONCLUSIONS

Katepensaurus goicoecheai is a new taxon of diplodocoid sauropod dinosaur from the Upper Cretaceous (Cenomanian–Turonian) Lower Member of the Bajo Barreal Formation of south-central Chubut Province, central Patagonia, Argentina. The holotypic specimen is an incomplete but associated axial skeleton that includes cervical, dorsal, and caudal vertebrae. Diagnosed by multiple autapomorphies of the middle-posterior dorsal vertebrae, *Katepensaurus* is the first diplodocoid from the San Jorge Basin to be identified to the generic level. Based on morphological comparisons with other diplodocoid taxa and its possession of several synapomorphic character states, *Katepensaurus* is regarded as a member of Rebbachisauridae, possibly as part of the subclade Limaysaurinae. The discovery of the new taxon adds to the globally sparse rebbachisaurid fossil record and augments our knowledge of central Patagonian terrestrial vertebrate assemblages during the early Late Cretaceous. When considered in light of other rebbachisaurid occurrences from this interval, *Katepensaurus* suggests that these distinctive sauropods may have reached the pinnacle of their taxonomic diversity within a few million years of their extinction.

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