VOL. 52 | ISSUE 4

TRIASSIC VERTEBRATES
A new continental fauna from the Late Triassic of Argentina: Cynodonts, turtles, pseudosuchians, and dinosauromorphs.

JURASSIC SAUROPODS
Remains from the Late Jurassic of Chile indicates high sauropod diversity in South America.

WOODS AND FUNGI
Jurassic coniferous wood from western Argentina and the role of basidiomycetes in wood decay during the Mesozoic in Gondwana.

NEW MATERIAL OF *KATEPENSAURUS GOICOECHEAI* (SAUROPODA: DIPLODOCOIDEA) AND ITS SIGNIFICANCE FOR THE MORPHOLOGY AND EVOLUTION OF REBBACHISAURIDAE

LUCIO M. IBIRICU[1]
GABRIEL A. CASAL[2]
RUBÉN D. MARTÍNEZ[2]
MATTHEW C. LAMANNA[3]
MARCELO LUNA[2]
LEONARDO SALGADO[4]

[1]Laboratorio de Paleontología, Centro Nacional Patagónico (CENPAT-CONICET), Boulevard Almirante Brown 2915, 9120 Puerto Madryn, Chubut, Argentina.
[2]Laboratorio de Paleovertebrados, Universidad Nacional de la Patagonia San Juan Bosco, C.C. 360, 9000 Comodoro Rivadavia, Chubut, Argentina.
[3]Section of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213 U.S.A.
[4]CONICET, Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro, Av. General Roca 1242, 8332 General Roca, Río Negro, Argentina.

PLEASE SCROLL DOWN FOR ARTICLE

Also appearing in this issue:

TRIASSIC VERTEBRATES
A new continental fauna from the Late Triassic of Argentina: Cynodonts, turtles, pseudosuchians, and dinosauromorphs.

JURASSIC SAUROPODS
Remains from the Late Jurassic of Chile indicates high sauropod diversity in South America.

WOODS AND FUNGI
Jurassic coniferous wood from western Argentina and the role of basidiomycetes in wood decay during the Mesozoic in Gondwana.

NEW MATERIAL OF *KATEPENSAURUS GOICOECHEAI* (SAUROPODA: DIPLODOCOIDEA) AND ITS SIGNIFICANCE FOR THE MORPHOLOGY AND EVOLUTION OF REBBACHISAURIDAE

LUCIO M. IBIRICU[1], GABRIEL A. CASAL[2], RUBÉN D. MARTÍNEZ[2], MATTHEW C. LAMANNA[3], MARCELO LUNA[2] AND LEONARDO SALGADO[4]

[1]Laboratorio de Paleontología, Centro Nacional Patagónico (CENPAT-CONICET), Boulevard Almirante Brown 2915, 9120 Puerto Madryn, Chubut, Argentina. *ibiricu@cenpat-conicet.gob.ar*

[2]Laboratorio de Paleovertebrados, Universidad Nacional de la Patagonia San Juan Bosco, C.C. 360, 9000 Comodoro Rivadavia, Chubut, Argentina. *paleogac@yahoo.com.ar*; *rudaframartinez@gmail.com*; *paleoambiental@yahoo.com*

[3]Section of Vertebrate Paleontology, Carnegie Museum of Natural History, 4400 Forbes Avenue, Pittsburgh, Pennsylvania 15213 U.S.A. *lamannam@carnegiemnh.org*

[4]CONICET, Instituto de Investigación en Paleobiología y Geología, Universidad Nacional de Río Negro, Av. General Roca 1242, 8332 General Roca, Río Negro, Argentina. *lsalgado@unrn.edu.ar*

Abstract. Cretaceous outcrops in southern South America preserve a rich and evolutionarily important record of sauropod dinosaurs. Among Sauropoda, South American titanosaurs have garnered particular interest due to their abundance and taxonomic diversity. Nevertheless, the fossil record of rebbachisaurids has also improved significantly in recent years, and consequently so has knowledge of the group. However, many aspects of the anatomy and phylogenetic relationships of Rebbachisauridae remain unresolved, due in large part to the fragmentary nature of many members of the clade. Within this context, we describe new fossils of *Katepensaurus goicoecheai* Ibiricu, Casal, Martínez, Lamanna, Luna, and Salgado, a recently-named rebbachisaurid from the Upper Cretaceous (Cenomanian/Turonian) Bajo Barreal Formation of central Patagonia (Argentina). Based on these additional materials, we propose two new autapomorphies of this taxon: (1) ventral portion of posterior articular surface of anterior dorsal vertebral centrum wider than dorsal portion, conferring a 'teardrop-shaped' contour; and (2) ovoid fossa on dorsal aspect of anterior to middle dorsal vertebral transverse processes. These features enhance our understanding of morphological diversity within Rebbachisauridae and augment the diagnosis of *Katepensaurus*. Furthermore, phylogenetic analysis confirms the assignment of this taxon to the rebbachisaurid subclade Limaysaurinae. *Katepensaurus* is the southernmost record of a rebbachisaurid that is identifiable to the generic level.

Key words. Rebbachisauridae. *Katepensaurus goicoecheai*. Late Cretaceous. Bajo Barreal Formation. Sauropoda.

Resumen. NUEVO MATERIAL DE *KATEPENSAURUS GOICOECHEAI* (SAUROPODA: DIPLODOCOIDEA) Y SU IMPORTANCIA PARA LA MORFOLOGÍA Y EVOLUCIÓN DE REBBACHISAURIDAE. Afloramientos Cretácicos en el sur de América del Sur preserva un rico y evolutivamente importante registro fósil de dinosaurios saurópodos. Dentro de este grupo, los titanosaurios adquieren particular interés debido a su abundancia y diversidad taxonómica. Sin embargo, en los últimos años, se ha producido un marcado incremento del registro fósil de los rebaquisauridos, y por lo tanto el conocimiento del grupo se ha incrementado. A pesar de esto, muchos aspectos relacionados con su anatomía, dispersión y relaciones filogenéticas permanecen sin resolver, debido en parte a la naturaleza fragmentaria de muchos de sus integrantes. En este contexto, se describen nuevos materiales de *Katepensaurus goicoecheai* Ibiricu, Casal, Martínez, Lamanna, Luna, and Salgado, un rebaquisaurido recientemente descripto del Cretácico Superior (Cenomaniano/Turoniano) de la Formación Bajo Barreal en la Patagonia central (Argentina). En base a estos nuevos materiales, dos nuevas autapomorfias son propuestas; (1) porción ventral del centro dorsal anterior con la superficie articular posterior más ancha que la porción dorsal lo cual le confiere un "aspecto de gota de agua"; (2) fosa con forma ovoide sobre el aspecto dorsal de los procesos transversos dorsales anterior a medios. Estos rasgos incrementan nuestro conocimiento acerca de la diversidad morfológica del grupo pero también apoyan la revisión de la diagnosis de *Katepensaurus*. Asimismo, nuestro análisis filogenético confirma la asignación de *Katepensaurus* como miembro del subsubclado Limaysaurinae. *Katepensaurus* es el registro más austral de un rebaquisaurido a nivel genérico.

Palabras clave. Rebbachisauridae. *Katepensaurus goicoecheai*. Cretácico Superior. Formación Bajo Barreal. Sauropoda.

KNOWLEDGE of rebbachisaurid sauropods has improved in recent years with the discoveries of multiple new representatives of this non-avian dinosaur group (*e.g.*, Carballido *et al.*, 2012; Fanti *et al.*, 2013; Ibiricu *et al.*, 2013a). Neverthe-

less, many aspects of the radiation of Rebbachisauridae remain inadequately understood, a situation that is due in large part to the fact that most taxa are represented by very incomplete fossils such as *Cathartesaura anaerobica*,

Histriasaurus boscarollii, *Nopcsaspondylus alarconensis* and *Rayososaurus agrioensis* (Nopcsa, 1902; Bonaparte, 1996; Dalla Vecchia, 1998; Gallina and Apesteguía, 2006; Apesteguía, 2007; Carballido *et al.*, 2010). This dearth of morphological information has hindered our understanding of rebbachisaurid evolution, which has, in turn, frustrated attempts to decipher the paleobiogeographic history of the clade.

The fossil record of unquestioned rebbachisaurids extends from the Early Cretaceous (late Hauterivian/early Barremian; Dalla Vecchia, 1998, 1999, 2005) to the early Late Cretaceous (late Cenomanian/Turonian; Garrido, 2010; Haluza *et al.*, 2012; Ibiricu *et al.*, 2012a, 2013a). Rebbachisaurid fossils have been discovered in both northern (*i.e.*, Europe) and southern (South America, Africa) hemispheres (*e.g.*, Salgado and Bonaparte, 2007; Mannion, 2009; Carballido *et al.*, 2010, 2012; Torcida Fernández-Baldor *et al.*, 2011; Fanti *et al.*, 2013). Phylogenetic analyses suggest that Rebbachisauridae originated during the Late Jurassic (Whitlock, 2011; Carballido *et al.*, 2012; Gallina *et al.*, 2014).

Katepensaurus goicoecheai (Ibiricu *et al.*, 2013a) is a recently named rebbachisaurid from the Bajo Barreal Formation (Late Cretaceous; Cenomanian/Turonian) of central Patagonia, Argentina (Fig. 1). Ibiricu *et al.* (2013a) tentatively interpreted this taxon as belonging to the South American rebbachisaurid subclade Limaysaurinae, but did not propose a more detailed phylogenetic position. Recent excavations at the *Katepensaurus* type locality resulted in the discovery of new fossils of this sauropod. Here we describe these new materials and use them (in conjunction with previously described fossils) to revisit the phylogenetic affinities of this rebbachisaurid taxon.

Institutional abbreviations. **CCC**, Casa de Cultura do Municipio de Coroatá, Coroatá, Brazil; **MACN,** Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MIWG,** Museum of Isle of Wight Geology, Sandown, United Kingdom; **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.

SYSTEMATIC PALEONTOLOGY

SAUROPODA Marsh, 1878

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

REBBACHISAURIDAE Bonaparte, 1997

Genus ***Katepensaurus*** Ibiricu, Casal, Martínez, Lamanna, Luna and Salgado, 2013a

Type species. *Katepensaurus goicoecheai* Ibiricu, Casal, Martínez, Lamanna, Luna and Salgado, 2013a.

Holotype. UNPSJB-PV 1007, an associated partial skeleton (Fig. 2) consisting of three anterior to middle cervical vertebrae (UNPSJB-PV 1007/1–3), three middle to posterior dorsal vertebrae (UNPSJB-PV 1007/4–6), and two caudal vertebrae (UNPSJB-PV 1007/7 and 1007/8). Material of the holotype newly identified herein includes a fragment of the right frontal (UNPSJB-PV 1007/29, regarded as an indeterminate element by Ibiricu *et al.*, 2013a), an indeterminate neural arch fragment and partial cervical ribs (UNPSJB-PV 1007/35–36), an incomplete anterior dorsal vertebra (UNPSJB-PV 1007/13), an incomplete anterior to middle dorsal vertebra (UNPSJB-PV 1007/12), an incomplete anterior to middle dorsal neural arch (UNPSJB-PV 1007/31), three incomplete anterior caudal vertebrae (UNPSJB-PV 1007/9–11), a possible metapodial fragment (UNPSJB-PV 1007/33), a possible fragment of the right astragalus
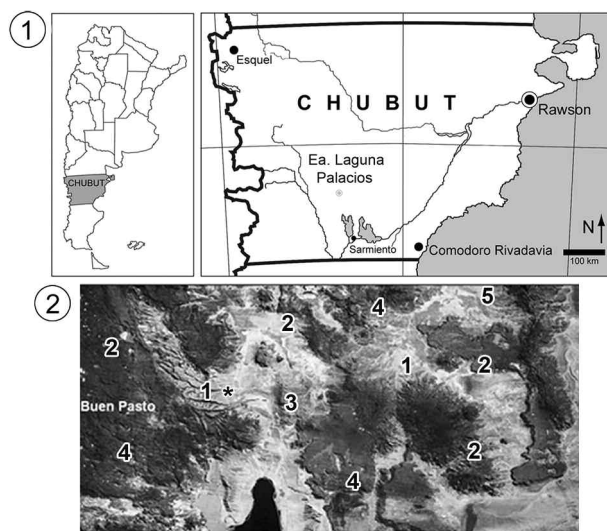

Figure 1. Geographic and geological context of *Katepensaurus goicoecheai*. **1,** location of southern Chubut Province, central Patagonia, Argentina, with gray circle indicating the site that yielded *Katepensaurus goicoecheai* (modified from Ibiricu *et al.*, 2013b); **2,** satellite image of the area. Numbers indicate: **1,** Chubut Group; **2,** Neogene basalt; **3,** retro-arc basalt; **4,** alluvial and colluvial deposits; **5,** Quaternary alluvium. Black asterisk indicates the site of procedence of *Katepensaurus goicoecheai*.
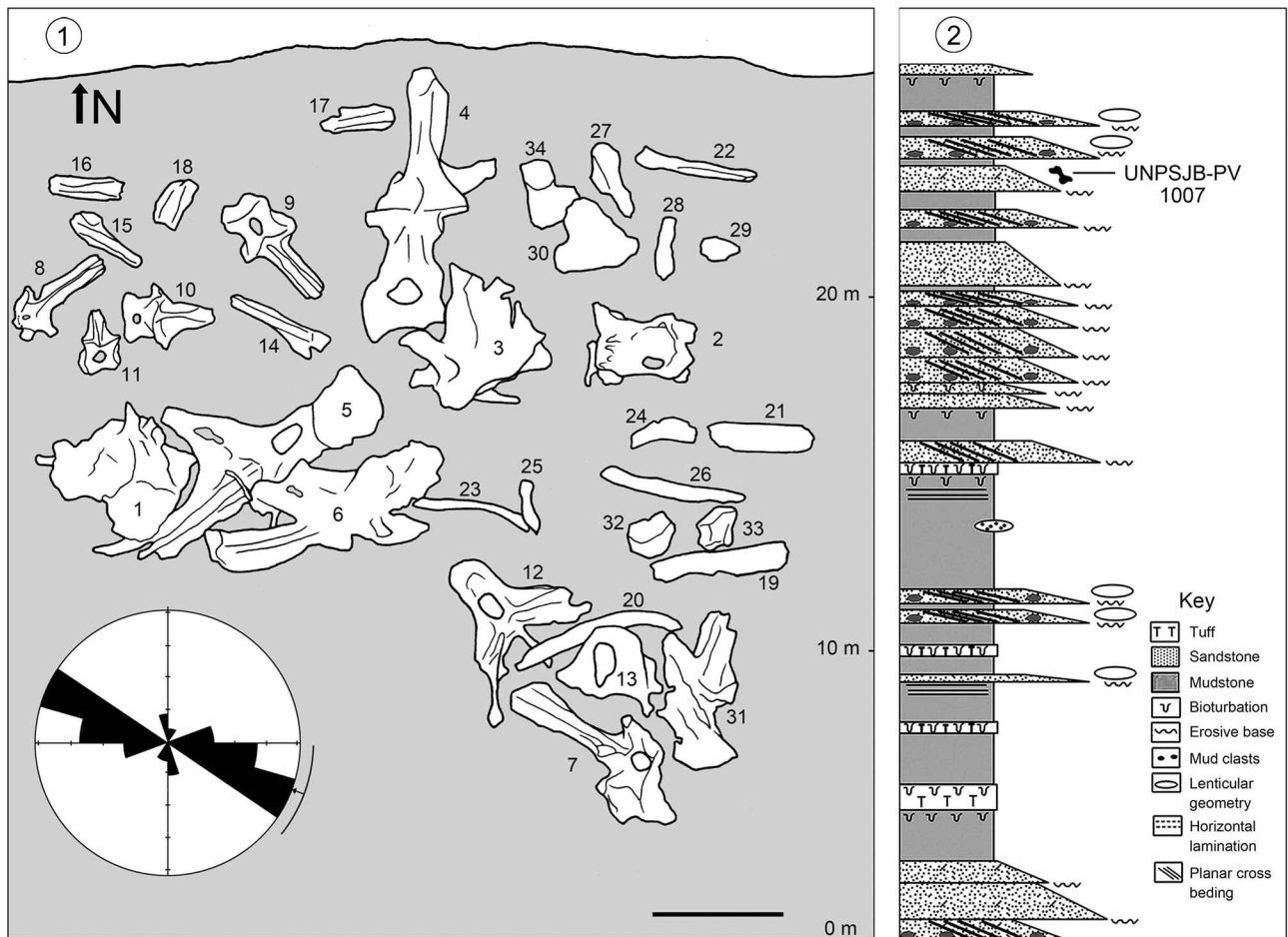
Figure 2. Quarry map and stratigraphic setting. **1,** map of the type locality (the '2005 Quarry') of *Katepensaurus goicoecheai* in the Estancia Laguna Palacios, with numbers indicating bones of the holotype (UNPSJB-PV 1007); **2,** stratigraphic section showing the level from which *Katepensaurus goicoecheai* was collected (modified from Ibiricu *et al.*, 2013a, 2014). Scale bar= 30 cm.

(UNPSJB-PV 1007/32), and numerous indeterminate elements (UNPSJB-PV 1007/19–28,30,32 and 34). Many of these indeterminate elements (*e.g.*, UNPSJB-PV 1007/14–16) are probably partial dorsal or anterior caudal neural spines.

Locality and horizon. All *Katepensaurus* fossils were recovered from the '2005 Quarry' (44°54′ 23.82″ S; 69°22′ 43.67″ W), in the Estancia Laguna Palacios in south-central Chubut Province, central Patagonia, Argentina (Figs. 1, 2). The specimens come from the upper part of the lower member of the Bajo Barreal Formation (Late Cretaceous; Fig. 2) of the Chubut Group. The age of this member is regarded as middle Cenomanian–Turonian (*e.g.*, Bridge *et al.*, 2000; Lamanna *et al.*, 2002; Casal and Ibiricu, 2010; Ibiricu *et al.*, 2012a, b). UNPSJB-PV 1007 was recovered from the base of a 1.25 m thick, fining-upward fluvial deposit of lenticular

geometry and erosive base (see Ibiricu *et al.*, 2013a).

Revised diagnosis. As proposed by Ibiricu *et al.* (2013a), *Katepensaurus goicoecheai* has the following autapomorphic characters in the middle to posterior dorsal vertebrae: (1) internal lamina dividing lateral pneumatic fossa of centrum (autapomorphic within Rebbachisauridae but shared with the non-rebbachisaurid diplodocoids *Dinheirosaurus lourinhanensis* and *Supersaurus vivianae*); (2) vertical ridges on lateral surface of vertebra overlying neurocentral junction; (3) pair of laminae in parapophyseal centrodiapophyseal fossa; and (4) well-defined rounded fossae on lateral aspect of postzygapophyses. Additionally, two new autapomorphies of the anterior to middle dorsal vertebrae are proposed herein: (5) posterior articular surface of centrum with ventral portion wider than dorsal portion, rendering it 'teardrop-shaped' in contour; and (6) ovoid fossa on dorsal

aspect of transverse processes in anterior to middle dorsal vertebrae and dorsal transverse processes perforated by elliptical fenestrae in middle to posterior dorsal vertebrae (see Discussion).

Comments. All of the new elements were recovered in close proximity to the original material of the *Katepensaurus goicoecheai* holotype, and from the same stratigraphic horizon (Fig. 2). The new specimens do not overlap in anatomical position with those previously described. Moreover, their size and morphology (*e.g.*, of the dorsal zygapophyses and neural arch laminae, as well as the development of presumably pneumatic features of the transverse processes) are closely compatible with this specimen. Therefore, we regard the newly collected bones as additional elements of the *Katepensaurus goicoecheai* holotype.

Comparative description

Frontal. A portion of the right frontal is preserved (UNPSJB-PV 1007/29; Fig. 3). The dorsal surface is slightly convex and rugose (Fig. 3.1), unlike that of the recently described flagellicaudatan diplodocoid *Kaatedocus siberi*, which is flat and relatively smooth (Tschopp and Mateus, 2012). The lateral edge (Fig. 3.2), which contributes to the dorsal margin of the orbit, is markedly rugose as in most sauropods. Although they appear less marked than in UNPSJB-PV 1007/29, similar rugosities are also present on the dorsal surface of the frontal of the South American rebbachisaurid *Limaysaurus tessonei* (see Calvo and Salgado, 1995: fig. 3). The ventral surface of the *Katepensaurus* frontal fragment is concave and smooth (Fig. 3.3).

Cervical ribs. Two probable cervical rib fragments were recovered, adhered to a piece of a presacral neural arch (UNPSJB-PV 1007/35,36; Fig. 4). Unfortunately, these rib fragments are not completely preserved; therefore, we cannot describe the relationship between cervical rib and centrum length. The ribs are interpreted as belonging to the posterior part of the cervical sequence, based on the size and length of the portions recovered (see Sereno *et al.*, 2007: fig. 3b). The cervical ribs are cylindrical and maintain the same thickness througout the preserved portion of the shaft. They are ovoid in cross-section, with the dorsoventral axis longer than the mediolateral axis. These features resemble those described in the cervical ribs of the European rebbachisaurid *Demandasaurus darwini* (Pereda-Suberbiola
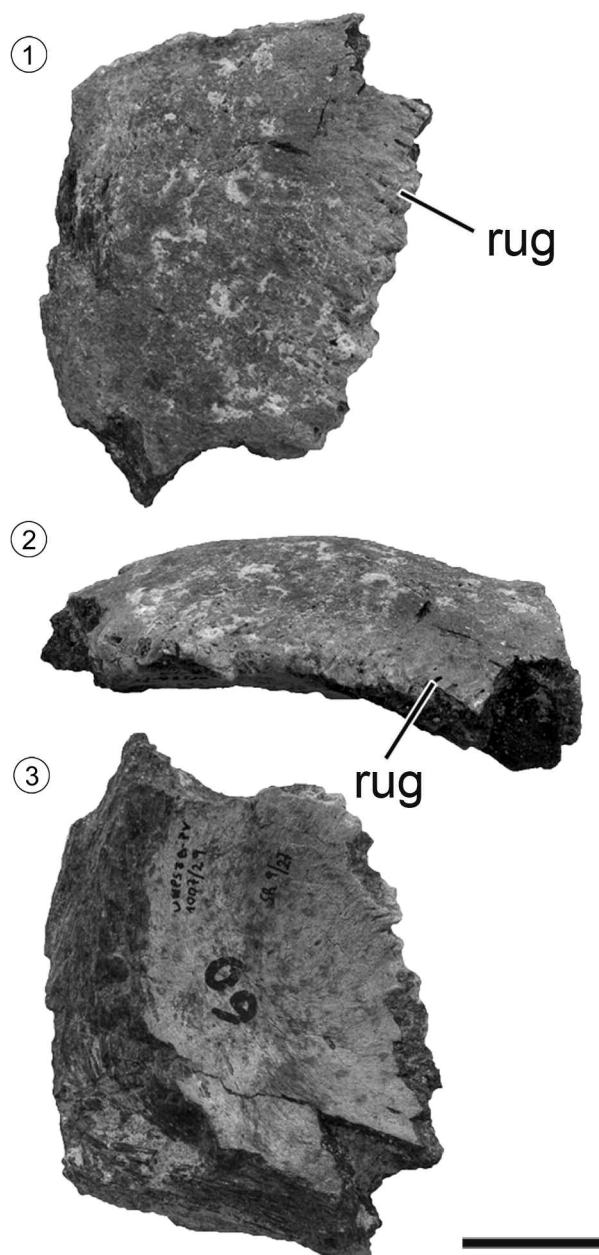

Figure 3. *Katepensaurus goicoecheai*, UNPSJB-PV 1007/29, fragment of right frontal. **1,** dorsal view; **2,** lateral view; **3,** ventral view. Anterior is towards the top of the page. Abbreviation: **rug,** rugosities. Scale bar= 2 cm.

et al., 2003; Torcida Fernández-Baldor *et al.*, 2011).

Dorsal vertebrae. The new material includes an anterior dorsal vertebra (UNPSJB-PV 1007/13; Fig. 5) and two anterior to middle dorsal vertebrae (UNPSJB-PV 1007/12, /31; Figs. 6–7). Unfortunately, the dorsal vertebrae have been taphonomically affected, and the positions of the parapophyses cannot be determined. Therefore, the interpretation of the

positions of these vertebrae in the dorsal column is based on comparisons with other vertebrae of the *Katepensaurus goicoecheai* holotype as well as with better-represented dorsal vertebral sequences of other diplodocoids. For example, the interpretation of UNPSJB-PV 1007/13 as an anterior dorsal is based on morphological features such as its slightly opisthocoelous centrum, well-defined lateral pneumatic fossae ('pleurocoels'), and relatively short transverse process. UNPSJB-PV 1007/12 was found closely associated with UNPSJB-PV 1007/13 (Fig. 2); furthermore, its diapophyses are less elevated than in the middle or posterior dorsal UNPSJB-PV 1007/5 (see Ibiricu *et al.*, 2013a), which suggests the identification of the former vertebra as an anterior to middle dorsal. UNPSJB-PV 1007/31 is considered an anterior to middle dorsal vertebra based on its possession of short dorsal transverse processes, as in anterior dorsal vertebrae of *Comahuesaurus windhauseni* (Salgado *et al.*, 2004; Carballido *et al.*, 2012) and the unnamed Patagonian rebbachisaurid MMCH-Pv 49 (see Haluza *et al.*, 2012).

The slightly opisthocoelous condition of the centrum of UNPSJB-PV 1007/13 is shared with the anterior dorsal vertebrae of *Amazonsaurus maranhensis* (Carvalho *et al.*, 2003; see also Mannion *et al.*, 2012), *Comahuesaurus* (Salgado *et al.*, 2004; Carballido *et al.*, 2012), and MMCH-Pv 49 (Apesteguía *et al.*, 2010; Haluza *et al.*, 2012). In contrast, the anterior dorsal centra are strongly opisthocoelous in *Limaysaurus* (Calvo and Salgado, 1995). The preserved portion of the posterior articular surface is concave and 'teardrop-shaped' in posterior view (*i.e.*, the ventral portion is transversely wider than the dorsal portion; see Fig. 5). Conversely, in other rebbachisaurids for which anterior dorsal vertebrae are known, such as *Comahuesaurus*, *Limaysaurus*, *Nigersaurus taqueti* (Sereno *et al.*, 1999, 2007), and MMCH-Pv 49, the posterior articular surface is subcircular to circular in outline, being almost as high as wide. As in the other dorsal centra of the *Katepensaurus goicoecheai* holotype (see Ibiricu *et al.*, 2013a), UNPSJB-PV 1007/13 is anteroposteriorly compressed with an anteroposteriorly concave ventral surface. These conditions are shared with *Comahuesaurus*, *Limaysaurus*, and *Nigersaurus*. In the Brazilian taxon *Amazonsaurus*, by contrast, the dorsal centra are comparatively low and elongate (Carvalho *et al.*, 2003).

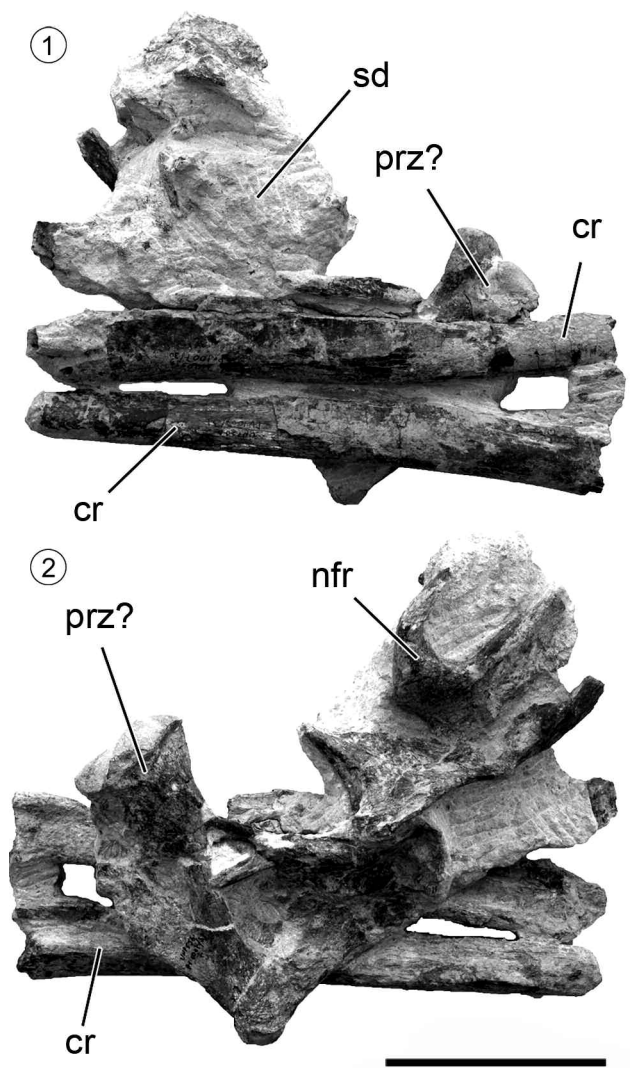The left lateral side of the anterior dorsal centrum, which

Figure 4. *Katepensaurus goicoecheai*, UNPSJB-PV 1007/35-36, fragments of cervical ribs and indeterminate neural arch fragment. **1,** lateral view; **2,** medial view. Abbreviations: **cr,** cervical rib; **nfr,** neural arch fragment; **prz?,** prezygapophysis?; **sd,** sediment. Scale bar= 10 cm.

is the best preserved, is excavated by a well-defined pneumatic fossa (*i.e.*, a 'pleurocoel'). This fossa is ovate in outline and extends anteroposteriorly for approximately three-quarters of the total length of the centrum. Although the general shape of the pneumatic fossa is similar to those in dorsal centra of other rebbachisaurids (*e.g.*, *Comahuesaurus*, *Limaysaurus*, *Nigersaurus*), it particularly resembles those described in *Amazonsaurus* and MMCH-Pv 49 (see Haluza *et al.*, 2012: fig. 3o). The preserved left transverse process of UNPSJB-PV 1007/13 has been taphonomically displaced. However, it appears to be less dorsally oriented than those
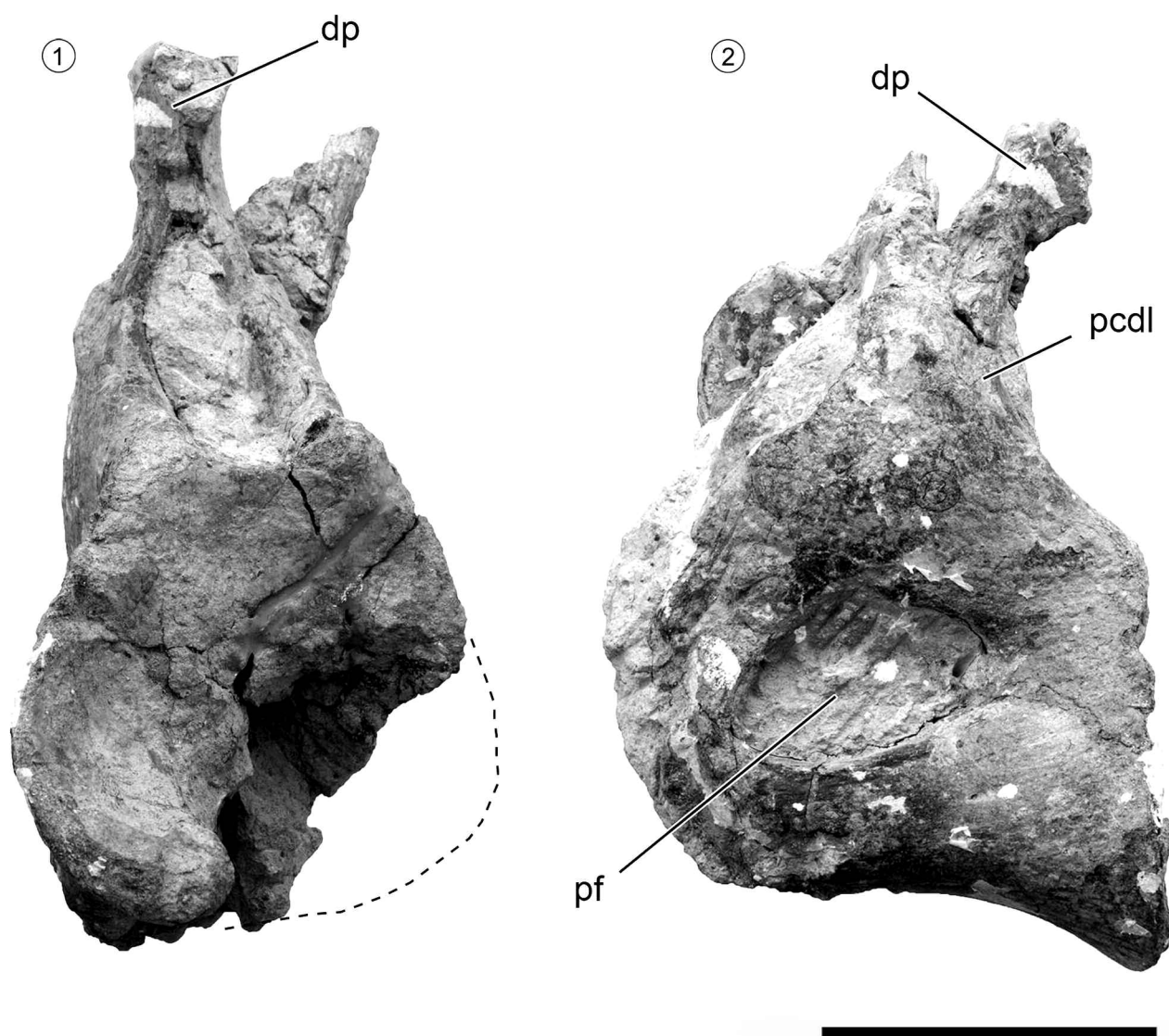
Figure 5. *Katepensaurus goicoecheai*, UNPSJB-PV 1007/13, anterior dorsal vertebra. **1,** posterior view; **2,** left lateral view. Abbreviations: **dp,** diapophysis; **pcdl,** posterior centrodiapophyseal lamina; **pf,** pneumatic fossa. Scale bar= 10 cm.

of UNPSJB-PV 1007/12 (see below) and the three *Katepensaurus* dorsal vertebrae described by Ibiricu *et al.* (2013a; *i.e.*, UNPSJB-PV 1007/4, 1007/5, and 1007/6). Furthermore, the transverse process of UNPSJB-PV 1007/13 is notably short. Together with its orientation and size, this supports an anterior position in the dorsal sequence for this vertebra.

Parts of the centrum and neural arch are preserved in UNPSJB-PV 1007/12 (Fig. 6). The neural canal is proportionally large and ovoid. Two well-developed centroprezygapophyseal laminae are evident in anterior view. These

laminae form the lateral margins of a deep fossa that, following Wilson *et al.* (2011), we regard as the centroprezygapophyseal fossa. The neural canal and centroprezygapophyseal fossa are separated by a transverse ridge. On both the left and right sides of the neural arch, the anterior centrodiapophyseal, centroprezygapophyseal, and prezygodiapophyseal laminae surround a deep, bilateral fossa, here identified as the prezygapophyseal centrodiapophyseal fossa (Wilson *et al.*, 2011). The large, wide prezygapophyses of UNPSJB-PV 1007/12 are united, forming a continu-

ous articular surface. A short intraprezygapophyseal lamina appears ventromedial to the prezygapophyses, rendering them 'V-shaped' in anterior view. The general morphology of the prezygapophyses (*e.g.*, the coalesced prezygapophyseal rami and the resulting continuous articular surface) most closely resembles that in the unnamed rebbachisaurid from the Huincul Formation at Las Campanas creek in Neuquén Province, Argentina (MMCH-Pv 49, see Apesteguía *et al.*, 2010; Haluza *et al.*, 2012). Conversely, *Comahuesaurus*, *Demandasaurus*, *Histriasaurus*, an isolated posterior dorsal neural arch from Brazil (CCC 017, Castro *et al.*, 2007; see also Whitlock, 2011), and another isolated partial dorsal vertebra from the Early Cretaceous of Patagonia (MACN PV N 35; Apesteguía, 2007) all have divided prezygapophyses. The preserved portion of the prespinal lamina resembles that of other rebbachisaurids. Just lateral to the prezygapophysis, the dorsal aspect of the right transverse process of UNPSJB-PV 1007/12 exhibits a deep, well-defined, ovoid depression that we term the laterodiapophyseal fossa. This fossa does not penetrate through the entire transverse process, unlike the laterodiapophyseal fenestrae of the middle to posterior dorsal vertebrae UNPSJB-PV 1007/4, 1007/5, and 1007/6 (see Ibiricu *et al.*, 2013a, and below). The left transverse process of UNPSJB-PV 1007/12 is broken, but it also appears to possess a laterodiapophyseal fossa. These structures, probably related to pneumaticity, have not been documented in other rebbachisaurids (see below). The transverse processes are dorsolaterally projected, as in middle and posterior dorsal vertebrae of many diplodocoids (Ibiricu *et al.*, 2013a). The diapophyses are positioned well dorsal to the zygapophyses.

UNPSJB-PV 1007/31 (Fig. 7) has been taphonomically distorted; however, several salient morphological features can be identified. The preserved left transverse process is short, a feature supporting an anterior position in the dor-
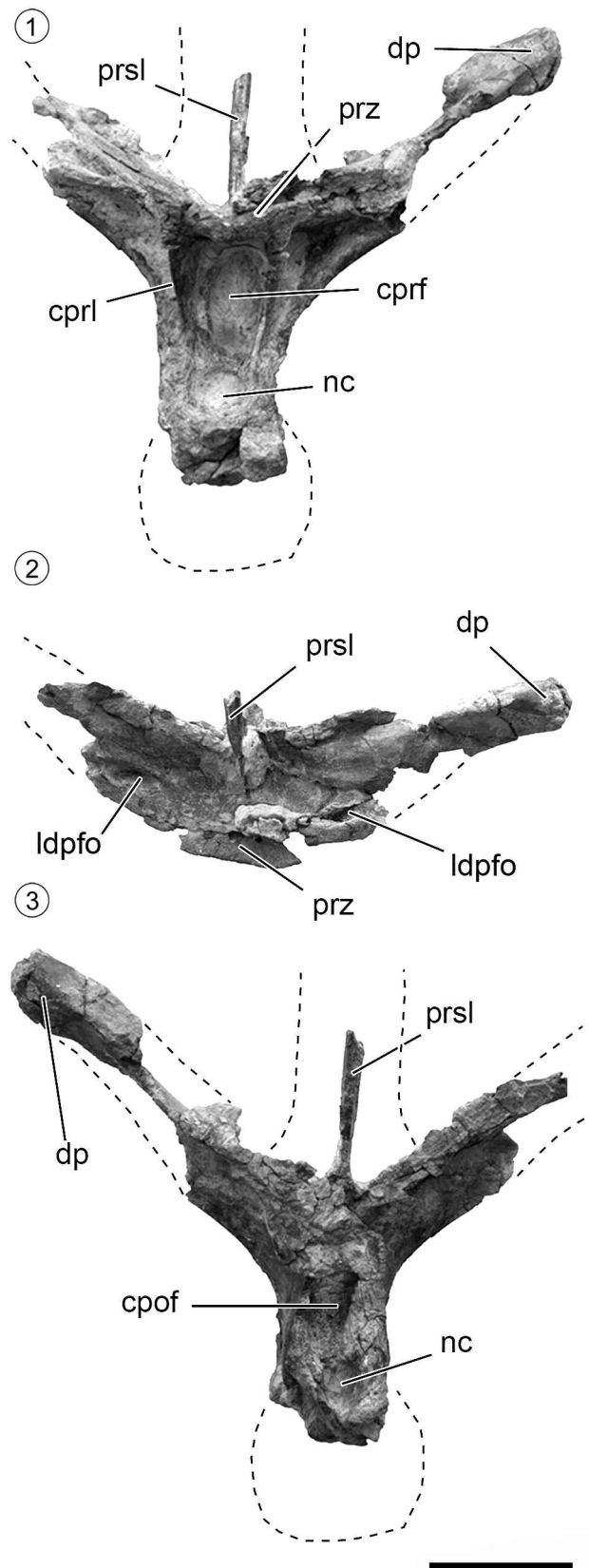

Figure 6. *Katepensaurus goicoecheai*, UNPSJB-PV 1007/12, anterior to middle dorsal vertebra. **1,** anterior view; **2,** dorsal view; **3,** posterior view. Abbreviations: **cpof,** centropostzygapophyseal fossa; **cprf,** centroprezygapophyseal fossa; **cprl,** centroprezygapophyseal lamina; **dp,** diapophysis; **ldpfo,** laterodiapophyseal fossa; **nc,** neural canal; **prsl,** prespinal lamina; **prz,** prezygapophysis. Scale bar= 10 cm.

sal sequence for this vertebra. The anterior surface of the preserved portion of the neural spine bears two parallel, robust, and well-marked spinoprezygapophyseal laminae. More laterally, the laterodiapophyseal fossa occupies about two-thirds the total length of the transverse process. Only one of the postzygapophyses is preserved in UNPSJB-PV 1007/31. Its facet is robust and oriented ventrolaterally. Unlike the condition in the dorsal vertebrae of the *Katepensaurus goicoecheai* holotype described by Ibiricu *et al.* (2013a), the well-marked lateral spinopostzygapophyseal lamina does not surpass the dorsoventral plane of the dorsal margin of the transverse process. A deep spinopostzygapophyseal fossa is present medial to this lamina. A relatively robust postzygodiapophyseal lamina and a thin but clearly observed spinodiapophyseal lamina are also present.

Caudal vertebrae. The new material includes three partial caudal vertebrae, UNPSJB-PV 1007/9–11 (Fig. 8). Based on comparisons with well-preserved rebbachisaurid caudal sequences (*e.g.*, *Limaysaurus*) and other caudal vertebrae described in the *Katepensaurus goicoecheai* holotype (Ibiricu *et al.*, 2013a), we interpret these elements belonging to the anterior portion of the tail. The morphology of the new caudal elements (*i.e.*, UNPSJB-PV 1007/9–11) does not differ notably from those described by Ibiricu *et al.* (2013a). Nevertheless, all major features are smaller in size. Therefore, these caudals may have been placed posterior to those described by Ibiricu *et al.* (2013a).

The neural canal is oval. The robust transverse processes are wing-like, particularly those of the most anterior vertebra in this set (UNPSJB-PV 1007/9), as in several rebbachisaurids (*e.g.*, *Cathartesaura*, *Comahuesaurus*, *Demandasaurus*). The dorsolaterally projected left transverse process of UNPSJB-PV 1007/9 arises, dorsally, from near the level of the prezygapophyses. As in UNPSJB-PV 1007/7 (Ibiricu *et al.*, 2013a) and caudals of several other diplodocoids, the
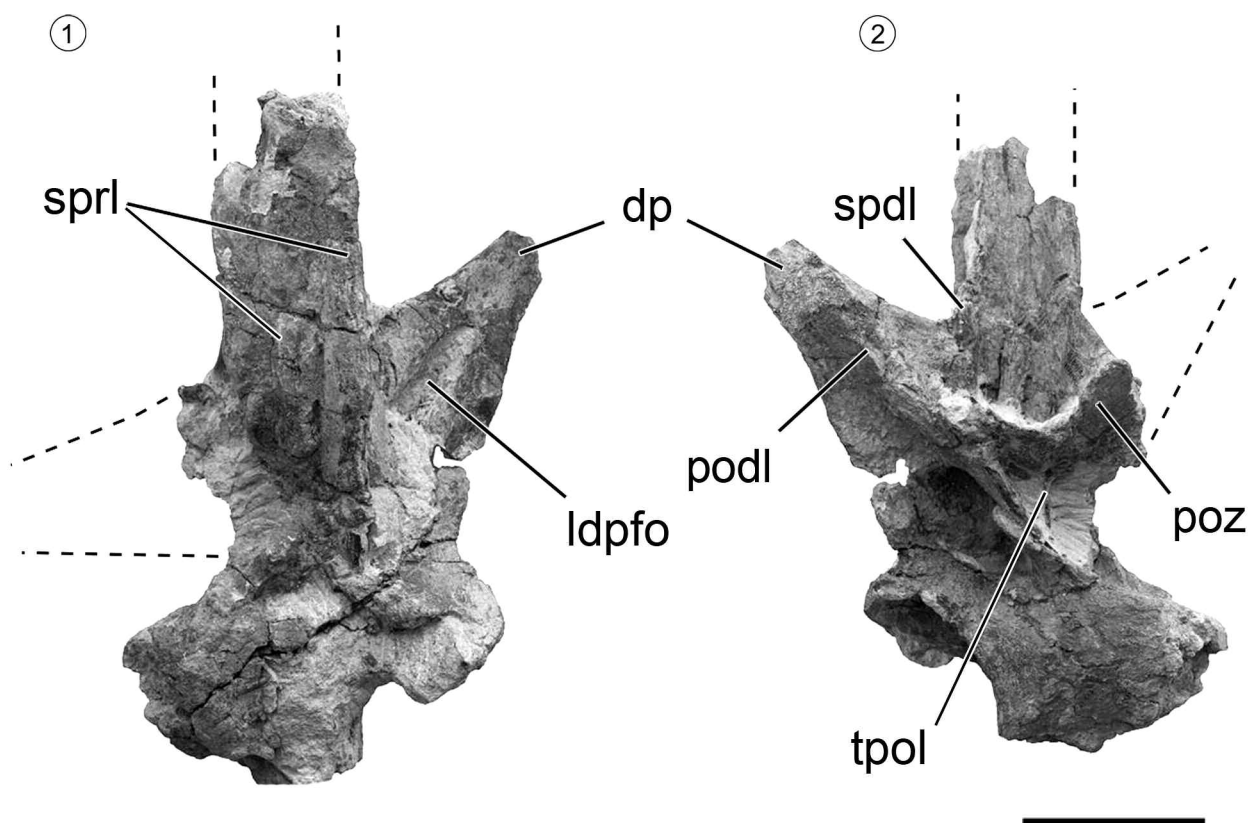

Figure 7. *Katepensaurus goicoecheai*, UNPSJB-PV 1007/31, anterior to middle dorsal neural arch. **1,** anterior view; **2,** posterior view. Abbreviations: **dp,** diapophysisipozl, infrapostzygapophyseal lamina; **ldpfo,** laterodiapophyseal fossa; **podl,** postzygodiapophyseal lamina; **poz,** postzygapophysis; **spdl,** spinodiapophyseal lamina; **sprl,** spinoprezygapophyseal lamina. Scale bar= 10 cm.

anterior surface of the transverse process is excavated by a fairly deep prezygapophyseal centrodiapophyseal fossa. The dorsal edge of the transverse process of UNPSJB-PV 1007/9 is formed by a thin prezygodiapophyseal lamina. This lamina dorsally frames the prezygapophyseal centro-diapophyseal fossa. This fossa is interrupted by a relatively robust prezygapophyseal centrodiapophyseal fossa lamina (see Ibiricu *et al.*, 2013a). This lamina arises from the base of the fossa and reaches the dorsal distal end of the transverse process. The three caudal vertebrae display robust (*i.e.*, transversely broad) prespinal laminae and well-marked spinoprezygapophyseal fossae. However, the spinoprezy-gapophyseal fossa seen in UNPSJB-PV 1007/10 is larger and deeper than those of UNPSJB-PV 1007/9 and 11, particu-larly toward its ventral end. In posterior view, only a vestige of the postspinal lamina is preserved. A well-marked and deep spinopostzygapophyseal fossa is observed in these caudal vertebrae. Although it is present in all of these cau-dals, that observed in UNPSJB- 1007/9 is larger than those of UNPSJB-PV 1007/10 and UNPSJB-PV 10 1007/11. In lateral view, only a portion of the lateral lamina is preserved. There-fore, it can not be determined if this lamina is formed by the fusion of the spinoprezygapophyseal and spinopostzy-gapophyseal laminae, as in UNPSJB-PV 1007/7 (see Ibiricu *et al.*, 2013a). The zygapophyses are eroded; however, the prezygapophyses are slightly elongate anteriorly and their facets are ovoid. The postzygapophyses are slightly shorter than the prezygapophyses, and their facets are posterodor-sally projected.

UNPSJB-PV 1007/9 preserves a vertical ridge that ex-tends from the neural canal ventrally to the spinoprezy-gapophyseal fossa dorsally (see Fig. 8.1). This vertical ridge is present only in this caudal vertebra. Conversely, in the caudal remains of the holotype of *Katepensaurus goicoecheai* and the new materials described here where it can be ob-served, the prezygapophyses are united by a short in-traprezygapophyseal lamina as in several diplodocoids. This relatively robust vertical ridge slightly surpasses the neural canal.

Indeterminate bones. Several additional bones associated with the newly described materials were collected (UNPSJB-PV 1007/14 to UNPSJB-PV 1007/28, 30 and UNPSJB-PV 1007/32 to 34, see Fig. 2.1). These elements can not be identified with confidence, but UNPSJB-PV 1007/33 re-
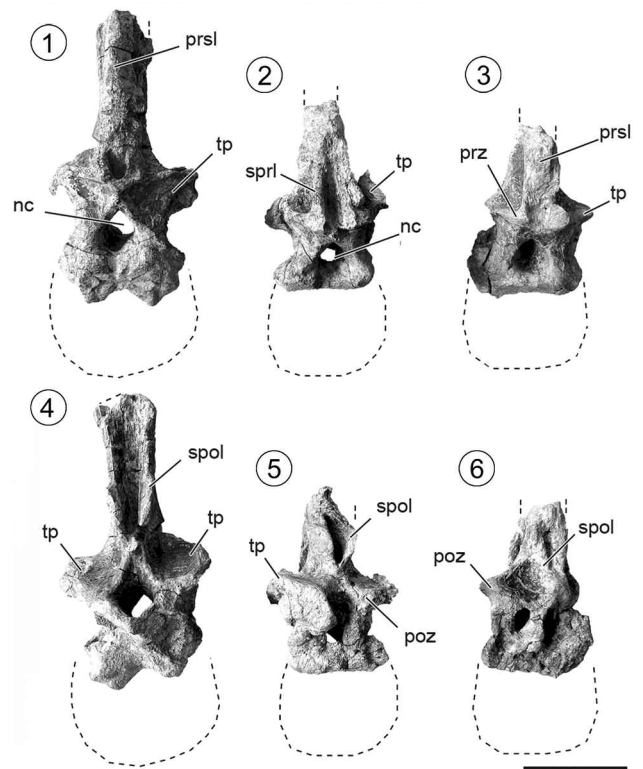

Figure 8. *Katepensaurus goicoecheai*, UNPSJB-PV 1007/9–11, ante-rior caudal neural arches. **1–3,** anterior view; **4–6,** posterior view. Abbreviations: **nc,** neural canal; **poz,** postzygapophysis; **prsl,** prespinal lamina; **prz,** prezygapophysis; **spol,** spinopostzygapophyseal lamina; **sprl,** spinoprezygapophyseal lamina; **tp,** transverse process. Scale bar= 10 cm.

sembles a right metapodial and UNPSJB-PV 1007/32 is ten-tatively interpreted as a fragment of the right astragalus. The remainder of the material probably consists of fragments of dorsal and caudal neural spines (Fig. 9) and dorsal ribs.

DISCUSSION

The relationships of Rebbachisauridae and the phylogenetic position of Katepensaurus

To evaluate the phylogenetic affinities of *Katepensaurus goicoecheai* we performed a phylogenetic analysis using TNT (Tree analysis using New Technology) version 1.1 (Goloboff *et al.*, 2008). We used the data matrix published by Mannion *et al.* (2012), which was based on the matrix originally compiled by Whitlock (2011). All characters were treated as unordered following analysis I of Mannion *et al.* (2012). Characters 75, 128, and 148 were re-scored follow-ing Carballido *et al.* (2012; see Appendix 1). An equally-weighted parsimony analysis using the Traditional Search

function of TNT yielded 39 most parsimonious trees (MPTs) of 345 steps. The consistency index (CI) obtained was 0.603, whereas the retention index (RI) was 0.770. Bremer and bootstrap supports were calculated and potential taxon instabilities and character conflicts were tested using Iter PCR (a script for TNT; see Pol and Escapa, 2009).

The strict consensus tree (Fig. 10) posits *Amazonsaurus* as the basalmost rebbachisaurid, the sister taxon to a polytomy consisting of *Zapalasaurus bonapartei* (Salgado *et al.*, 2006), *Rebbachisaurus*, *Histriasaurus*, and a clade containing all other rebbachisaurids in the analysis. As in many recent phylogenetic analyses (*e.g.*, Whitlock, 2011; Carballido *et al.*, 2012; Mannion *et al.*, 2012; Fanti *et al.*, 2013; Gallina *et al.*, 2014), Rebbachisauridae consists of two monophyletic subclades: the South American Limaysaurinae and the Afro-European Nigersaurinae [recently proposed as Rebbachisaurinae (*Nigersaurus* + *Demandasaurus*) + *Rebbachisaurus*, see Wilson and Allain, in press]. *Katepensaurus* is placed within Limaysaurinae in a polytomy with the two other limaysaurine genera *Limaysaurus* and *Cathartesaura*. This result is consistent with the conclusions of Ibiricu *et al.* (2013a), who proposed that *Katepensaurus* is a probable member of Limaysaurinae.

Limaysaurinae is supported by the following synapomorphies: accessory lamina connecting postzygodiapophyseal and spinoprezygapophyseal laminae in posterior cervical vertebrae (an ambiguous synapomorphy); contact of spinoprezygapophyseal and spinopostzygapophyseal laminae forming robust lateral lamina on lateral aspect of anterior caudal neural spines; and length of scapular acromion at least half of total scapular length (ambiguous synapomorphy). In *Katepensaurus*, only the contact between the spinoprezygapophyseal and spinopostzygapophyseal laminae in anterior caudal vertebrae can be definitively evaluated (*i.e.*, in our matrix, the other two characters are scored as unknown for this taxon).

To summarize, we confirm the assignment of *Katepensaurus* to Limaysaurinae, a systematic position that was tentatively advanced by Ibiricu *et al.* (2013a). Our analysis underscores the presently low phylogenetic resolution within Rebbachisauridae and the weak support for most proposed relationships within this diplodocoid group. This situation is almost certainly related to the incomplete nature of the majority of rebbachisaurid taxa (*e.g.*, *Amazonsaurus* and *Zapalasaurus* have completeness values of only 11% and 17%, respectively; see Mannion and Upchurch, 2010; Mannion *et al.*, 2012). The large amount of missing data within Rebbachisauridae is a major reason for the poorly resolved phylogeny of the group and the low Bremer and bootstrap support values that characterize our consensus tree (Fig. 10).

Implications of Katepensaurus for rebbachisaurid morphology

The additional dorsal vertebrae of *Katepensaurus* reported herein display characters that we interpret as newly recognized autapomorphies of this taxon. The posterior articular surface of the centrum of the anterior dorsal vertebra UNPSJB-PV 1007/13 is transversely wider ventrally than dorsally, conferring a 'teardrop-shaped' outline to this surface (Fig. 11.1). Although a portion of the centrum has been lost to taphonomic processes, there is no evidence of lithostatic deformation, and the smooth, undamaged margin of the preserved part of the centrum strongly suggests that this contour is a natural feature. The vertebra UNPSJB-PV 1007/12 possesses another character that was previously undocumented within Rebbachisauridae: the
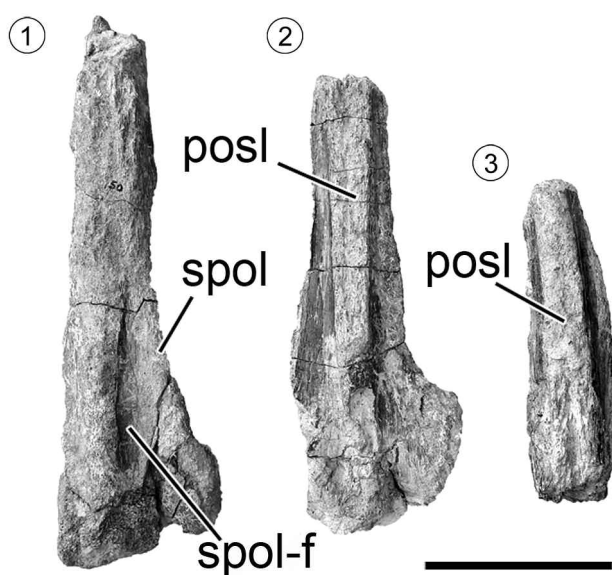

Figure 9. *Katepensaurus goicoecheai*, UNPSJB-PV 1007/14-15-16, probable fragments of neural spines. **1, 2, 3,** posterior view. Abbreviations: **posl,** postspinal lamina; **spol,** spinopostzygapophyseal lamina; **spol-f,** spinopostzygapophyseal lamina fossa. Scale bar= 10 cm.
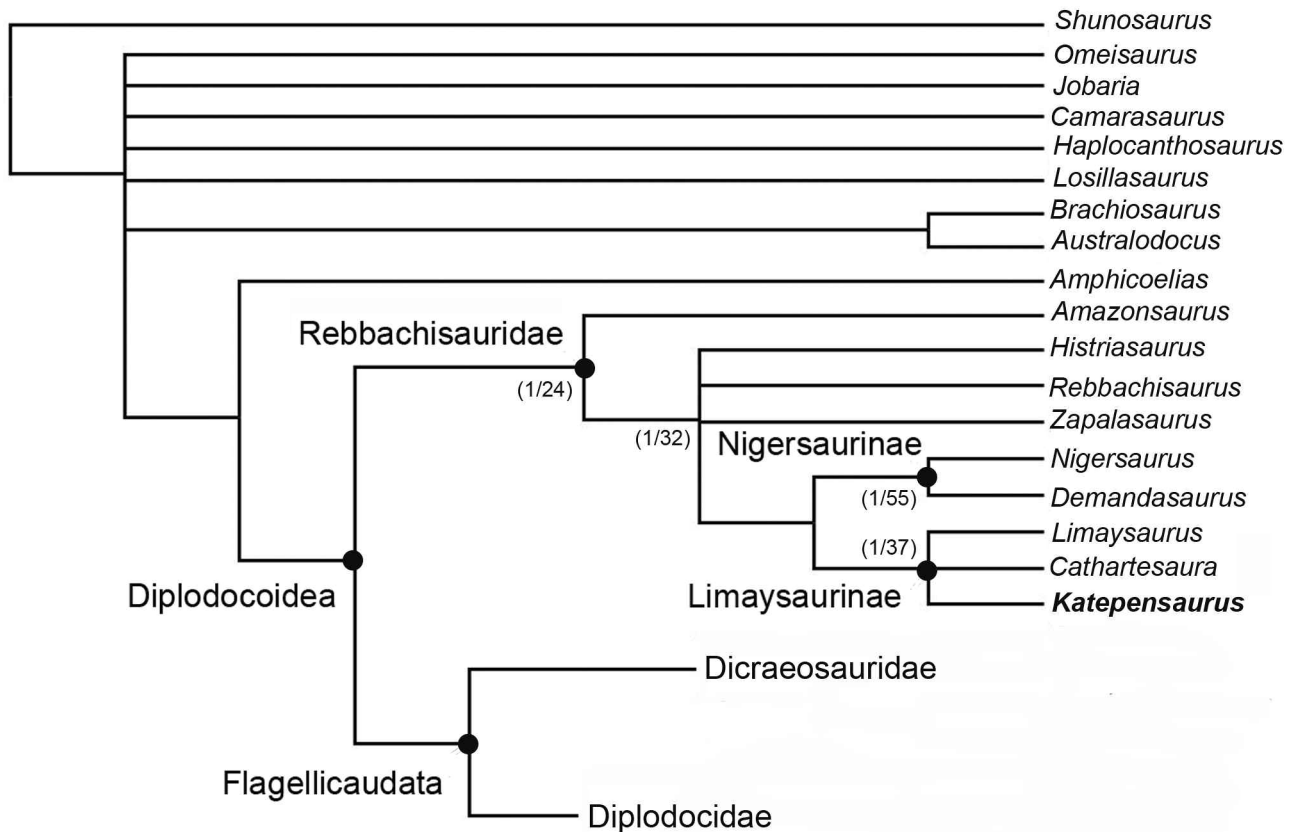
Figure 10. Strict consensus tree showing hypothesized phylogenetic relationships of *Katepensaurus goicoecheai*. The robustness of individual nodes within Rebbachisauridae is indicated in parentheses (Bremer and bootstrap values, respectively).

presence of a fossa, here termed the laterodiapophyseal fossa, on the dorsal surface of the right transverse process (Fig. 11.2–3). Although the corresponding region of the left transverse process is not completely preserved, this fossa is almost certainly a bilateral structure. The laterodiapophyseal fossa is also present on the preserved left transverse process of another of the newly described dorsal vertebrae, UNPSJB-PV 1007/31. As stated above, we identify these elements as anterior to middle dorsal vertebrae, whereas the three *Katepensaurus* dorsal vertebrae previously described by Ibiricu *et al.* (2013a; UNPSJB-PV 1007/4, 1007/5, and 1007/6) occupy positions in the middle to posterior regions of the column. Therefore, the laterodiapophyseal fossa in anterior to middle dorsal vertebrae (UNPSJB-PV 1007/12, 1007/31) may represent a serial homologue of the laterodiapophyseal fenestra in middle to posterior dorsal vertebrae (UNPSJB-PV 1007/4, 1007/5, 1007/6). Stated differently, it appears that the anterior to middle dorsal

transverse processes of *Katepensaurus* are excavated by fossae, whereas more posterior dorsal transverse processes are pierced by fenestrae. The shape of the posterior articular surface of the anterior dorsal centrum and the laterodiapophyseal fossa of the anterior to middle dorsal neural arches are features that have not been documented in other rebbachisaurids; therefore, both characters are herein proposed as new autapomorphies of *Katepensaurus*.

The presence of hyposphene-hypantrum accessory intervertebral articulations in dorsal vertebrae is considered a synapomorphy of Saurischia, and is consequently regarded as a plesiomorphic character in Sauropoda (Apesteguía, 2005; Carballido *et al.*, 2012). *Histriasaurus* has frequently been recovered as a basal member of Rebbachisauridae primarily because the holotypic dorsal vertebra retains a well-developed hyposphene, a plesiomorphic condition that, where scorable, is missing in other named genera within the clade (Whitlock, 2011). Among likely rebbachisaurid fossils,
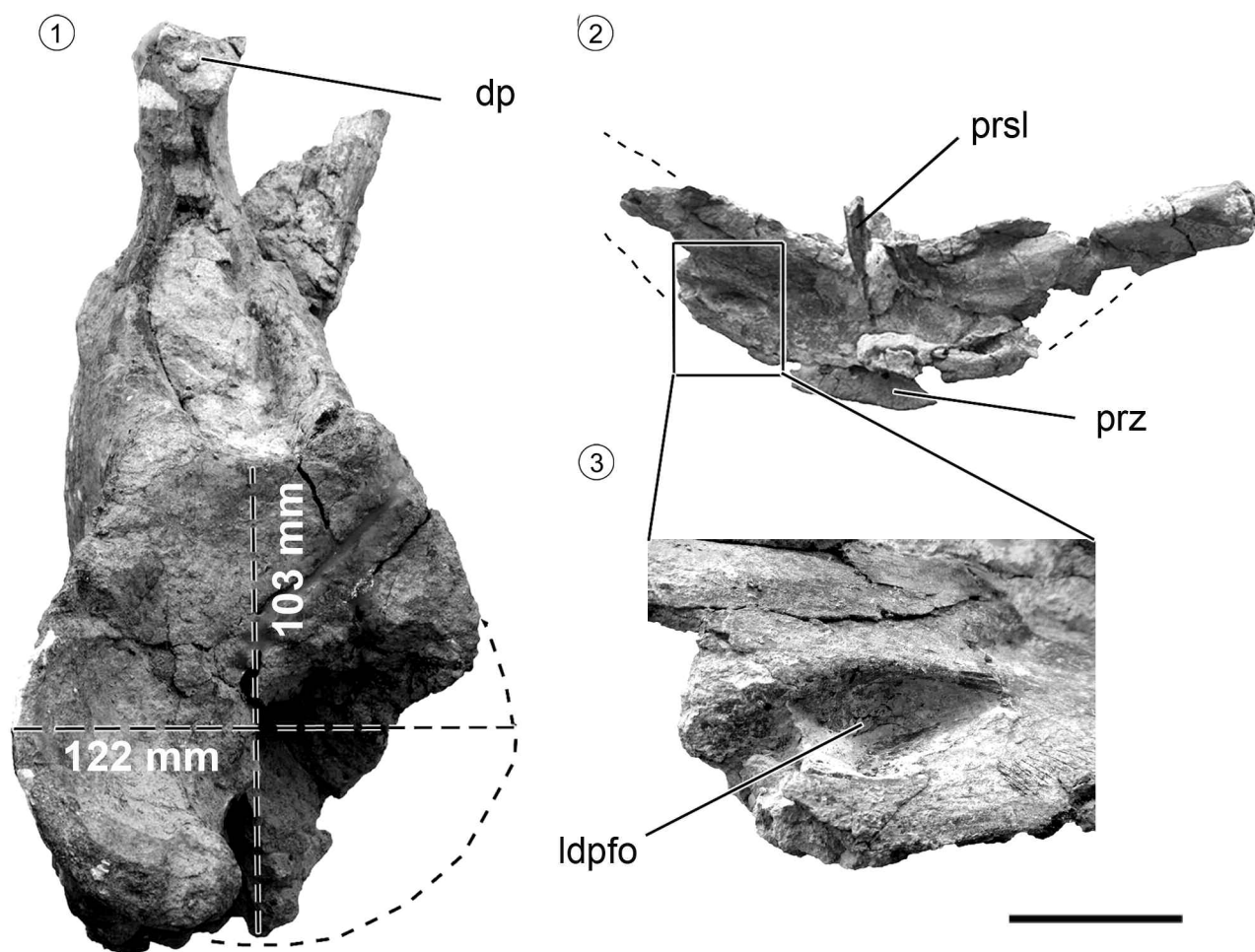
Figure 11. Newly proposed autapomorphies of *Katepensaurus goicoecheai*. UNPSJB-PV 1007/13, anterior dorsal vertebra. **1,** posterior view, with dorsoventral and transverse dimensions of posterior articular surface of centrum. UNPSJB-PV 1007/12, anterior to middle dorsal neural arch; **2,** anterodorsal view; **3,** detail of laterodiapophyseal fossa. Abbreviations: **dp,** diapophysis; **ldpfo,** laterodiapophyseal fossa; **prsl,** prespinal lamina; **prz,** prezygapophysis. Scale bar= 10 cm.

this morphology has otherwise been documented only in two unnamed dorsal neural arches from the Cretaceous of South America: MACN PV N35 from the Barremian of Argentina (Apesteguía, 2007) and possibly CCC 017 from the Albian of Brazil (Castro *et al.*, 2007). Accordingly, these specimens have been regarded as belonging to basal rebbachisaurids, either firmly (MACN PV N35; Apesteguía, 2007) or tentatively (CCC 017; Whitlock, 2011). Dorsal vertebrae of *Comahuesaurus*, *Demandasaurus*, and *Nigersaurus* exhibit a 'laminar hyposphene' (Torcida Fernández-Baldor *et al.*, 2011) or 'hyposphenal ridge' (*i.e.*, a morphologically simpler, linear structure that is shaped differently than the triangular or diamond-shaped hyposphene of basal rebbachisaurids; see Carballido *et al.*, 2012: fig. 13). *Katepensaurus*

exhibits a well-marked infrapostzygapophyseal lamina (see Ibiricu *et al.*, 2013a: fig. 8). This lamina is similar in morphology to the one described in the unnamed rebbachisaurid from Las Campanas Creek (MMCH-Pv 49, Apesteguía *et al.*, 2010; Haluza *et al.*, 2012). As such, rebbachisaurid dorsal vertebrae may presently be grouped into three evolutionary 'grades' based on the morphology of their accessory intervertebral articulations: (1) a group comprised of *Histriasaurus* and MACN PV N35, with a well-developed, subtriangular hyposphene (Fig. 12.1–2); (2) a group with a 'laminar hyposphene' or 'hyposphenal ridge' that includes *Comahuesaurus* and the nigersaurines (rebbachisaurines) *Demandasaurus* and *Nigersaurus* (Fig. 12.3–4); and (3) a group with a well defined infrapostzygapophyseal lamina,
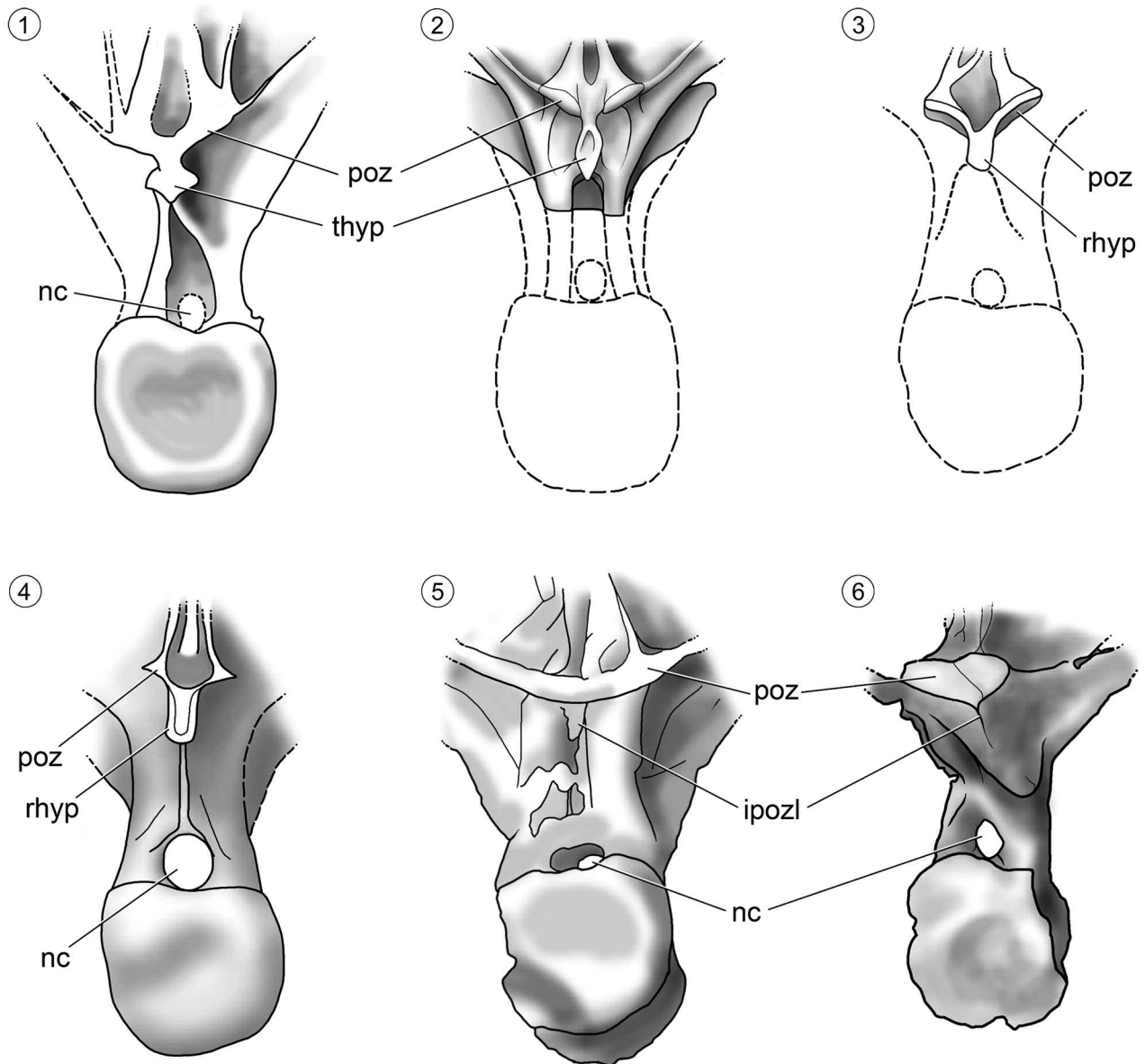
Figure 12. Comparative line drawings of rebbachisaurid posterior dorsal vertebrae in posterior view, showing the development of the hyposphene-hypantrum complex [modified and re-drawn from Carballido *et al.* (2012)]. **1**, *Histriasaurus*; **2**, MACN PV N35; **3**, *Comahuesaurus*; **4**, *Nigersaurus*; **5**, MMCH-Pv 49 [after Haluza *et al.* (2012)]; **6**, *Katepensaurus* [after Ibiricu *et al.* (2013a)]. Abbreviations: **ipozl,** infrapostzygapophyseal lamina; **nc,** neural canal; **poz,** postzygapophysis; **rhyp,** ridge-shaped hyposphene; **thyp,** triangular hyposphene. Not to scale.

encompassing *Katepensaurus*, and MMCH-Pv 49 (Fig. 12.5–6). The anatomical difference between these last two groups (*i.e.*, *Comahuesaurus* and nigersaurines and the group including *Katepensaurus* and MMCH-Pv 49), is the column-like, robust and likely intervertebral articulation present in *Comahuesaurus* and nigersaurines, rather than the thin lamina present in the two other Patagonian taxa.

Finally, in anterior caudal neural spines of *Katepensaurus*, the spinoprezygapophyseal and spinopostzygapophyseal laminae merge to form a robust lateral lamina (Fig. 13). This feature is shared with other members of Limaysaurinae (*i.e.*, *Cathartesaura* and *Limaysaurus*). On the other hand, contact between these laminae is absent in basal rebbachisaurids (*e.g.*, *Zapalasaurus*) and several Lower Cretaceous Afro-European members of the clade (*Demandasaurus*, *Nigersaurus*, the

recently described Tunisian rebbachisaurid *Tataouinea hannibalis* [Fanti *et al.*, 2013], and an isolated anterior caudal vertebra from the Isle of Wight [MIWG 5384; Mannion *et al.*, 2011]).

Ibiricu *et al.* (2012a) described several rebbachisaurid specimens from the Bajo Barreal Formation and assigned them to Rebbachisauridae indet. Among these were an isolated anterior caudal vertebra (UNPSJB-PV 580) and a fragmentary but associated anterior and middle caudal sequence (UNPSJB-PV 1004). Ibiricu *et al.* (2012a) suggested that the lateral lamina of these specimens was formed by the coalesced spinoprezygapophyseal and spinodiapophyseal laminae. Nevertheless, after further study and consideration, we now regard the lateral lamina of UNPSJB-PV 580 and 1004 as being formed from the spinoprezygapophyseal and spinopostzygapophyseal laminae. In the phylogenetic topology recovered herein, this character is the only unambiguous synapomorphy of Limaysaurinae. As such, we consider UNPSJB-PV 580 and 1004 to belong to this South American rebbachisaurid subclade. Whether or not these two specimens are referable to *Katepensaurus* remains unclear, so we regard them as Limaysaurinae indet.

Paleobiogeographic overview of Rebbachisauridae

Within Diplodocoidea, the clade Flagellicaudata is regarded as the sister taxon of Rebbachisauridae. The oldest definitive flagellicaudatans date from the Late Jurassic (Harris and Dodson, 2004; Harris, 2006), which implies that both this clade and Rebbachisauridae must have originated by that time (Remes, 2006; Carballido *et al.*, 2010, 2012; Whitlock, 2011; Mannion *et al.*, 2012). The most ancient undoubted rebbachisaurid is *Histriasaurus*, from late Hauterivian–early Barremian deposits in Istria, Croatia (Dalla Vecchia, 1998, 1999, 2005). Consequently, assuming that the higher-level relationships of Rebbachisauridae have been accurately reconstructed, the first *ca.* 30 million years (Late Jurassic–early Hauterivian) of the evolutionary history of the clade are missing from the fossil record (Whitlock, 2011; Mannion *et al.*, 2012). Due largely to the current lack of Jurassic and earliest Cretaceous rebbachisaurid fossils, the precise area of origin of the clade remains unclear (see Remes, 2006; Whitlock, 2011). Nevertheless, as described below, fossil evidence (*i.e.*, the occurrences of the earliest and basalmost rebbachisauids) suggests that much of the early history of the clade may have taken place in Gond-

wana, possibly in the western region of this supercontinent, in areas that are now part of South America and Africa.

Recent phylogenetic analyses of Diplodocoidea (Sereno *et al.*, 2007; Carballido *et al.*, 2010, 2012; Torcida Fernández-Baldor *et al.*, 2011; Whitlock, 2011; Mannion *et al.*, 2012; Fanti *et al.*, 2013; Gallina *et al.*, 2014) have postulated *Histriasaurus* as a basal rebbachisaurid; moreover, several of these (Sereno *et al.*, 2007; Carballido *et al.*, 2010; Torcida Fernández-Baldor *et al.*, 2011; Whitlock, 2011) have regarded this form as the most plesiomorphic member of the clade yet discovered. Given its Croatian provenance, this taxon is typically regarded as European in origin (*e.g.*, Sereno *et al.*, 2007; Carballido *et al.*, 2010; Whitlock, 2011; Mannion, *et al.*, 2012; Fanti *et al.*, 2013). Nevertheless, as discussed by Dalla Vecchia (2005), the area of Croatia that yielded this rebbachisaurid was part of the Adriatic-Dinaric Carbonate Platform during the Early Cretaceous, a region which is thought to have had biotic affinities with continental Africa. Thus, and as previously suggested by Torcida Fernández-Baldor *et al.* (2011) and Carballido *et al.* (2012), *Histriasaurus* is more appropriately considered an African form (*i.e.*, a Gondwanan taxon).

A number of other recent phylogenetic analyses, including our own, have regarded the Aptian–Albian Brazilian taxon *Amazonsaurus* as the basalmost known rebbachisaurid (*e.g.*, Carballido *et al.*, 2012; Mannion *et al.*, 2012; Fanti *et al.*, 2013; Gallina *et al.*, 2014; Wilson and Allain, in press). Furthermore, and as mentioned above, two dorsal vertebral neural arches from the Early Cretaceous of South America, MACN PV N35 and CCC 017, are also considered as belonging to basal rebbachisaurids. If these systematic assessments are correct, then four of the most archaic rebbachisaurids yet discovered are South American (*Amazonsaurus*, MACN PV N35, CCC 017) or effectively African (*Histriasaurus*) in provenance.

Katepensaurus is the southernmost record of Rebbachisauridae that is identifiable to the genus level. The results of our phylogenetic analysis support the hypothesis that this central Patagonian taxon is a 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 of southernmost South America, especially toward the end of that period. At least three limaysaurine genera (*Katepen-*
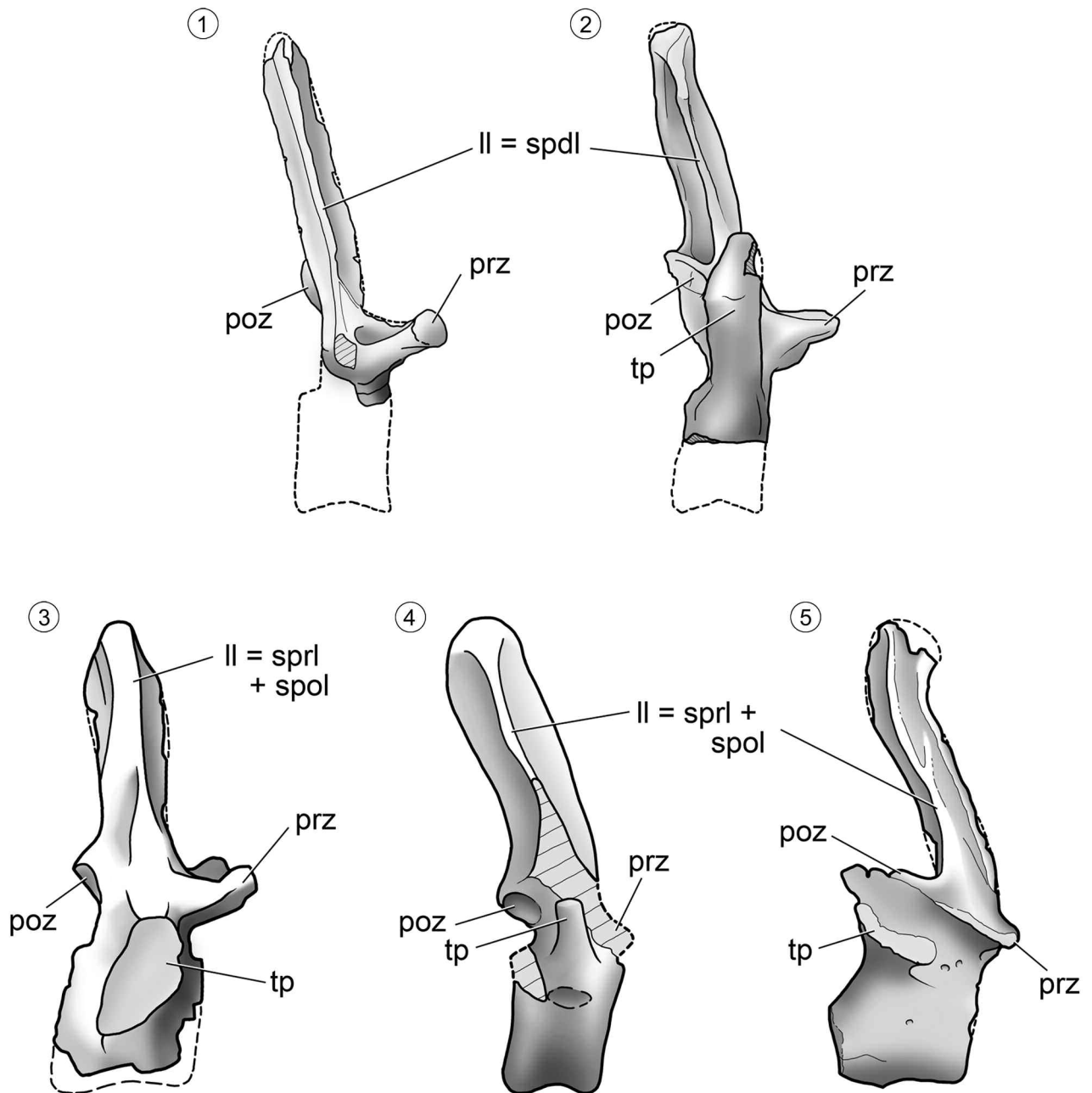
Figure 13. Comparative line drawings of rebbachisaurid anterior caudal vertebrae in lateral view, showing the different configurations of the lateral lamina [modified and re-drawn from Mannion *et al.* (2011)]. **1**, *Amazonsaurus*; **2**, MIWG 5384 [reversed, after Mannion *et al.* (2011)]; **3**, *Katepensaurus* [reversed, after Ibiricu *et al.* (2013a)]; **4**, *Limaysaurus*; **5**, *Cathartesaura*. Abbreviations: **ll**, lateral lamina; **poz**, postzygapophysis; **prz**, prezygapophysis; **spdl**, spinodiapophyseal lamina; **spol**, spinopostzygapophyseal lamina; **sprl**, spinoprezygapophyseal lamina; **tp**, transverse process. Not to scale.

saurus, *Cathartesaura* and *Limaysaurus*) are known from the Cenomanian–Turonian of Patagonia; this number would increase to four, five, or even six if, as seems likely, the fragmentary *Nopcsaspondylus* (Nopcsa, 1902; Apesteguía, 2007), *Rayososaurus* (Carballido *et al.*, 2010), and/or the generically unidentified rebbachisaurid MMCH-Pv 49 (Apesteguía *et al.*, 2010; Haluza *et al.*, 2012) are also part of this radiation. Consequently, the diversification of Limaysaurinae in South America during the mid-Cretaceous apparently constituted another key phase in rebbachisaurid evolution.

ACKNOWLEDGMENTS

REFERENCES

Apesteguía, S. 2005. Evolution of the hyposphene-hypantrum complex within Sauropoda. In: V. Tidwell, and K. Carpenter (Eds.), *Thunder-Lizards: The Sauropodomorph Dinosaurs*. Indiana University, Bloomington, Indiana, p. 248–267.

Apesteguía, S. 2007. The sauropod diversity of the La Amarga Formation (Barremian), Neuquén (Argentina). *Gondwana Research* 12: 533–546.

Apesteguía, S., Gallina, P.A., and Haluza, A. 2010. Not just a pretty face: anatomical peculiarities in the postcranium of rebbachisaurids (Sauropoda: Diplodocoidea). *Historical Biology* 22: 165–174.

Bonaparte, J.F. 1996. Cretaceous tetrapods of Argentina. *Münchner Geowissenschaftliche Abhandlungen* A 30: 73–130.

Bonaparte, J.F. 1997. *Rayososaurus agrioensis* Bonaparte 1995. *Ameghiniana* 34: 116.

Bridge, J.S., Jalfin, G.A., and Georgieff, S.M. 2000. Geometry, lithofacies, and spatial distribution of Cretaceous fluvial sandstone bodies, San Jorge Basin, Argentina: outcrop analog for the hydrocarbon-bearing Chubut Group. *Journal of Sedimentary Research* 70: 341–359.

Calvo, J.O., and Salgado, L. 1995. *Rebbachisaurus tessonei* sp. nov. a new Sauropoda from the Albian-Cenomanian of Argentina; new evidence on the origin of the Diplodocidae. *Gaia* 11: 13–33.

Carballido, J.L., Garrido, A.C., Canudo, J.I., and Salgado, L. 2010. Redescription of *Rayososaurus agrioensis* Bonaparte (Sauropoda, Diplodocoidea), a rebbachisaurid from the early Late Cretaceous of Neuquén. *Geobios* 43: 493–502.

Carballido, J.L., Salgado, L., Pol, D., Canudo, J.I., and Garrido, A.C. 2012. A new basal rebbachisaurid (Sauropoda, Diplodocoidea) from the Early Cretaceous of the Neuquén Basin; evolution and biogeography of the group. *Historical Biology* 24: 631–654.

Carvalho, I.S., Avilla, L.S., and Salgado, L. 2003. *Amazonsaurus maranhensis* gen. et sp. nov. (Sauropoda, Diplodocoidea) from the Lower Cretaceous (Aptian–Albian) of Brazil. *Cretaceous Research* 24: 697–713.

Casal, G.A., and Ibiricu, L.M. 2010. Materiales asignables a *Epachthosaurus* Powell, 1990 (Sauropoda: Titanosauria), de la Formación Bajo Barreal, Cretácico Superior, Chubut, Argentina. *Revista Brasileira de Paleontología* 13: 1–10.

Castro, D.F., Bertini, R.J., Santucci, R.M., and Medeiros, M.A. 2007. Sauropods of the Itapecuru Group (lower/middle Albian), São Luís-Grajaú Basin, Maranhão State, Brazil. *Revista Brasileira de Paleontología* 10: 195–200.

Dalla Vecchia, F.M. 1998. Remains of Sauropoda (Reptilia, Saurischia) in the Lower Cretaceous (upper Hauterivian/lower Barremian) limestones of SW Istria (Croatia). *Geologica Croatica* 51: 105–134.

Dalla Vecchia, F.M. 1999. Atlas of the sauropod bones from the upper Hauterivian–lower Barremian of Bale/Valle (SW Istria, Croatia). *Natura Nascosta* 18: 6–41.

Dalla Vecchia, F.M. 2005. Between Gondwana and Laurasia: Cretaceous sauropods in an intraoceanic carbonate platform. In: V. Tidwell, and K. Carpenter (Eds.), *Thunder Lizards: The Sauropodomorph Dinosaurs*. Indiana University, Bloomington, Indiana. p. 395–429.

Fanti, F., Cau, A., Hassine, M., and Contessi, M. 2013. A new sauropod dinosaur from the Early Cretaceous of Tunisia with extreme avian-like pneumatization. *Nature Communications*. Doi:10.1038/ncomms3080.

Gallina, P.A., and Apesteguía, S. 2006. *Cathartesaura anaerobica* gen. et sp. nov., a new rebbachisaurid (Dinosauria, Sauropoda) from the Huincul Formation (Upper Cretaceous), Río Negro, Argentina. *Revista del Museo Argentino de Ciencias Naturales* 7: 153–166.

Gallina, P.A., Apesteguía, S., Haluza, A., and Canale, J.I. 2014. A diplodocid sauropod survivor from the Early Cretaceous of South America. *PLoS ONE*. Doi:10.1317/journal.pone.0097128.

Garrido, A.C. 2010. Estratigrafía del Grupo Neuquén, Cretácico Superior de la Cuenca Neuquina (Argentina): nueva propuesta de ordenamiento litoestratigráfico. *Revista del Museo Argentino de Ciencias Naturales* 12: 121–177.

Goloboff, P., Farris, J., and Nixon, K. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.

Haluza, A., Canale, J.I., Otero, A., Pérez, L.M., and Scanferla, C.A. 2012. Changes in vertebral laminae across the cervicodorsal transition of a well-preserved rebbachisaurid (Dinosauria, Sauropoda) from the Cenomanian of Patagonia, Argentina. *Journal of Vertebrate Paleontology* 32: 219–224.

Harris, J.D. 2006. The axial skeleton of the dinosaur *Suuwassea emilieae* (Sauropoda: Flagellicaudata) from the Upper Jurassic Morrison Formation of Montana, USA. *Palaeontology* 49: 1091–1121.

Harris, J.D., and Dodson, P. 2004. A new diplodocoid sauropod dinosaur from the Upper Jurassic Morrison Formation of Montana, USA. *Acta Palaeontologica Polonica* 49: 197–210.

Ibiricu, L.M., Casal, G.A., Lamanna, M.C., Martínez, R.D., Harris, J.D., and Lacovara, K.J. 2012a. The southernmost records of Rebbachisauridae (Sauropoda: Diplodocoidea), from early Late Cretaceous deposits in central Patagonia. *Cretaceous Research* 34: 220–232.

Ibiricu, L.M., Martínez, R.D., and Casal, G.A. 2012b. The first record of Pterosauria in the Bajo Barreal Formation (Upper Cretaceous), central Patagonia, Argentina. *Ameghiniana* 49: 657–661.

Ibiricu, L.M., Casal G.A., Martínez, R.D., Lamanna, M.C., Luna, M., and Salgado, L. 2013a. *Katepensaurus goicoecheai* gen. et sp. nov., a Late Cretaceous rebbachisaurid (Sauropoda, Diplodocoidea) from central Patagonia, Argentina. *Journal of Vertebrate Paleontology* 33: 1351–1366.

Ibiricu, L.M., Martínez, R.D., Casal, G.A., and Cerda, I.A. 2013b. The behavioral implications of a multi-individual bonebed of a small theropod dinosaur. *PLoS ONE*. Doi:10.1371/journal.pone.0064253.

Ibiricu, L.M., Martínez, R.D., Luna, M., and Casal, G.A. 2014. A reappraisal of *Notohypsilophodon comodorensis* (Ornithischia: Ornithopoda) from the Late Cretaceous of Patagonia, Argentina. *Zootaxa* 3786: 401–422.

Lamanna, M.C., Martínez, R.D., and Smith, J.B. 2002. A definitive

abelisaurid theropod dinosaur from the early Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology* 22: 58–69.

Mannion, P.D. 2009. A rebbachisaurid sauropod from the Lower Cretaceous of the Isle of Wight, England. *Cretaceous Research* 30: 521–526.

Mannion, P.D., and Upchurch, P. 2010. Completeness metrics and the quality of the sauropodomorph fossil record through geological and historical time. *Paleobiology* 36: 283–302.

Mannion, P.D., Upchurch, P., and Hutt, S. 2011. New rebbachisaurid (Dinosauria: Sauropoda) material from the Wessex Formation (Barremian, Early Cretaceous) Isle of Wight, United Kingdom. *Cretaceous Research* 32: 774–780.

Mannion, P.D., Upchurch, P., Mateus, O., Barnes, R.N., and Jones, M.E.H. 2012. New information on the anatomy and systematic position of *Dinheirosaurus lourinhanensis* (Sauropoda: Diplodocoidea) from the Late Jurassic of Portugal, with a review of European diplodocoids. *Journal of Systematic Palaeontology* 10: 521–551.

Marsh, O.C. 1878. Principal characters of American Jurassic dinosaurs. Part I. *American Journal of Science, Series Three* 16: 411–416.

Marsh, O.C. 1884. Principal characters of American Jurassic dinosaurs. Part VII. On the Diplodocidae, a new family of the Sauropoda. *American Journal of Science, Series Three* 27: 161–167.

Nopcsa, F. 1902. Notizen über cretacische Dinosaurier. 3. Wirbel eines südamerikanischen Sauropoden. *Sitzungsberichte der Kais. Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Classe Wien* 111: 108–114.

Pereda Suberbiola, X., Torcida, F., Izquierdo, L.A., Huerta, P., Montero, D., and Pérez, G. 2003. First rebbachisaurid dinosaur (Sauropoda, Diplodocoidea) from the Early Cretaceous of Spain: palaeobiogeographical implications. *Bulletin de la Société Géologique de France* 174: 471–479.

Pol, D., and Escapa, I.H. 2009. Unstable taxa in cladistic analysis: identification and the assessment of relevant characters. *Cladistics* 25: 1–13.

Remes, K. 2006. Revision of the Tendaguru sauropod dinosaur *Tornieria africana* (Fraas) and its relevance for sauropod paleobiogeography. *Journal of Vertebrate Paleontology* 26: 651–669.

Salgado, L., and Bonaparte, J.F. 2007. Sauropodomorpha. In: Z. Gasparini, L. Salgado, and R.A. Coria (Eds.), *Patagonian Mesozoic Reptiles*. Indiana University, Bloomington, Indiana, p. 188–228.

Salgado, L., Garrido, A.C., Cocca, S., and Cocca, J.R. 2004. Lower Cretaceous rebbachisaurid sauropods from Cerro Aguada del León (Lohan Cura Formation), Neuquén Province, northwestern Patagonia, Argentina. *Journal of Vertebrate Paleontology* 24: 903–912.

Salgado, L., Carvalho, I.S., and Garrido, A.C. 2006. *Zapalasaurus bonapartei*, un nuevo dinosaurio saurópodo de la Formación La Amarga (Cretácico Inferior), noroeste de Patagonia, Provincia de Neuquén, Argentina. *Geobios* 39: 695–707.

Sereno, P.C., Beck, A.L., Dutheil, D.B., Larsson, H.C.E., Lyon, G.H., Moussa, B., Sadleir, R.W., Sidor, C.A., Varricchio, D.J., Wilson, G.P., and Wilson, J.A. 1999. Cretaceous sauropods from the Sahara and the uneven rate of skeletal evolution among dinosaurs. *Science* 286: 1342–1347.

Sereno, P.C., Wilson, J.A., Witmer, L.M., Whitlock, J.A., Maga, A., Ide, O., and Rowe, T.A. 2007. Structural extremes in a Cretaceous dinosaur. *PLoS ONE*. doi:10.1371/journal.pone.0001230.

Torcida Fernández-Baldor, F., Canudo, J.I., Huerta, P., Montero, D., Pereda Suberbiola, X., and Salgado, L. 2011. *Demandasaurus darwini*, a new rebbachisaurid sauropod from the Early Cretaceous of the Iberian Peninsula. *Acta Palaeontologica Polonica* 56: 535–552.

Tschopp, E., and Mateus, O. 2012. The skull and neck of a new flagellicaudatan sauropod from the Morrison Formation and its implications for the evolution and ontogeny of diplodocid dinosaurs. *Journal of Systematic Palaeontology* 11: 853–888.

Upchurch, P. 1995. The evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London, Series B* 349: 365–390.

Whitlock, J.A. 2011. A phylogenetic analysis of Diplodocoidea (Saurischia: Sauropoda). *Zoological Journal of the Linnean Society* 161: 872–915.

Wilson, J.A., and Allain, R. In press. Osteology of *Rebbachisaurus garasbae* Lavocat, a diplodocoid (Dinosauria: Sauropoda) from the early Late Cretaceous-aged Kem Kem beds of southeastern Morocco. *Journal of Vertebrate Paleontology*.

Wilson, J.A., D'Emic, M.D., Ikejiri, T., Moacdieh, E.M., and Whitlock, J.A. 2011. A nomenclature for vertebral fossae in sauropods and other saurischian dinosaurs. *PLoS ONE*. doi:10.1371/journal.pone.0017114.

APPENDIX 1

Character scores of *Katepensaurus goicoecheai* based on the data matrix proposed by Mannion *et al.* (2012).

?? ????????0?1110010???0?0?0?0???010??????????0?11?0?1?1110?1? ?11?1100?1?1111?????01?11000?0?????1???????????????????????? ????????????????????

Note:

Character 75 was re-scored in all rebbachisaurids following Carballido *et al.* (2012), this lamina is identified as the PODL-SPRL lamina [for more detail see Carballido *et al.* (2012); Supplementary 1, character 119].

Character 128 was re-scored in *Zapalasaurus bonapartei* following Carballido *et al.* (2012) as caudal neural spines without triangular lateral processes.

Character 148 was re-scored in *Zapalasaurus bonapartei* following Carballido *et al.* (2012); the anterior caudal transverse processes, triangular in shape and tapering distally.