Extreme postcranial pneumaticity in sauropod dinosaurs from South America

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Abstract Birds are unique among living tetrapods in possessing pneumaticity of the postcranial skeleton, with invasion of bone by the lung and air-sac system. Postcranial skeletal pneumaticity (PSP) has been reported in numerous extinct archosaurs including pterosaurs and non-avian dinosaurs. Here we report a case of extreme PSP in a group of small-bodied, armored sauropod dinosaurs from the Upper Cretaceous of South America. Based on osteological data, we report an extensive invasion of pneumatic diverticula along the vertebral column, reaching the distal portion of the tail. Also, we provide evidence of pneumaticity in both pectoral and pelvic girdles. Our study reveals that the extreme PSP in archosaurs is not restricted to pterosaurs and theropod dinosaurs.

Keywords Sauropoda · Titanosauria · Upper Cretaceous · Air-sac system · Appendicular pneumaticity

Introduction

Birds are the only extant group of vertebrates that possesses a pneumatic postcranal skeleton, which results from invasion of bone by extensions (diverticula) from the lung and air-sac system (Britt 1993; Duncker 1971). This feature has also been reported in numerous extinct archosaurs including pterosaurs and non-avian dinosaurs (Benson et al. 2011; Britt 1993; Buttler et al. 2009; Claessens et al. 2009; Janensch 1947; O’Connor 2006; Wedel 2003; Yates et al. 2012). In sauropod dinosaurs, the postcranial skeletal...
pneumaticity (PSP) has been commonly identified in the presacral axial skeleton (including dorsal ribs) and, in some groups, in the sacrum and the proximal and middle caudal vertebrae (Janensch 1947; Schwarz et al. 2007; Wedel et al. 2000; Wedel 2003, 2007, 2009). Pneumatization of the pelvic girdle has been proposed for some Neosauropoda taxa (Carvalho et al. 2003; Hocknull et al. 2009; Wedel 2009; Wilson and Upchurch 2009; Woodward and Lehman 2009; Xu et al. 2006), but based on non-conclusive evidence, and pneumaticity in the pectoral girdle has definitely never been reported in sauropodomorphs.

Several osteological correlates of PSP have been previously proposed for the determination of this feature in fossil groups (Britt 1993). However, recent studies on extant tetrapods have demonstrated that the correlation between many of these purported osteological features (i.e., blind fossae) with PSP is ambiguous (O’Connor 2006; O’Connor and Claessens 2005). The only unambiguous indicators of pneumaticity are large cortical openings (foramina) connected directly with large internal cavities (camerae or camellae) within the bone. Using this anatomical criterion, we study the PSP in a derived clade of titanosaurian sauropods from the Upper Cretaceous of South America [Saltasaurini (Salgado and Bonaparte 2007, Saltasaurinae sensu Salgado et al. 1997, Saltasaurinae sensu Powell 2003)], which actually includes Saltasaurus loricatus from Northwestern Argentina (Bonaparte and Powell 1980; Powell 2003) and Neuquensaurus australis and Rocasaurus muniozi from Northern Patagonia (Powell 2003; Salgado and Azpilicueta 2000).

Institutional abbreviations

APB: Museo de la Asociación Paleontológica de Bariloche, Río Negro Province, Argentina; MLP-CS, Museo de La Plata, Cinco Saltos Collection, La Plata, Argentina; MLP-Ly: Museo de La Plata, Lydekker’s Collection; PVL: Paleovertebrate collection of Instituto “Miguel Lillo”, Tucumán Province, San Miguel de Tucumán, Argentina. MPCA-Pv: Paleovertebrate Collection of Museo Provincial “Carlos Ameghino”, Cipolletti, Río Negro Province, Argentina; MCS-Pv, Paleovertebrate Collection of Museo Regional Cinco Saltos, Río Negro Province, Argentina.

Materials and methods

The examined material of Saltasaurus includes all the specimens referred to by Powell (2003) and identified as PVL 4017 and PVL 4740 (see Powell 2003 for a complete list of the specimens). The material was collected from the Upper Cretaceous (?upper Campanian-Maastrichtian) sediments of the Lecho Formation at the locality of El Brete (south of Salta Province, Argentina) (Bonaparte and Powell 1980; Powell 2003). The specimens of Neuquensaurus were recovered from the localities of Cinco Saltos and Lago Pellegrini (Río Negro Province, Argentina), from sediments of the Anacleto Formation (lower Campanian) (Powell 2003; Salgado et al. 2005; Otero 2010). We examined postcranial elements assigned to Neuquensaurus identified as MCS-Pv 5 (Salgado et al. 2005), MLP-Ly and MLP-CS (see Powell 2003 for a complete list of the materials housed in Museo de La Plata). The assignation of the studied specimens to Neuquensaurus has been previously discussed by several authors (McIntosh 1990; Powell 2003; Wilson and Upchurch 2003; Salgado et al. 2005; Otero 2010). The Rocasaurus material includes the holotype (MPCA-Pv 46) and all the referred material (MPCA-Pv 47-51, MPCA-Pv 56-60 and APB 2887). These specimens were collected from sediments of the Allen Formation (middle Campanian-lower Maastrichtian) of the locality of Salitral Moreno (Río Negro Province, Argentina) (Salgado and Azpilicueta 2000).

The internal structure of the examined bones was studied by observation of: fortuitous breaks in specimens (all the three taxa); mechanical sections (Saltasaurus) and non-destructive computed tomography (CT) (vertebrae of Neuquensaurus and Rocasaurus). Obtaining images by CT scanning was not possible for Saltasaurus, because of the
prevalent heavy elements in its sedimentary matrix. The CT scanning of the different bones was conducted on a Pro Speed helicoidal scanner (99783 Pro Gp serie) housed at Policlínico Neuquén (Neuquén Province, Argentina). Vertebrae laminae and fossae terminology follows Wilson (2000) and Wilson et al. (2011). Pneumatic structure nomenclature follows Britt (1993) and Wedel et al. (2000).

Results

Saltasaurini titanosaurs show evidence of PSP in both the axial and appendicular skeleton. Given that PSP in the precaudal axial skeleton of sauropod dinosaurs has been largely described previously (Britt 1993; Janensch 1947; Schwarz et al. 2007; Wedel 2003, 2007, 2009), we focused our description on the caudal vertebrae and the appendicular skeleton of Saltasaurini titanosaurs. The centra and neural arches of anterior and middle caudal vertebra of Saltasaurus and Rocasaurus have a camellate (“honeycomb”-like) internal structure consisting of a large number of small (~5–20-mm-diameter) internal chambers (camellae) that are observed on broken and abraded surfaces and in CT imagery (Fig. 1). Posterior caudal neural arches also possess an internal camellate architecture, but the posterior centra are semicamellate, with large (~20 mm diameter) camerae that divide into a numerous smaller camerae (Fig. 1a–n). Large (~5–45 mm diameter) foramina are observed on the lateral and ventral surfaces of the centrum and in different positions of the neural arch (i.e., the spinoprezygapophyseal fossa, base of the prezygapophysis) (Fig. 1b–d, i–l). As observed in Saltasaurus and Rocasaurus, the caudal neural arches of Neuquensaurus are internally composed of camellate tissue. However, the internal architecture of the caudal centra differs from the typical “honeycomb” morphology described for the other taxa. Instead, the internal cavities have a quite variable morphology and size (larger cavities reach ~45 mm diameter) (Fig. 1o, p). Also, while the pneumatized caudal vertebrae of Saltasaurus and Rocasaurus are perforated by foramina in both centra and neural arches, caudal centra of Neuquensaurus lack these openings. The cortical foramina observed in Neuquensaurus are commonly located in the spinoprezygapophyseal fossa and in the posterior end of the neural spine (between or above the postzygapophysis) (Fig. 1q–t). Another important difference between Neuquensaurus and the other Saltasaurini titanosaurs lies in the intraspecific variation with regard to the extension of the pneumaticity in the caudal series. While in all the examined specimens of Saltasaurus and Rocasaurus the internal cavities are present even in the posterior portion of the tail, some specimens of Neuquensaurus (e.g., MLP-CS 1320) lack pneumatic structures in this portion of the skeleton. The pectoral girdle is at least pneumatized in Saltasaurus and Neuquensaurus (it is not preserved in Rocasaurus) (Fig. 2). A broken scapula (PVL 4017-153) of Saltasaurus exhibits a camellate internal structure, with large (more than 20 mm diameter) and elongated cavities (Fig. 2a, b). No pneumatic foramina were recorded in this element. The two preserved coracoids of Saltasaurus (PVL 4017-100 and PVL 4017-101) also possess a camellate architecture, with well-developed internal cavities (~10–20 mm diameter). The cortical pneumatic foramina of the coracoids are small (5–10 mm), and they are located on the medial surface, near the coracoid foramen (Fig. 2c–e). Pneumaticity in the scapular girdle of Neuquensaurus is well observed in an incomplete scapulocoracoid (MLP-CS 1298). This element reveals internal cavities in both fused bones. A prominent pneumatic foramen (9 mm diameter) is observed on the medial surface of the scapula, at the level of the glenoid fossa, toward the dorsal margin (Fig. 2f–h).

Pneumaticity of the pelvic girdle is restricted to the ilium in Saltasaurini titanosaurs (Fig. 3). This element exhibits camellate tissue in the three examined taxa. Although the exact distribution of the camellate tissue in the ilia cannot be determined, the broken surfaces of the examined elements indicate that large camellae (more than 10 mm diameter) are mainly distributed in the anterior and middle portion of the iliac blade, but they do not invade the pubic peduncle (Fig. 3a–i). Pneumatic foramina are observed in a specimen of Neuquensaurus (MLP-CS 1057) and in the holotype of Rocasaurus (MPCA-Pv 46-12). In Rocasaurus, a prominent foramen of 31 mm is located on the dorsal margin of the acetabulum (Fig. 3e, f). In the Neuquensaurus specimen, a small (9-mm-diameter) cortical foramen is observed on the medial surface of the ilium, at the level of the pubis peduncle, between two successive sacral rib facets (possibly the third and the fourth) (Fig. 3h, i).

Discussion

Appendicular pneumaticity

Among sauropod dinosaurs, internal cavities (camerae and camellae) have been previously reported in the pelvic girdle (ilia) of several taxa, including Euhelopus zdanskyi (Wilson and Upchurch 2009; Wiman 1929), Lirainosaurus astibiae (Sanz et al. 1999), Amazonsaurus maranhensis (Carvalho et al. 2003), Sonidosaurus saihangaobiensis (Xu et al. 2006), Diamantinasaurus matildae (Hocknull et al. 2009) and Alamossaurus sanjuanensis (Woodward and Lehman 2009). These cavities have been interpreted by some authors as pneumatic (Carvalho et al. 2003; Hocknull et al. 2009; Wedel 2009; Wilson and Upchurch 2009; Woodward and Lehman 2009; Xu et al. 2006). However, at
present, there are no reports in sauropodomorphs of cortical foramina communicating with the internal cavities of the ilia. As has been previously stated, the only unambiguous indicators of pneumaticity are large foramina connected directly with large internal cavities (camerae or camellae) within the bone (O’Connor 2006; O’Connor and Claessens 2005). Our finding gives the first report of a cortical foramen communicated with internal cavities in the ilium and supports the previous hypothesis of the invasion of pneumatic diverticula in the pelvic girdle in some Neosauropoda taxa. We note that in several badly damaged Saltasaurini bones (e.g., Saltasaurus scapula PVL 4017-153, Neuquensaurus ilium MLP-CS 1259, Rocasaurus ilium MPCA-Pv 46-13), the camellate tissue is present but the pneumatic foramina could not be found. We infer that the pneumatic foramina were actually present but obscured by the poor preservation of the bones. The same explanation could be applied to those non-Saltasaurini sauropods for which camellate tissue has been reported in the ilium. Hence, as has been previously proposed by Wedel (2003, 2005, 2009), the invasion of pneumatic diverticulae in the ilium appears to be an extended character within derived neosauropod dinosaurs.

With regard to the pneumatic invasion in the pectoral girdle of Saltasaurus and Neuquensaurus, there are no previous reports of internal cavities in this portion of the skeleton of sauropodomorph dinosaurs. Thus, Saltasaurini titanosaurs are the only known group of sauropodomorph dinosaurs with this character. Given that the scapular girdle is not preserved in Rocasaurus, it is not possible to determine if pneumatic features in this element are present by direct observation. However, since Neuquensaurus is the sister group of the clade formed by Rocasaurus + Saltasaurus (Calvo et al. 2007a, b; González Riga et al. 2009), we hypothesize that camellate tissue and cortical foramina were actually present in the scapula and coracoides of Rocasaurus.

Caudal pneumaticity

Previous studies have documented the existence of pneumatic features in the anterior and even in the middle caudal vertebrae of some Neosauropoda taxa (Janensch 1947; Salgado et al. 2006; Wedel 2009). However, pneumaticity in the distal portion of the tail as described here for Saltasaurini titanosaurs has not been previously reported in sauropodomorph dinosaurs. Our data reveal an unexpected caudal extension of the pneumatic diverticula from the respiratory system, only comparable to some lineages of non-avian theropods (Benson et al. 2011).

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**Fig. 2** Pneumatic features in the pectoral girdle of *S. loricatus* (a-e) and *N. australis* (f-h). a Incomplete left scapula (PVL 4017-153) in medial view. b Broken surface of the same specimen (dashed lines in a) showing the camellate internal bone. c, Left coracoid (PVL 4017-101) in medial view. d Broken surface of the same specimen revealing the distribution of the camellate tissue. e Close-up of the pneumatic foramina in PVL 4017-101 (box inset in e). Note the presence of internal camellae communicated with the larger foramina. f Fragment of scapulocoracoid (MLP-CS 1298) in medial view. g Detail of the pneumatic foramina in the medial surface. h MLP-CS 1298 in anterior view. Note the presence of pneumatic cavities in the broken surface. cf Coracoid foramen, gs glenoid surface, pc pneumatic cavities.
Body size and postcranial pneumaticity

Since the development of PSP is thought to have been very important in the achievement of giant size in sauropodomorph dinosaurs (Sander et al. 2011), the extreme pneumaticity in Saltasaurini is rather unexpected. Saltasaurini titanosaurs represent one of the few cases of phylogenetic decrease in body size among dinosaurs (Wilson 2005). This group has been considered as the “smallest of the giants,” with body lengths that probably did not exceed 7 m. Our data reveal that one of the smallest sauropod clades actually has the most developed PSP. In this sense, although body size seems to be important in the development of PSP in sauropod dinosaurs (Britt 1993; Wedel 2003), this is not the only factor governing the evolution of pneumaticity. A detailed analysis on a larger data set, including species-level information, is necessary to elucidate which are the main factors involved in the development of PSP in sauropod dinosaurs.

Structure of respiratory system

The identification of postcranial pneumaticity in fossil groups indicates the presence of an avian-like, heterogeneously partitioned pulmonary system, composed of both exchange (lung) and non-exchange (air sac) regions (O’Connor 2006; O’Connor and Claessens 2005). In extant birds, the air sac system includes the cervical, clavicular (= interclavicular), anterior thoracic, posterior thoracic and abdominal air sacs (Duncker 1971; Perry et al. 2011). Recent work has demonstrated that strict correlations exist between specific air sacs and the axial elements that they pneumatize in living birds (O’Connor 2006; O’Connor and Claessens 2005; contra Sereno et al. 2008).
When the postcranial skeleton is pneumatized, the cervical vertebrae/ribs and the anterior dorsal vertebrae are pneumatized by diverticula of the cervical air sacs; in turn, diverticula of the abdominal air sacs pneumatize pelvic girdle and hind limb elements and the posterior dorsal, sacral and caudal vertebrae; finally, diverticula from the clavicular air sac pneumatize pectoral girdle and forelimb elements, whereas dorsal vertebrae and ribs are pneumatized directly by the lung. Anterior thoracic air sac diverticula often pneumatize the sternum and sternal ribs, and posterior thoracic air sacs never pneumatize the skeleton. Previous studies used this conservative pattern of PSP in living birds to infer the presence of specific air sacs in extinct archosaurs, including pterosaur, sauropodomorph and non-avian theropods (Claessens et al. 2009; O’Connor 2006; O’Connor and Claessens 2005; Wedel 2009; Yates et al. 2012). Following this reasoning, the pneumatic features observed in the postcranial skeleton of Saltasaurini implies the presence of cervical, abdominal and clavicular air sacs in this clade (Fig. 4). Although previous studies of PSP have proposed that cervical and abdominal air sacs were actually present in sauropodomorph dinosaurs (Wedel et al. 2000; Wedel 2007, 2009; Yates et al. 2012), anatomical evidence for clavicular air sacs has never been reported in this group.

Although the presence of PSP is indicative of air sacs and diverticula, the lack of pneumaticity does not indicate the absence of such pulmonary specializations (O’Connor 2006; Wedel 2003, 2007, 2009). Hence, it is very plausible that the clavicular air sac was actually present in a more inclusive clade of sauropodomorph dinosaurs, but its osteological correlates were only present in Saltasaurini titanosaurs. A similar hypothesis has been proposed for the cervical and abdominal air sacs in basal sauropodomorph dinosaurs, for which unambiguous correlates of PSP are absent or poorly documented (Butler et al. 2012; Wedel 2007, 2009; Yates et al. 2012).

Since PSP has been recorded in different lineages of ornithodiran archosaurs (pterosaurs, sauropodomorph and
non-avian theropod dinosaurs), several authors have proposed that the presence of a heterogeneously partitioned pulmonary system is primitive for ornithodiran archosaurs (Benson et al. 2011; Britt 1993; Butler et al. 2012; Wedel 2003, 2007; Yates et al. 2012). The extreme PSP reported here for Saltasaaurini titanosaurs, with evidence of cervical, abdominal and clavicular air sacs, reinforces this idea. The independent acquisition of appendicular pneumaticity in pterosaurs (Claessens et al. 2009) and dinosaurs (theropods and derived sauropodomorphs) (Benson et al. 2011; Wedel 2009) emphasizes the tendency for ornithodirans to extensively pneumatize the postcranial skeleton (Benson et al. 2011; Butler et al. 2012).

Conclusions

Osteological features of the axial and appendicular skeleton in Saltasaaurini titanosaurs reveal extreme pneumaticity that is unparalleled in other sauropodomorph dinosaurs, with invasion of pneumatic diverticula in the pectoral girdle and the distal portion of the tail. Our result indicates that, besides pterosaurs and theropod dinosaurs, extensive pneumaticity was also reached independently in Sauropodomorpha. Our data also strengthen the hypothesis for the presence of posterior abdominal air sacs in sauropod dinosaurs and provide the first evidence for a clavicular air sac in this lineage. Finally, the record of extreme PSP in Saltasaaurini titanosaurs contributes to the growing evidence of widespread, repeated evolution of appendicular and posterior axial skeletal pneumaticity in ornithodiran archosaurs, which in turn indicates that a heterogeneously partitioned pulmonary system is primitive for this group.

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References

Benson, R.B.J., R.J. Butler, M.T. Carrano, and P.M. O’Connor. 2011. Air-filled postcranial bones in theropod dinosaurs: Physiological implications and the ‘reptile’–’bird’ transition. Biological Reviews of the Cambridge Philosophical Society. doi:10.1111/j.1469-185X.2011.0190.x.

Bonaparte, J.F. and Powell, J.E. 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda-Coelurosauria-Carnosauria-Aves). Mémories de la Socie´eté Géologique de France 139:19–28.

Butler, R.J. 1993. Pneumatic postcranial bones in dinosaurs and other archosaurs. Dissertation, University of Calgary.

Butler, R.J., P.M. Barrett, and D.J. Gower. 2009. Postcranial skeletal pneumaticity and air-sacs in the earliest pterosaurs. Biology Letters 5: 557–560. doi:10.1098/rsbl.2009.0139.

Butler, R.J., P.M. Barrett, and D.J. Gower. 2012. Reassessment of the evidence for postcranial skeletal pneumaticity in Triassic archosaurs, and the early evolution of the avian respiratory system. PLoS One 7(3): e34094. doi:10.1371/journal.pone.0034094.

Calvo, J.O., B.J. González Riga, and J.D. Porfíri. 2007a. A new titanosaur sauropod from the Late Cretaceous of Neuquén, Patagonia, Argentina. Arquivos do Museu Nacional 65: 485–504.

Calvo, J.O., J.D. Porfíri, B.J. González Riga, and A.W.A. Kellner. 2007b. A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. Anais da Academia Brasileira de Ciencias 79: 529–541.

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

Claessens, L.P.A., P.M. O’Connor, and D.M. Unwin. 2009. Respiratory evolution facilitated the origin of pterosaur flight and aerial gigantism. PLoS One 4: e4497. doi:10.1371/journal.pone.0004497.

Duncker, H.-R. 1971. The lung air-sac system of birds. Advances in Embryology and Cell Biology 45: 1–171.

Gonzáles Riga, B.J., E. Previtera, and C.A. Pirrone. 2009. Malar- guesaurus florenciae gen. et sp. nov., a new titanosauriform (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza, Argentina. Cretaceous Research 30: 135–148.

Hocknull, S.A., M.A. White, T.R. Tischler, A.G. Cook, N.D. Calleja, T. Sloan, and E.A. Elliott. 2009. New Mid-Cretaceous (Late Albian) Dinosaurs from Winton, Queensland, Australia. PLoS One 4(7): e6190. doi:10.1371/journal.pone.0006190.

Jansens, W. 1947. Pneumatization bei Wirbeln von Sauropoden und anderen saursichien. Palaeontographica 53: 1–25.

Mcintosh, J.S. 1990. Sauropoda. In The Dinosauria 1st edn, eds. D.B. Weishampel, P. Dodson & H. Osmolska, 345–401. Bloomington and Indianapolis: Indiana University Press.

O’Connor, P.M. 2006. Postcranial pneumaticity: An evaluation of soft-tissue influences on the postcranial skeleton and the reconstruction of pulmonary anatomy in archosaurs. Journal of Morphology 267: 1199–1226. doi:10.1002/jmor.10470.

O’Connor, P.M., and L.P.A. Claessens. 2005. Basic avian pulmonary design and flow-through ventilation in nonavian theropod dinosaurs. Nature 436: 253–256. doi:10.1038/nature03716.

Otero, A. 2010. The appendicular skeleton of Nequensaurus, a Late Cretaceous saltasaurine sauropod from Patagonia, Argentina. Acta Palaeontologica Polonica 55: 399–426.

Perry, S.F., T. Breuer, and N. Pajor. 2011. Structure and function of the sauropod respiratory system. In Biology of the sauropod dinosaurs: Understanding the life of giants, ed. N. Klein, K. Remes, C.T. Gee, and P.M. Sander, 83–93. Bloomington and Indianapolis: Indiana University Press.

Powell, J.E. 2003. Revision of South American Titanosaurid dinosaurs: Palaeobiological, palaeobiogeographical and phylogenetic aspects. Records of the Queen Victoria Museum 111: 1–173.

Salgado, L., S. Aposteguia, and S.E. Heredia. 2005. A new specimen of Nequensaurus australis, a Late Cretaceous saltasaurine titanosaur from North Patagonia. Journal of Vertebrate Paleontology 25: 623–634.
Salgado, L., and C. Azpílizcueta. 2000. Un nuevo saltasaurino (Sauropoda, Titanosauridae) de la Provincia de Río Negro (Formación Allen, Cretácico Superior), Patagonia, Argentina. *Ameghiniana* 37: 259–264.

Salgado, L., R.A. García, and J.D. Daza. 2006. Consideraciones sobre las láminas neurales de los dinosaurios saurópodos y su significado morfofuncional. *Revista del Museo Argentino de Ciencias Naturales* 8: 69–79.

Salgado, L., and J.F. Bonaparte. 2007. Sauropodomorpha. In *Patagonian Mesozoic reptiles*, ed. Z. Gasparini, L. Salgado, and R.A. Coria, 188–228. Indiana: Indiana University Press.

Salgado, L., R.A. Coria, and J.O. Calvo. 1997. Evolution of titanosaurid sauropods. I: Phylogenetic analysis based on the postcranial evidence. *Ameghiniana* 34: 3–32.

Sander, P.M., A. Christian, M. Clauss, R. Fechner, C.T. Gee, E.M. Griebeler, H.C. Gunga, J. Hummel, H. Mallison, S.F. Perry, H. Preuschoft, O.W.M. Rauhut, K. Remes, T. Tütken, O. Wings, and U. Witzel. 2011. Biology of the sauropod dinosaurs: The evolution of gigantism. *Biological Reviews of the Cambridge Philosophical Society* 86: 117–155. doi: 10.1111/j.1469-185X.2010.00137.x.

Sanz, J.L., J.E. Powell, J. Le Loeuff, R. Martínez, and X. Pereda Suberbiola. 1999. Sauropod remains from the Upper Cretaceous of Lango (northcentral Spain). Titanosaur phylogenetic relationships. *Estudios del Museo de Ciencias Naturales de Lava* 14: 235–255.

Sereno, P.C., R.N. Martínez, J.A. Wilson, D.J. Varrichio, O.A. Alcober, and H.C.E. Larsson. 2008. Evidence for avian intrathoracic air sacs in a new predatory dinosaur from Argentina. *PLoS One* 3: e3303. doi: 10.1371/journal.pone.0003303.

Schwarz, D., E.D. Frey, and C. Meyer. 2007. Pneumatics and soft-tissue reconstructions in the neck of diplodocid and dicraeosaurid sauropods. *Acta Palaeontologica Polonica* 52: 167–1188.

Wedel, M.J. 2007. What pneumaticity tells us about ‘prosauropods’, and vice versa. *Special Papers in Palaeontology* 77: 207–222.

Wedel, M.J. 2009. Evidence for bird-like air-sacs in saurischian dinosaurs. *Journal of Experimental Zoology A* 311: 611–628. doi:10.1002/jez.513.