A novel form of postcranial skeletal pneumaticity in a sauropod dinosaur: Implications for the paleobiology of Rebbachisauridae

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In dinosaurs and other archosaurs, the presence of foramina connected with internal chambers in axial and appendicular bones is regarded as a robust indicator of postcranial skeletal pneumaticity (PSP). Here we analyze PSP and its paleobiological implications in rebbachisaurid diplodocoid sauropod dinosaurs based primarily on the dorsal vertebrae of Katepensaurus goicoecheai, a rebbachisaurid from the Cenomanian–Turonian (Upper Cretaceous) Bajo Barreal Formation of Patagonia, Argentina. We document a complex of interconnected pneumatic foramina and internal chambers within the dorsal vertebral transverse processes of Katepensaurus. Collectively, these structures constitute a form of PSP that has not previously been observed in sauropods, though it is closely comparable to morphologies seen in selected birds and non-avian theropods. Parts of the skeletons of Katepensaurus and other rebbachisaurid taxa such as Amazonsaurus maranhensis and Tataouinea hannibalis exhibit an elevated degree of pneumaticity relative to the conditions in many other sauropods. We interpret this extensive PSP as an adaptation for lowering the density of the skeleton, and tentatively propose that this reduced skeletal density may also have decreased the muscle energy required to move the body and the heat generated in so doing. Given that several rebbachisaurids inhabited tropical to subtropical paleolatitudes during the extreme warmth of the mid-Cretaceous, increased PSP may have better enabled these sauropods to cope with extraordinarily high temperatures. Extensive skeletal pneumaticity may have been an important innovation in Rebbachisauridae, and perhaps also in saltasaurine titanosaurs, which evolved an even greater degree of PSP. This may in turn have contributed to the evolutionary success of rebbachisaurids, which were the only diplodocoids to survive into the Late Cretaceous.

Key words: Dinosauria, Rebbachisauridae, Katepensaurus, air sac system, postcranial skeletal pneumaticity, pulmonary system, Cretaceous, Bajo Barreal Formation, Argentina.

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Introduction

Studies of archosauromorph anatomy demonstrate that the presence of foramina connected with internal chambers in axial and appendicular bones is a consistent indicator of postcranial skeletal pneumaticity (PSP) (Janensch 1947; Britt 1997; Wedel et al. 2000; Wedel 2003, 2009; O’Connor 2004, 2006; O’Connor and Claessens 2005; Sereno et al.
Pneumatic diverticula arise from the cervical air sacs in intrapulmonary bronchi (O’Connor 2004). One single (the clavicular) and four paired (the cervical, anterior and posterior thoracic, and abdominal) air sacs are recognized in most birds, although a minority of avian species deviate from this pattern (Duncker 1972; Wedel 2003; O’Connor 2004). The lungs, which are fixed on the dorsal portion of the body cavity and attached to the thoracic vertebrae, are comparatively rigid structures that are united to a series of thin-walled air sacs by intrapulmonary bronchi (O’Connor 2004). One single (the clavicular) and four paired (the cervical, anterior and posterior thoracic, and abdominal) air sacs are recognized in most birds, although a minority of avian species deviate from this pattern (Duncker 1972; Wedel 2003; O’Connor 2004). The pneumatic diverticula (a network of epithelial “connector structures” that originate from the lungs and air sacs and insert in the walls of soft tissues and bones (O’Connor 2006)) have been divided into four categories: visceral, intermuscular, subcutaneous, and intraosseous (O’Connor 2004). Intraosseous diverticula arising from the cervical air sacs pneumatize the cervical vertebrae and ribs and the anterior thoracic vertebrae, whereas diverticula from the abdominal air sacs pneumatize the posterior thoracic, sacral, and caudal vertebrae plus the pelvic girdle and hind limbs (O’Connor and Claessens 2005; O’Connor 2006). The pectoral girdle and forelimbs are pneumatized by diverticula from the clavicular air sac, whereas some thoracic vertebrae and ribs are pneumatized by the lung itself. Diverticula from the anterior thoracic air sacs often pneumatize the sternum and sternal ribs, but the posterior thoracic air sacs do not pneumatize bones (Duncker 1972; Perry et al. 2011). Functionally, PSP has frequently been regarded as a weight-reducing specialization in large-bodied and/or flying avian taxa (e.g., O’Connor 2004, 2009; Benson et al. 2012). Air sacs and their respective diverticula are also generally associated with the following functions in birds: ventilation, buoyancy, vocalization, and display (Wedel 2003, 2006; Henderson 2004; Perry et al. 2009).

Rebbachisauridae is a clade of small to medium-sized, morphologically peculiar diplodocoid sauropod dinosaurs known from the Early and mid-Cretaceous of Europe, South America, and Africa. Previous works have attempted to elucidate the paleobiology of rebbachisaurids based on the skeletal anatomy of these unusual sauropods (e.g., Apesteguía 2005; Sereno and Wilson 2005; Sereno et al. 2007; Apesteguía et al. 2010; Fanti et al. 2013, 2015; Wilson and Allain 2015; Paulina Carabajal et al. 2016). Nevertheless, many aspects of rebbachisaurid paleobiology remain poorly understood, a circumstance that is due in large part to the highly incomplete nature of most fossils of these dinosaurs (Ibiricu et al. 2012). Although PSP has been described in members of various sauropod lineages, particularly by Wedel (2003), rebbachisaurids have received comparatively little attention in this regard (but see Fanti et al. 2013, 2015).

Katepensaurus goicoecheai (Ibiricu et al. 2013a, 2015) is a recently-named rebbachisaurid that was recovered from an exposure of the Cenomanian–Turonian (Upper Cretaceous) Bajo Barreal Formation in the Cañadón de Las Horquetas on the Estancia Laguna Palacios in Chubut Province, central Patagonia, Argentina. Katepensaurus, the southern-most-known rebbachisaurid taxon, was recently assigned to the subclade Limaysaurinae (Ibiricu et al. 2015); however, Fanti et al.’s (2015) phylogenetic analysis recovered this taxon as a member of Rebbachisaurinae (= Nigersaurinae; see Wilson and Allain 2015). Here, we analyze rebbachisaurid PSP and its paleobiological implications, based primarily on the dorsal vertebrae of Katepensaurus. Most notably, we document and describe a form of PSP—pneumatic chambers connected to foramina within the dorsal vertebral transverse processes—that has not previously been observed in sauropods.
Material and methods

We studied the holotypic partial skeleton of *Katepensaurus goicoecheai* (UNPSJB-PV 1007) from the Cenomanian–Turonian Bajo Barreal Formation of Chubut Province, Argentina. We examined the specimen firsthand. Furthermore, we subjected three dorsal vertebrae of the *Katepensaurus* holotype to computed tomographic (CT) scanning to evaluate their internal structures. The scans were performed at the Instituto del Diagnóstico del Este del Chubut, in Puerto Madryn, Chubut Province, Argentina, and at the Sanatorio Asociación Española S.M. in Comodoro Rivadavia, also in Chubut. Because of their relatively good preservation, the vertebrae selected for scanning were UNPSJB-PV 1007/4, /5, and /12 (which are anterior to middle [UNPSJB-PV 1007/12] and middle to posterior [UNPSJB-PV 1007/4, /5] dorsal vertebrae, respectively). Images in DICOM format were imported in 3D Slicer (visualization software; www.slicer.org). Soft tissues such as ligaments, muscles, cartilage, and pneumatic diverticula are almost never directly preserved in the fossil record; however, such tissues often leave traces on bones. We utilized these osteological correlates as evidence to infer the presence of these soft tissues (following, for example, Witmer 1995).

We focused on the dorsal vertebrae of *Katepensaurus* that exhibit the hypothesized pneumatic morphologies that are most relevant to this study (see Ibiricu et al. 2013a, 2015 for detailed descriptions and comparisons of these and other bones). The nomenclature of vertebral fossae employed here is that of Wilson et al. (2011), whereas that of vertebral laminae is from Wilson (1999).

Histological sections of a dorsal rib of *Katepensaurus* (UNPSJB-PV 1007/28) were prepared, based on the methodology outlined by Chinsamy and Raath (1992), in the petrographic laboratory of the Universidad Nacional de San Luis, in San Luis, San Luis Province, Argentina. The sections were studied using a Nikon E400 petrographic polarizing microscope. Nomenclature and definitions of osteohistological structures are derived from Francillon-Vieillot et al. (1990) and Chinsamy-Turan (2005).

Results

Pneumatic dorsal vertebral structures in *Katepensaurus*—The external osteological evidence for the presence of
soft tissues in extinct animals such as sauropod dinosaurs includes vertebral fossae (including blind [= non-communicating] and communicating fossae), cortical foramina, grooves, sulci, rugosities, and bone excavations in general (O’Connor 2006; Organ 2006; Schwarz-Wings 2009). Recently, Ibiricu et al. (2015) described new fossils of \textit{Katepensaurus goicoecheai}; among these are one anterior and two anterior to middle dorsal vertebrae (specimen numbers UNPSJB-PV 1007/13, /12, and /31, respectively; Figs. 2A, B, 3). In the anterior dorsal vertebra UNPSJB-PV 1007/13, the left lateral side of the centrum, which is the best preserved, is excavated by a well-defined fossa (i.e., a “pleurocoel” of many previous works). This fossa is ovate in outline and extends anteroposteriorly for approximately three-fourths the preserved length of the centrum (Ml, 87.9 mm; Mh, 50 mm). Closely comparable fossae are associated with pneumatic invasion by the pulmonary system in many extant birds (O’Connor 2004).

Both transverse processes of the anterior to middle dorsal vertebra UNPSJB-PV 1007/12 exhibit a deep, well-defined ovoid fossa that penetrates to the ventral floor of the bone (the laterodiaphyseal fossa of Ibiricu et al. 2015). The right laterodiaphyseal fossa of this vertebra has a Ml of 52.1 mm and a Mh of 24.8 mm. Furthermore, as shown by CT imagery, much of the interior of the left diaphysis of vertebra UNPSJB-PV 1007/12 is hollow (Fig. 3B). A laterodiaphyseal fossa is also present on the preserved left transverse process of another of the recently described \textit{Katepensaurus} anterior to middle dorsal vertebrae, UNPSJB-PV 1007/31. Nevertheless, in this latter vertebra, the orientation and shape of the fossa differ from those in UNPSJB-PV 1007/12. These differences may be related to the distinct positions of these vertebrae along the dorsal column, since UNPSJB-PV 1007/12 is thought to be situated slightly more posteriorly in the sequence. However, these distinctions might also be due to variation in the distribution and/or morphology of pneumatic diverticula and their associated osteological correlates independent of serial position. For instance, in the holotypic partial skeleton of the Tunisian rebbachisaurid \textit{Tatouinea hannibalisa}, the sacrum, caudal vertebrae, and ischia exhibit asymmetrical pneumatization, with the development of probable pneumatic features being more extensive on the left side of the animal than the right (Fanti et al. 2013, 2015). Moreover, in another sauropod group, saltasaurine titanosaurs, variation in the presence of fossae and foramina between specimens, vertebral sequences, and the left and right halves of individual vertebrae also appears to be related to the distribution of pneumatic diverticula and does not always vary systematically according to serial position (Zurriaguz and Álvarez 2014; Zurriaguz and Powell 2015).

The \textit{Katepensaurus} holotype also includes three middle to posterior dorsal vertebrae (UNPSJB-PV 1007/4–6; Ibiricu et al. 2013a, 2015; Figs. 2C, D, 4, 5). In UNPSJB-PV 1007/4, the lateral sides of the centrum are invaded by large, well-defined, ovate fossae ("pleurocoels") that extend anteroposteriorly for approximately half its length (Ml of the right fossa: 75.4 mm; Mh: 54.2 mm). The right fossa is rel-

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**Fig. 3.** Partial anterior to middle dorsal vertebra (UNPSJB-PV 1007/12) of the rebbachisaurid sauropod \textit{Katepensaurus goicoecheai} Ibiricu, Casal, Martínez, Lamanna, Luna, and Salgado, 2013a from the Cenomanian–Turonian Bajo Barreal Formation of Chubut Province, Argentina. **A.** Computed tomography (CT)-based digital reconstruction in left anterolateral view. **B.** Axial CT “slice” in anterior view, with hypothesized pneumatic structures indicated by arrows. Note internal cavity in left diapophysis.
atively deep and internally partitioned by a thin, dorsoventrally-oriented lamina. Similarly, although it is smaller and shallower, an ovate lateral fossa is present in the centrum of UNPSJB-PV 1007/5 (see Ibiricu et al. 2013a).

Perhaps the most distinctive features of the middle to posterior dorsal vertebrae of *Katepensaurus goicoecheai* Ibiricu, Casal, Martínez, Lamanna, Luna, and Salgado, 2013a from the Cenomanian–Turonian Bajo Barreal Formation of Chubut Province, Argentina. A. Computed tomography (CT)-based reconstruction of the transverse process and diapophysis in posterior view, with black rectangle indicating location of axial CT “slice” shown in B. B. Axial CT “slice” showing intradiapophyseal chamber, with black and white arrowheads indicating cortical and trabecular tissues, respectively. Reconstruction of the transverse process and diapophysis in medial (C) and posterior (D) views. Black rectangle indicates location of sagittal CT “slice” shown in E. E. Sagittal CT “slice” through intradiapophyseal chamber.

The right laterodiapophyseal fenestra of UNPSJB-PV 1007/5 has a Ml of 84.8 mm and a Mh of 24.4 mm. Interestingly, and as revealed by CT images, this fenestra is united directly to a pneumatic chamber within the distal (i.e., lateral) end of the transverse process, which is here termed the intradiapophyseal chamber (Fig. 4; see also Discussion). Most of the intradiapophyseal chamber is surrounded by solid but relatively thin cortical bone; however, trabecular bone is present at the distal end of the chamber. As observed in and reconstructed from CT images, the intradiapophyseal chamber extends to the distal end of the transverse process, which
is eroded. This pneumatic structure is dorsoventrally taller laterally than it is medially, and exhibits a total internal \( M_l \) of 58.8 mm, a \( M_h \) of 23.7 mm, and a maximum anteroposterior width of 18.5 mm (Fig. 4). The estimated volume (from the distal [= lateral] end of the laterodiapophyseal fenestra to that of the transverse process, which in turn, represents the reconstructed air space) of the chamber is 20 534 mm\(^3\) (= 20.534 cm\(^3\)).

In the vertebra UNPSJB-PV 1007/4, the posterior centroparapophyseal and posterior centrodiaiaphyseal laminae delimit the deep parapophyseal centrodiaiaphyseal fossa. This fossa is subdivided by two accessory laminae, the dorsal and ventral parapophyseal centrodiaiaphyseal fossa laminae of Ibiricu et al. (2013a). The lateral surfaces of the neural arch also exhibit deep, ovoid cavities, the postzygapophyseal centrodiaiaphyseal fossa and the parapophyseal centroprezygapophyseal fossa. In UNPSJB-PV 1007/5, there are also well-defined, rounded fossae placed lateral to the articular facets of the postzygapophyses (the lateral postzygapophyseal fossae of Ibiricu et al. 2013a). The right lateral postzygapophyseal fossa of UNPSJB-PV 1007/5 has a \( M_l \) of 31.2 mm and a \( M_h \) of 19.5 mm.

The middle to posterior dorsal vertebral neural spines display wide, bilateral fossae, the prezygapophyseal spino-diaphyseal and spinopostzygapophyseal lamina fossae. These shallow fossae exhibit flat “floors”. The lateral spinopostzygapophyseal lamina separates the comparatively mediolaterally narrow, dorsomedially positioned spinopostzygapophyseal lamina fossa from the wider, ventrolaterally situated postzygapophyseal spinodiapophyseal fossa (see Ibiricu et al. 2013a).

In sum, the dorsal vertebral sequence of *Katepensaurus* includes anterior to middle dorsals with laterodiapophyseal fossae (i.e., UNPSJB-PV 1007/12, 31) and middle to posterior dorsals with laterodiapophyseal fenestrae (UNPSJB-PV 1007/4–6). Stated another way, the anterior to middle dorsal vertebral transverse processes of *Katepensaurus* are excavated by fossae, whereas the more posterior dorsal transverse processes are pierced by fenestrae (see Ibiricu et al. 2015). Moreover, the system of fossae in the dorsal vertebral neural arches is well-developed.

**Histological context and ontogenetic assessment.**—To assess the minimum ontogenetic age of the *Katepensaurus* type specimen, a transverse histological thin section was taken from a dorsal rib (UNPSJB-PV 1007/28). Although the ontogenetic stages of sauropod specimens have usually been deduced from long bone histology (e.g., Klein and...
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Sander 2008), dorsal ribs have recently been demonstrated to be useful for at least minimum age estimation (Waskow and Sander 2014).

The rib has a relatively thick cortex that surrounds a small marrow cavity that is filled with cancellous bone (Fig. 6A). There is no evidence of pneumatic cavities. The perimedullary cortex gradually transforms into cancellous bone. The inner cortex is highly remodeled, exhibiting several generations of secondary osteons (Fig. 6B). This remodeling is clearly more pronounced on one side of the rib, in which secondary osteons reach the outer cortex. The inner cortex is highly remodeled, exhibiting several generations of secondary osteons (Fig. 6B). This remodeling is clearly more pronounced on one side of the rib, in which secondary osteons reach the outer cortex. Primary bone consists of well-vascularized fibrolamellar bone tissue (Fig. 6C). Primary osteons are mostly longitudinally oriented (Fig. 6D). Osteocyte lacunae are rounded or slightly elongate. Sharpey’s fibers are mostly observed on both the anterior and posterior regions of the rib. Fibrolamellar bone is interrupted by growth marks (annuli and lines of arrested growth; i.e., LAGs) (Fig. 6E). Seven growth marks are evident from the innermost cortex to the periosteal surface. Spacing between concentric growth marks diminishes moderately towards the periphery. There are no significant changes in the intrinsic fiber orientation and the density of vascular spaces in the outer cortex.

Based on the number of growth marks, we interpret a minimum age of seven years for the *Katepensaurus* holotype. Furthermore, judging from the absence of a strong decrease in the spacing of the peripheral growth marks, we infer that the individual represented by this specimen died during an active phase of growth; in other words, that the *Katepensaurus* holotype was not fully grown when it died.

**Discussion**

**Reconstruction of rebbachisaurid pulmonary anatomy.**—The axial skeleton of *Katepensaurus* displays a suite of hypothesized pneumatic features that are, in most respects, comparable to those seen in other rebbachisaurid taxa. For instance, the dorsal vertebral centra of this Patagonian form are excavated by well-defined lateral fossae (“pleurocoels”), a feature that is shared with many other sauropods, including all other rebbachisaurids for which this part of the skeleton has been described (i.e., *Amazonsaurus maranhensis*, Carvalho et al. 2003, *Comahuesaurus windhaussen*, Carballido et al. 2012, *Demandasaurus darwini*, Torcida Fernández-Baldor et al. 2011, *Histriasaurus boscobollei*, Dalla Vecchia 1999, *Limaysaurus tessonei*, Calvo and Salgado 1995, *Nigersaurus taqueti*, Sereno et al. 2007, *Nopcsaspondylus alarconensis*, Nopcsa 1902; Apesteguía

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**Fig. 6.** Histology of a dorsal rib (UNPSJB-PV 1007/28) of the holotype of the rebbachisaurid sauropod *Katepensaurus goicoecheai* Ibiricu, Casal, Martínez, Lamanna, Luna, and Salgado, 2013a from the Cenomanian–Turonian Bajo Barreal Formation of Chubut Province, Argentina. A. Complete cross section of the rib sampled for histology. B. Detail of the dense Haversian bone in the cortex. C. General view of fibrolamellar bone tissue. D. Detail of fibrolamellar bone tissue. Note the abundance of longitudinally oriented vascular spaces in C and D. E. Four of the seven growth marks preserved in the primary bone tissue (indicated by arrowheads).
2007, *Rebbachisaurus garasbae*, Wilson and Allain 2015, and several unidentified or unnamed forms, e.g., MMCH-Pv 49, Haluza et al. 2012, MOZ-Pv 1240, Salgado et al. 2012). Moreover, in *Katepensaurus*, the general morphology of the dorsal neural arches and their associated complex of laminae and fossae closely resembles those of other rebbachisaurids such as *Limaysaurus*, *Nopcsaspondylus*, *Rebbachisaurus*, and especially MMCH-Pv 49 (Apesteguía et al. 2010; Haluza et al. 2012). These neural arch fossae are probably related to the presence of pneumatic diverticula associated with the dorsal column. Evidence consistent with this hypothesis is present in the form of numerous, irregular foramina and fossae in the middle to posterior dorsal neural arches of *Rebbachisaurus* that Wilson and Allain (2015) regarded as pneumatic in origin. Additionally, Torcida Fernández-Baldor et al. (2011) documented the occurrence of foramina that penetrate entirely through the dorsal neural arch pedicels of the Spanish rebbachisaurid *Demandasaurus*, and interpreted these as pneumatic structures as well. Torcida Fernández-Baldor et al. (2011) also reported evidence of pneumaticity in the area of the capitulotubercular web in dorsal ribs of *Demandasaurus*.

*Katepensaurus* offers additional, compelling evidence that the dorsal series of at least some rebbachisaurids was pneumatized by diverticula from the pulmonary system. As detailed above, the middle to posterior dorsal neural arches of this Patagonian taxon display features that have not been documented elsewhere within Sauropoda, most notably the laterodiapophyseal fenestrae and their associated intradiapophyseal chambers. As demonstrated by CT images, the right laterodiapophyseal fenestra of the middle to posterior dorsal vertebra UNPSJB-PV 1007/5 is united to the intradiapophyseal chamber, an internal cavity that extends to the distal (= lateral) end of the transverse process. The intradiapophyseal chamber is surrounded by solid cortical bone that terminates distally in trabecular bone (Fig.
anaerobica cervical vertebrae have been described (i.e., as is also the case in all other rebbachisaurids for which
fined fossae (Fig. 7; see also Ibiricu et al. 2013a: figs. 3–5), this rebbachisaurid are excavated by several deep, well-de-
caudal vertebrae. The cervical centra and neural arches of
the holotype of vertebral transverse processes of
apot yseal fossae present in the anteri or to mi ddl e dorsal
(Cerda et al. 2012).

Similarly, following from the PP concept, the laterodi-
apophyseal fossae present in the anterior to middle dorsal vertebral transverse processes of *Katepensaurus* may also be an indicator of pneumaticity. As demonstrated by CT imagery, much of the interior of the left diapophysis of the anterior to middle dorsal vertebra UNPSJB-PV 1007/12 is hollow, indicating the presence of an intradiapophyseal chamber (Fig. 3B). Unfortunately, the area that would have linked the left laterodiapophyseal fossa with the remainder of the transverse process is broken in this vertebra; therefore, it is not possible to definitively establish an internal connection between the fossa and chamber. However, assuming that, as seems likely, these fossae and chambers are indeed indicators of pneumatic invasion of the anterior to middle dorsal vertebrae of *Katepensaurus*, these verte-
brae may have been pneumatized by diverticula from the lungs and/or cervical air sacs (as has also been hypothe-
sized for this part of the skeleton in other sauropods, e.g., *Haplocanthosaurus*, *Saltasaurus*).

Although the focus of this study is the dorsal vertebrae, the holotype of *Katepensaurus* also includes cervical and caudal vertebrae. The cervical centra and neural arches of this rebbachisaurid are excavated by several deep, well-de-
defined fossae (Fig. 7; see also Ibiricu et al. 2013a: figs. 3–5), as is also the case in all other rebbachisaurids for which cervical vertebrae have been described (i.e., *Cathartesaura anaerobica*, Gallina and Apesteguía 2005, *Demandasaurus*, Torcida Fernández-Baldor et al. 2011, *Limaysaurus*, Calvo and Salgado 1995, *Nigersaurus*, Sereno et al. 2007, *Zapalasaurus bonapartei*, Salgado et al. 2006, and unidentified or unnamed forms, e.g., MMCH-Pv 49, Haluza et al. 2012, MOZ-Pv 1248, Salgado et al. 2012, UNPSJB-PV 1005, Ibiricu et al. 2012). These fossae almost certainly represent pneumatic structures associated with the presence of diverticu-
tica from the cervical air sacs, as has been reconstructed for many other saurischians, including other sauropods and basal sauropodomorphs (e.g., Wedel 2006, 2007, 2009; Cerda et al. 2012; Yates et al. 2012).

The most complete anterior caudal vertebra of *Kate-
pensaurus* (UNPSJB-PV 1007/7) exhibits a wing-like right transverse process, the anterior surface of which is excavated by a large prezygapophyseal centrodia
ophyseal fossa. This fossa is divided by a well-developed lamina, the prezyga-
ophyseal centrodia
ophyseal fossa lamina (Fig. 8A; see also Ibiricu et al. 2013a). The caudal vertebral neural arches are also excavated by several fossae that differ in their degrees of development (e.g., the spinodiapophyseal and spinopre-
zygapophyseal fossae). Unfortunately, however, the caudal centra of this rebbachisaurid are all missing or incomplete; therefore, it is not possible to observe any potentially pneumatic features in these elements. Consequently, the evidence for pneumaticity in the caudal series of *Katepensaurus* is not as robust as it is for the dorsal vertebrae.

Nevertheless, other rebbachisaurid taxa provide more convincing evidence for the invasion of the tail skeleton by pneumatic diverticula. In the holotypic specimen of *Tataouinea*, for example, the first 17 caudal vertebrae were preserved in articulation (Fanti et al. 2015). Of these, the centra of caudals 1–6 exhibit lateral foramina (i.e., “pleuro-
coels”), whereas those of vertebrae 14–16 possess well-de-
fined lateral fossae. Interestingly, the centra of vertebrae 7–13 lack lateral foramina or fossae (see Fantí et al. 2013, 2015). Fantí et al. (2015) interpreted this suite of features as evidence of pneumatic invasion of the most anterior and several of the medial caudal centra, interrupted by a pneumatic hiatus in the centra of vertebrae 7–13. Comparable lateral foramina are present in anterior caudal centra of *Comahuesaurus* (Carballido et al. 2012: fig. 7a, b) and in UNPSJB-PV 580, a rebbachisaurid caudal vertebra from the Bajo Barreal Formation that probably represents the first or second in the sequence (Ibiricu et al. 2012); given its nearly identical provenance, it is possible that this latter element may be referable to *Katepensaurus*, though this is presently unclear (Ibiricu et al. 2013a, 2015). Probable pneumatic excavations have been reported in the caudal vertebrae of other rebbachisaurid specimens as well; for instance, Torcida Fernández-Baldor et al. (2011: fig. 11a) identified the prezygapophyseal centrodiaaphyseal fossa of an anterior caudal of *Demandasaurus* as a “pneumatic depression”, whereas Medeiros and Schultz (2004) and Mannion and Barrett (2013) noted lateral fossae in the centra of isolated rebbachisaurid anterior caudals from the mid-Cretaceous of Brazil and Morocco, respectively. As such, and based on the morphological patterns observed in extant birds, the caudal vertebrae of rebbachisaurids may well have been pneumatized by the posterior diverticula of the abdominal air sacs, as has also been proposed for *Haplancanthosaurus* (Wedel 2009), diplodocids and brachiosaurids (Wedel and Taylor 2013), and saltasaurine titanosaurs (Cerda et al. 2012), among other sauropods. Within Rebbachisauridae, at least *Rebbachisaurus* and *Tataouinea* display evidence of sacral pneumaticity as well (see Fantí et al. 2013, 2015; Wilson and Allain 2015).

Compelling evidence for the presence of abdominal air sacs in Rebbachisauridae occurs in the form of probable pneumatic structures in the pelvises of selected members of the clade. Fantí et al. (2013, 2015) documented the existence of internal cavities in the pelvic elements of *Tataouinea*, specifically in several regions of the ilium (the preacetabular process, iliac blade, and pubic peduncle) and in most or all of the preserved parts of the ischium. These ischial cavities constitute a particularly persuasive indicator of PSP in that they are clearly connected to an external foramen (on the lateral side of the iliac peduncle of the ischium), thus satisfying all of the criteria specified in the Pneumaticity Profile of O’Connor (2006). Fantí et al. (2015: 39) also reported ischial pneumaticity in *Rebbachisaurus*, but this was not mentioned by Wilson and Allain (2015) in their detailed redescription of this taxon, so the condition in this animal remains unclear. Lastly, Carvalho et al. (2003) reported a pneumatic chamber in the region of the ischial peduncle of the ilium of *Amazonosaurus*. Significantly, most recent phylogenetic analyses that have included this taxon (e.g., Carballido et al. 2012; Mannion et al. 2012; Fantí et al. 2015; Ibiricu et al. 2015; Wilson and Allain 2015) have recovered it as the earliest-diverging rebbachisaurid, suggesting that pelvic pneumaticity may be synapomorphic for, and therefore probably widespread within, this sauropod clade. In extant birds, only the abdominal air sacs pneumatize pelvic elements; consequently, the occurrence of pneumatic ilia and ischia in at least some rebbachisaurids strongly suggests that abdominal air sacs were present in these dinosaurs.

Taking all of the above into account, it is possible to generate a hypothetical reconstruction of the rebbachisaurid pulmonary system (Fig. 9A). In addition to lungs, there is convincing evidence of the existence of cervical and abdominal air sacs in these sauropods, with the most compelling indicators of the latter being the pneumatized caudal and pelvic elements of selected genera (e.g., *Tataouinea*, probably *Amazonosaurus*). Cervical and abdominal air sacs have also been hypothesized in a variety of other neosauropods, such as *Haplancanthosaurus* (Wedel 2009), diplodocids and brachiosaurids (Wedel and Taylor 2013), and saltasaurine titanosaurs (Cerda et al. 2012). The existence of these air sacs may therefore represent the plesiomorphic condition for Neosauropoda, and indeed (given the probable occurrence of these structures in theropod dinosaurs) possibly a much more inclusive clade (e.g., Saurischia) as well. There is, however, no evidence of clavicular air sacs in rebbachisaurids, in contrast to what has been observed in saltasauroines (Cerda et al. 2012).

It is interesting to note that, in several rebbachisaurid taxa, there are indications of an extraordinary degree of invasion of postcranial skeletal elements by pneumatic diverticula relative to the conditions in many other sauropods. This appears particularly pronounced in the thoracic and abdominal regions: for instance, uniquely among sauropods, *Katepensaurus* has laterodiaphyseal fossae/fenestrae and intradiaphyseal chambers in the dorsal vertebral transverse processes, *Demandasaurus* has presumably pneumatic foramina that pass through the middle to posterior dorsal neural arch pedicles (Torcida Fernández-Baldor et al. 2011), and *Rebbachisaurus* has an abundance of pneumatic foramina in the laminae of the middle to posterior dorsal neural spines (Wilson and Allain 2015). Further, *Amazonosaurus*, *Tataouinea*, and possibly *Rebbachisaurus* show evidence of pneumatized pelvic elements, a condition that, in sauropods, is otherwise seen only in a few somphospondylans titanosaurs (see Cerda et al. 2012; Lamanna and Hasegawa 2014); pneumatic ischia are not definitively known elsewhere within Sauropoda. The potential implications of this extensive PSP are discussed below.

**Implications for rebbachisaurid paleobiology.**—Although deciphering the paleobiological implications of the extensive PSP seen in rebbachisaurids is necessarily speculative, some tentative inferences may be made by examining the significance of postcranial pneumaticity in the closest extant relatives of sauropods, modern birds. In birds, PSP lessens the density of bones by filling their internal cavities with air rather than marrow. By lightening the skeleton in this way, PSP reduces the muscle energy required to power the body,
thereby decreasing metabolic energy consumption, which may in turn be allocated to other purposes such as locomotion and foraging (O’Connor 2009). It therefore seems reasonable to infer that the extensive PSP seen in Katepensaurus and other rebbachisaurids may have provided similar energetic benefits to these sauropods. Since sauropods were obviously nonvolant, the selective pressure to reduce skeletal density may have been minimal in comparison to the same pressure in flying birds. From an energetics standpoint, however, the capacity to pneumatize parts of the skeleton may have been beneficial even to large-bodied, ground-dwelling animals such as rebbachisaurids (O’Connor 2009). Furthermore, as it is well-known that the contraction of vertebrate skeletal muscle produces heat (e.g., Huxley 1974), decreasing the amount of muscle energy required to support and move the body may have also reduced the amount of heat generated during these activities. This may in turn have provided additional benefit to rebbachisaurids, in that many, if not all, of these animals inhabited exceedingly warm paleoenvironments. For example, the northern South American rebbachisaurid Amazonsaurus and the North African Rebbachisaurus and Tataouinea lived at tropical to subtropical paleolatitudes during the Albian–Cenomanian (see paleogeographic reconstructions of these areas in Blakey 2008 and Seton et al. 2012), when global climates were exceptionally warm (Huber et al. 2002; Holz 2015); consequently, these sauropods would presumably have been routinely subjected to extraordinarily high temperatures (Fig. 10). Katepensaurus, though it comes from a higher paleolatitude, lived at approximately the Cenomanian–Turonian boundary—the time of the Cretaceous Thermal Maximum, one of the hottest intervals of the entire Phanerozoic (Clarke and Jenkyns 1999; Huber et al. 2002; Poulsen et al. 2003)—and therefore would likely have experienced greatly elevated temperatures as well.

The hypothesis that Katepensaurus frequently had to contend with extreme warmth is supported by reconstructions of its paleoenvironment. The holotype was recovered from an exposure of the Cenomanian–Turonian Bajo Barreal Formation on the Estancia Laguna Palacios in the Golfo San Jorge Basin of Chubut Province, Argentina. The Bajo Barreal Formation is interpreted as having been deposited by a low-sinuosity braided fluvial system (Rodriguez 1992; Figari et al. 1999; Uzamano et al. 2008, 2012; Casal et al. 2013) and is notable for its abundance of paleosols. Since arid climatic conditions inhibit the formation of paleosols (Retallack 1988), these data suggest the existence of a humid paleoclimate in this region during the early Late Cretaceous (see Casal et al. 2016). Plant fossils provide

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**Fig. 9.** Comparison of the reconstructed pulmonary systems of the sauropod clades Rebbachisauridae (Diplodocoidea) and Saltasaurinae (Titanosauria) in right lateral view. A. Reconstructed pulmonary anatomy of a generalized rebbachisaurid. Skeletal reconstruction based largely on *Nigersaurus taqueti* (Sereno et al. 2007: fig. 3a); pulmonary anatomy based on data presented herein, i.e., hypothesized osteological correlates of pneumaticity described in multiple rebbachisaurids, but primarily *Katepensaurus goicoecheai* (cervical and dorsal pneumaticity) and *Tataouinea hannibalis* (sacral, caudal, and pelvic pneumaticity). B. Reconstructed pulmonary anatomy of a saltasaurine (after Cerda et al. 2012: fig. 4a). Color coding of pulmonary structures is as follows: orange, lung; green, cervical air sac system; yellow, clavicular air sac system; blue, abdominal air sac system. Postcranial skeletal elements that are known to have been pneumatized are shown in gray; bones that were either apneumatic or for which this condition is uncertain are in white.
additional evidence that the Bajo Barreal Formation was deposited under a warm, humid paleoclimatic setting. Based on their study of fossil wood (pertaining to Araucariaceae, probably *Agathoxylon* sp.) from this unit, Pujana et al. (2007) proposed that the paleoclimate of central Patagonia during the early Late Cretaceous was characterized by an absence of seasonality. This inference is supported by the weakly defined boundaries of the growth rings in this wood, a feature that is associated with warm temperate to subtropical climates. Moreover, based on their studies of palynological assemblages, Archangelsky et al. (1994, 2009) and Barreda and Archangelsky (2006) also suggested the existence of a warm, humid paleoclimate in the Golfo San Jorge Basin during the Cenomanian.

Clearly, at least some rebbachisaurids habitually had to endure unusually hot temperatures. Although even the larger-bodied members of the clade were small compared to most other sauropods (e.g., the holotype of *Rebbachisaurus* is estimated at 7915–12 015 kg in body mass, Wilson and Allain 2015; that of *Tataouinea* was roughly 12 m long in life, Fanti et al. 2015), these were still very large (approx. elephant-sized) animals that had to function in what were presumably extraordinarily warm climates, and that therefore may have been susceptible to heat stress. Within this context, the extensive PSP of *Katepensaurus* and other rebbachisaurids may be plausibly, if cautiously, interpreted, at least in part, as an adaptive response to the exceptional warmth of the mid-Cretaceous. Minimizing the density of the skeleton through increased invasion of postcranial bones by air sac diverticula may have reduced the muscle power required to move the body and the heat energy produced in so doing. This may in turn have enabled these dinosaurs to better cope with exceptionally hot conditions. Bearing this in mind, it is perhaps not coincidental that several of the rebbachisaurids that exhibit the most extensive PSP yet documented within the clade—*Amazonsaurus*, *Rebbachisaurus*,
and *Tataouinea*—inhabited equatorial to near-equatorial habitats during the extreme warmth of the mid-Cretaceous.

Nevertheless, it is important to note that other sauropod taxa—that often exhibit greater overall body sizes and possibly lower “grades” of PSP—lived in the same paleoenvironments. For example, *Katepensaurus* shared its paleoecosystem with comparably-sized titanosaurs such as *Sarmientosaurus musacchii* (which was recovered from a near-equivalent horizon of the Bajo Barreal Formation at the same locality, the Estancia Laguna Palacios; see Martínez et al. 2016) and possibly *Epachthosaurus sciutoi*, which comes from the same member of the same formation but from a different locality approximately 40 km to the southwest (Martínez et al. 2004). Similarly, isolated material that indicates the presence of very large-bodied titanosaurs has been reported from the “Kem Kem beds” of Morocco (e.g., Lamanna and Hasegawa 2014; Ibrahim et al. 2016), the stratigraphic unit that yielded *Rebbachisaurus*. To conclude, although this hypothesis is weakly supported, we tentatively suggest that the extensive PSP seen in *Katepensaurus* and other rebbachisaurids may represent an adaptation for lightening the skeleton and lowering the body mass in response to the extremely warm climates of the mid-Cretaceous.

**Extensive pneumaticity in rebbachisaurids: convergence with saltasaurine titanosaurids.**—As documented above, rebbachisaurid diplodocoids such as *Katepensaurus* and *Tataouinea* exhibit manifestations of postcranial skeletal pneumaticity that are otherwise unknown within Sauropoda. Similarly, Cerda et al. (2012) and Zurriaguz and Cerda (2017) described the occurrence of elevated (“extreme”) PSP in another neosauropod clade, saltasaurine titanosaurids (i.e., *Neuquensaurus australis*, *Rocasaurus muniozi*, and *Saltasaurus loricatus*; Fig. 9B), although the patterns of pneumaticity in rebbachisaurids and saltasaurines differ significantly. For instance, pneumatic pectoral girdle elements are presently known in saltasaurines but not rebbachisaurids, whereas a pneumatized ischium is known in at least one rebbachisaurid (*Tataouinea*) but not in saltasaurines. Furthermore, like other titanosaurians, saltasaurines primarily exhibit camellate and semicamellate pneumatic bone tissue rather than the camerate tissue that predominates in rebbachisaurids and other diplodocoids.

Since, as noted above, PSP is widespread in Sauropodomorpha and other ornithodiran archosaur clades, it is clear that the common ancestor of Rebbachisauridae and Saltasaurinae would have possessed a pneumatized postcranial skeleton; in other words, that PSP is a plesiomorphic condition shared by these diplodocoid and titanosaurian groups. Nevertheless, both rebbachisaurids and saltasaurines exhibit a “grade” or degree of PSP that appears to be elevated in comparison to that of their closest relatives (Fig. 9). For example, as detailed above, the dorsal vertebrae of *Katepensaurus* possess laterodiaphyseal fossae/fenestrae and intradiaphyseal chambers, and *Tataouinea* and probably *Amazonsaurus* have pneumatic pelvic elements, characters that are otherwise unknown in Diplodocoidea. Similarly, saltasaurines are the only titanosauriforms known to possess pneumatic posterior caudal vertebral and pectoral elements. Evidently, then, the elevated degree of PSP seen in rebbachisaurids and saltasaurines (relative to other diplodocoids and titanosaurs, respectively) was convergently acquired.

Rebbachisaurids are the latest-surviving representatives of Diplodocoidea, having persisted until the mid-Cretaceous (Cenomanian–Turonian; Ibiricu et al. 2013a). Saltasaurines are also among the latest-surviving titanosaurians, with fossils having been recovered from deposits as recent as latest Cretaceous (Campanian–Maastrichtian) in age (Cerda et al. 2012; Zurriaguz and Cerda 2017), though other titanosaurian lineages persisted into the latest Cretaceous as well (e.g., Curry Rogers 2009; Lacovara et al. 2014). As such, the unusually well-developed postcranial skeletal pneumaticity of rebbachisaurids and saltasaurines—which in turn implies the presence of an extensive system of air sacs and pneumatic diverticula—may have provided some form of competitive advantage to these sauropods over many of their relatives. Elevated PSP may therefore have played an important role in the course of rebbachisaurid and saltasaurine evolution.

**Conclusions**

The type specimen of the Patagonian rebbachisaurid sauropod dinosaur *Katepensaurus goicoecheai* pertained to an individual with a minimum ontogenetic age of seven years at the time of its death. The dorsal vertebrae of *Katepensaurus* display a pneumatic configuration that has not been documented previously among sauropods, the laterodiaphyseal fenestrae and their associated intradiaphyseal chambers. This character complex constitutes an unambiguous indicator that, in this rebbachisaurid, the middle to posterior dorsal vertebral transverse processes were internally pneumatized. Within Sauropoda, this manifestation of postcranial skeletal pneumaticity is presently unique to *Katepensaurus*, and it is herein interpreted as an adaptation for minimizing the density of the skeleton.

*Katepensaurus* inhabited a warm, humid paleoenvironment at or near the Cretaceous Thermal Maximum, which was one of the hottest temporal intervals of the Phanerozoic. Interestingly, several other rebbachisaurids that also exhibit extensive PSP (e.g., *Amazonsaurus maranhensis*, *Rebbachisaurus garasbae*, *Tataouinea hannibalis*) lived at tropical to subtropical paleolatitudes during the mid-Cretaceous, and therefore would also have had to contend with extraordinarily warm conditions. We therefore tentatively propose that the decreased skeletal density afforded by the well-developed PSP of rebbachisaurids would have lowered the amount of energy required to move the bodies of these animals and the heat generated in so doing. As such, increased PSP may have enabled rebbachisaurids to better...
cope with extremely warm climatic conditions. Though PSP was undoubtedly widespread among sauropods and other ornithodirans, rebbachisaurid diplodocoids and saltasaurine titanosaurs independently evolved an elevated degree of PSP relative to other representatives of Diplodocoidea and Macronaria, respectively. Extensive PSP may therefore have contributed to the evolutionary success of rebbachisaurids and saltasaursines, both of which were among the latest-surviving representatives of their respective neosauropod clades.

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References


information on *Tatouineus hannibalis* from the Early Cretaceous of Tunisia and implications for the tempo and mode of rebbachisaurid sauropod evolution. *PloS ONE* 10: e0123475.


