

The origin of an invasive air sac system in sauropodomorph dinosaurs

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Abstract

One of the most remarkable features in sauropod dinosaurs relates to their pneumatized skeletons permeated by a bird-like air sac system. Many studies described the late evolution and diversification of this trait in mid to late Mesozoic forms but few focused on the origin of the invasive respiratory diverticula in sauropodomorphs. Fortunately, it is possible to solve this thanks to the boom of new species described in the last decade as well as the broad accessibility of new technologies. Here we analyze the unaysaurid sauropodomorph *Macrocollum itaquii* from the Late Triassic (early Norian) of southern Brazil using micro-computed tomography. We describe the chronologically oldest and phylogenetically earliest unambiguous evidence of an invasive air sac system in a dinosaur. Surprisingly, this species presented a unique pattern of pneumatization in non-sauropod sauropodomorphs, with pneumatic foramina in posterior cervical and anterior dorsal vertebrae. This suggests that patterns of pneumatization were not cladistically consistent prior to the arrival of Jurassic eusauropods. Additionally, we describe the protocamerae tissue, a new type of pneumatic tissue with properties of both camellae and camerae. This reverts the previous hypothesis which stated that the skeletal pneumatization first evolved into camerae, and derived into delicate trabecular arrangements. This tissue is evidence of thin camellate-like tissue developing into larger chambers. Finally, *Macrocollum* is an example

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of the gradual evolution of skeletal tissues responding to the fastly specializing Respiratory System of saurischian dinosaurs.

KEYWORDS

bone histology, ornithodira, respiratory system, South America, Triassic

1 | INTRODUCTION

Sauropods were an emblematic clade of long-necked dinosaurs that colonized all continents during the Jurassic and Cretaceous (Curry Rogers and Forster 2001; Cerda, Paulina Carabajal, et al., 2012; Ghilardi et al., 2016; Wiersma-Weyand et al., 2021; Rigby et al., 2021; Díez Díaz, 2022; Mo et al., 2023). Some lineages attained giant sizes, evolving into the largest animals to ever inhabit terrestrial landscapes (Carballido et al., 2017; González Riga et al., 2016; Lacovara et al., 2014; Otero et al., 2021). One of the features that allowed the body enlargement was a structural decrease of density caused by the presence of a bird-like air sac system (Perry et al., 2009; Sander et al., 2011). The identification of Postcranial Skeletal Pneumaticity (PSP) is the current method to identify the diverticular respiratory system in fossil taxa (Britt, 1994). The evaluation of unambiguous PSP requires the identification of deep vertebral fossae containing foramina connecting with internal pneumatic structures such as camerae and camellae (O'Connor, 2006). Unambiguous PSP has been extensively reported in neosauropods, especially titanosauriforms (Wedel et al., 2000; Wedel, 2003; Schwarz & Fritsch, 2006; Woodward and Lehman 2009; Cerda, Salgado, & Powell, 2012; Zurriaguz & Powell, 2015; Bandeira et al., 2016). In contrast, few studies have focused on the origins of these diverticula within early sauropodomorphs, and much of the knowledge on non-sauropod sauropodomorphs is based on scarce evidence (Butler et al., 2012; Wedel, 2007, 2009; Yates et al., 2012). Recent evidence showing the absence of PSP in the earliest dinosaurs (Aureliano et al., 2022) suggested this trait was not homologous in ornithodirans and that invasive air sacs evolved at least three times independently, in theropods, sauropodomorphs, and pterosaurs. This discovery encouraged additional research into how and when these structures emerged during the Late Triassic. Here we evaluate the unaysaurid sauropodomorph *Macrocollum itaquii* (Müller, Langer, & Dias-da-Silva, 2018), the oldest and largest long-necked sauropodomorph of the lower Norian Candelária Sequence in South Brazil (Müller, Langer, & Dias-da-Silva, 2018). The micro-computed tomography of the skeleton of *Macrocollum* brings novel insights

into the gradual evolution of the Respiratory System in dinosaurs.

2 | MATERIALS AND METHODS

Institutional abbreviations: CAPP/UFMS, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia, Universidade Federal de Santa Maria, São João do Polêsine, Rio Grande do Sul, Brazil; PVL, Paleovertebrate collection, Instituto “Miguel Lillo,” San Miguel de Tucumán, Salta, Argentina; NHM, Natural History Museum, London, United Kingdom; ULBRA, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia, Universidade Federal de Santa Maria, São João do Polêsine, Rio Grande do Sul, Brazil (previously Museu de Ciências Naturais, Universidade Luterana do Brasil, Canoas, Brazil).

2.1 | Specimen

The studied specimen corresponds to a paratype of *Macrocollum itaquii* (CAPP/UFMS 0001b), an almost complete articulated skeleton of an unaysaurid sauropodomorph (Müller, Langer, & Dias-da-Silva, 2018). This specimen was found associated with two other skeletons (holotype and paratype) resulting in the oldest evidence of gregarious behavior in dinosaurs. There are yet no histological thin sections to address the skeletochronology of this specimen, but the scapula and the coracoid are partially unfused. Some vertebrae present fused neurocentral sutures to a varied degree along the column, some neural arches remain not entirely merged, which suggests a subadult ontogenetic stage (Brochu, 1996; Müller et al., 2015).

2.2 | Locality and horizon

Macrocollum specimens were excavated at the Wachholz Site (29°36'46.42"S; 53°15'54.06"W), Agudo municipality, Rio Grande do Sul state, South Brazil (Müller et al., 2015). This site is part of the Upper Triassic (lower Norian) Candelária Sequence, Paraná Basin. Chronocorrelated strata were dated at 225.42 ± 0.37 Ma (Langer et al., 2018).

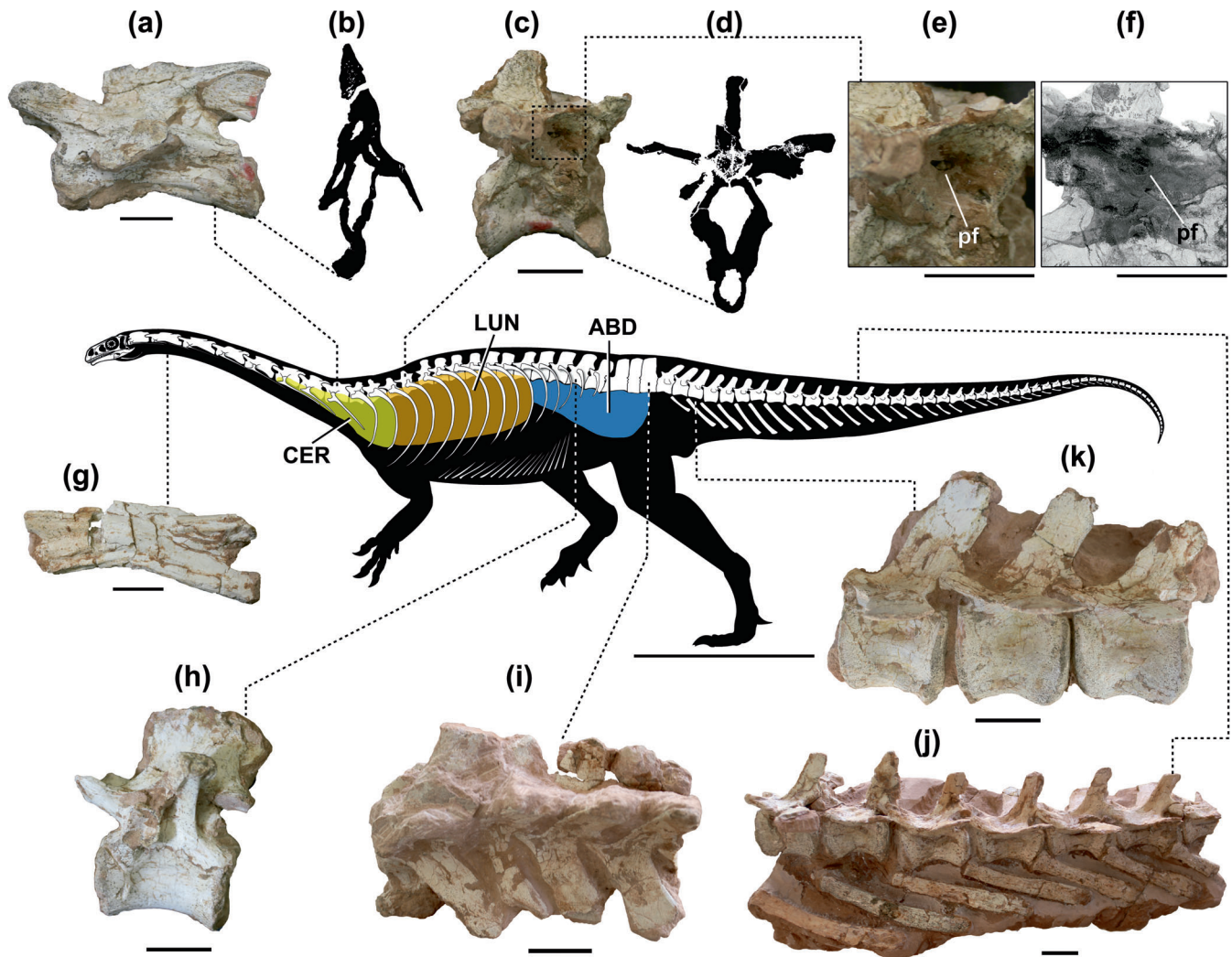


FIGURE 1 Skeletal reconstruction of the unaysaurid sauropodomorph *Macrocollum* (CAPPA/UFSM 0001b) showing vertebral elements along the spine and putative reconstruction of the air sac systems involved. (a) Pneumatic posterior cervical vertebra and a cross-section CT slice in b. (c) a pneumatized anterior dorsal vertebra with cross-section CT slice in d, and detail of the pneumatic foramen in e. (f) Detail of the pneumatic foramen in a reconstructed 3D model of the element. (g) Anterior cervical element (apneumatic). (h) Posterior dorsal vertebra shows no traces of PSP. The sacral series (i), as well as the anterior (k) and mid-caudal (j) series are apneumatic. a, g, h, j, and k are in left lateral view. c, e and f are in right lateral view. i is in dorsal view. ABD, abdominal diverticula; CER, cervical diverticula; LUN, lung; pf, pneumatic foramen. The reconstruction was made by Rodrigo T. Müller. Scale bar of the skeletal reconstruction = 500 mm; a–j = 20 mm.

2.3 | Taphonomic remarks

The CAPPA/UFSM 0001 series of specimens were moderately affected by taphonomic compression, showing both subtle diagenetic distortions and cracks (Müller, Garcia, et al., 2018). However, the external overall morphology is well preserved, except for smaller foramina, which will be further explained in the results section.

2.4 | Anatomical nomenclature and terminology

We apply Wilson's terms to describe vertebral laminae, fossae, and their landmarks (Wilson, 1999, 2012; Wilson

et al., 2011), Wedel's for vertebral pneumaticity (Wedel, 2003, 2007; Wedel et al., 2000), and O'Connor's method to evaluate unambiguous PSP (O'Connor, 2006).

2.5 | Microtomography (μ CT scan)

A posterior (eighth) cervical vertebra and an anterior (second) dorsal vertebra of *Macrocollum* were scanned in a Bruker-Skyscan 1,173 microtomographer (130 kV μ -focus X-ray source; voxel size = 0.15 mm). This μ CT scanner is located at the *Instituto do Petróleo e dos Recursos Naturais*, Universidade Católica do Rio Grande do Sul/PUCRS), Porto Alegre, Brazil. We used the open-source software *3D-Slicer* v5.2 (Fedorov et al., 2012) and

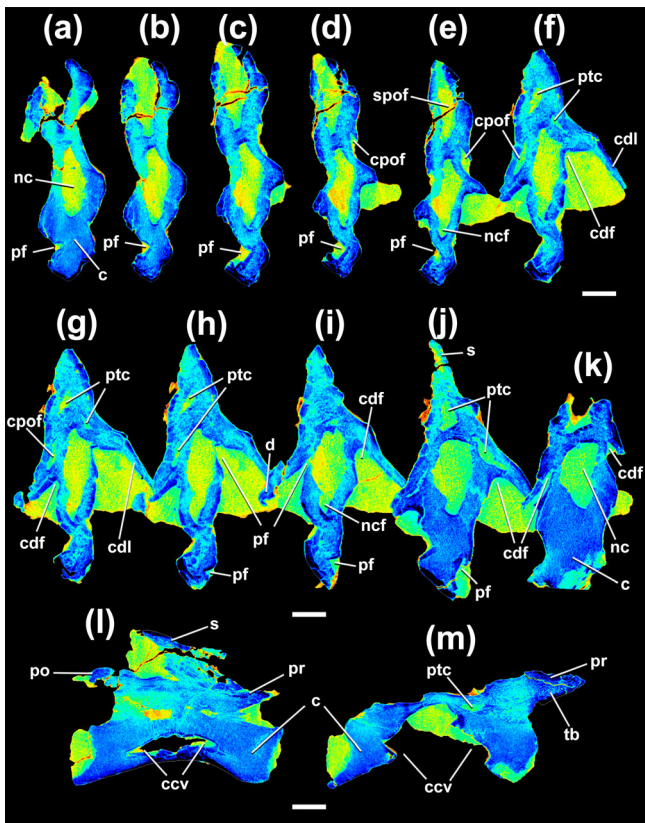


FIGURE 2 Micro-CT scan of the posterior (eighth) cervical vertebra of the unaysaurid sauropodomorph *Macrocollum* (CAPPA/UFSM 0001b) in cross-section (a–k) and lateral views (l, m). (a–k) presents a cross-section series from posterior to anterior-most positions, respectively. (l) and (m) show a narrow longitudinally-elongated chamber in the centrum and a decrease in trabecular density in the prezygapophysis and the neural spine. c, centrum; ccv, a chamber in the centrum; cdf, centrodiaepophyseal fossa; cdl, centrodiaepophyseal lamina; cpofo, centropostzygapophyseal fossa; d, diapophysis; nc, neural canal; ncf, neural canal foramen; pf, pneumatic foramen; po, postzygapophysis; pocdf, postzygacentrodiaepophyseal fossa; pr, prezygapophysis; prcdf, prezygacentrodiaepophyseal fossa; ptc, protocamera; s, neural spine/spof, spinopostzygapophyseal fossa. Scale bar = 10 mm.

CloudCompare v2.12.4 (CloudCompare, 2018) to process the data, to generate 3D reconstructions, and to apply density-based color grades based on bone tissues (Aureliano et al., 2020). *ImageJ* v1.52 (Schneider et al., 2012) was used for digital measurements. All microtomography data were uploaded to the Morphobank platform and is available through this link: <http://morphobank.org/permalink/?P4526>.

3 | RESULTS

We analyzed the vertebrae of the sauropodomorph *Macrocollum itaquii* employing both macroscopic inspection and computed tomography (Figure 1). The vertebral

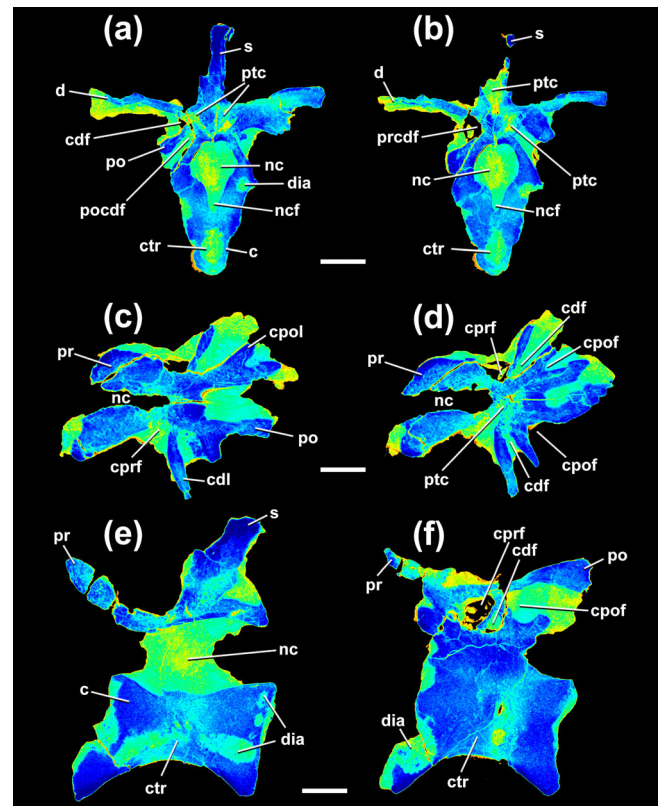


FIGURE 3 Micro-CT scan of the anterior (second) dorsal vertebra of the unaysaurid sauropodomorph *Macrocollum* (CAPPA/UFSM 0001b). (a) and (b) show cross-sections of the entire vertebra in anterior view at the approximate midpoint. (c) and (d) show midshaft slices in lateral view. (e) and (f) show narrow longitudinal slices in lateral view. (f) shows three fossae in the neural arch (cprf, cdf and cpofo). c, centrum; cdf, centrodiaepophyseal fossa; cdl, centrodiaepophyseal lamina; ctr, chaotic trabeculae; cpofo, centropostzygapophyseal fossa; cprf, centroprezygapophyseal fossa; d, diapophysis; dia, diagenetic artifact; nc, neural canal; ncf, neural canal foramen; pf, pneumatic foramen; po, postzygapophysis; pocdf, postzygacentrodiaepophyseal fossa; pr, prezygapophysis; prcdf, prezygacentrodiaepophyseal fossa; ptc, protocamera; s, neural spine. Scale bar = 10 mm.

tissue showed moderate evidence of diagenetic effects, mainly in the form of cracking and mineral infills, which altered the bone morphology slightly. This condition made it difficult to detect smaller nutritional foramina but, fortunately, did not affect the preservation of the larger pneumatic ones. It was thus possible to detect evidence of unambiguous PSP, which varies along the axial skeleton. Only presacral vertebrae demonstrated the presence of pneumatic foramina. The μ CT scan of the posterior cervical element (Figure 2) revealed that the centrum comprises mostly dense trabecular bone except for a narrow longitudinally-elongated chamber connecting with two lateral pneumatic foramina. There is also a decrease in trabecular density in the neural arch. Several fossae (spof, cpofo and cdf) connect with internal pneumatic

TABLE 1 Evaluation of postcranial skeletal pneumaticity in sauropodomorphs and the herrerasaurid *Gnathovorax*. Question marks indicate unknown information and/or elements.

Taxon/specimen	Age	Anterior cervical	Posterior cervical	Anterior dorsal	Posterior dorsal	Sacral	Anterior caudal	Reference
<i>Gnathovorax</i> (CAPPA/UFSM 0009)	Carnian	No	No	No	No	No	No	(Aureliano et al., 2022)
<i>Buriolestes</i> (CAPPA/UFSM 0035)	Carnian	No	No	No	No	No	No	(Aureliano et al., 2022)
<i>Pampadromaeus</i> (ULBRAPV016)	Carnian	?	?	No	?	?	?	(Aureliano et al., 2022)
<i>Macrocollum</i> (CAPPA/UFSM 0001b)	early Norian	No	Yes	Yes	No	No	No	This work
<i>Plateosaurus</i> (AMNH 6810)	late Norian - Rhaetian	No	Yes	No	No	No	No	Yates et al. (2012)
<i>Eucnemesaurus</i> (BP/1/6107)	late Norian - Rhaetian	?	?	?	Yes	?	?	Yates et al. (2012)
<i>Aardonyx</i> (BP/1/6566)	Hettangian	No	No	No	Yes	Yes	No	Yates et al. (2012)
<i>Antenonitrus</i> (BP/1/4952)	Sinemurian - Pliensbachian	?	?	No	Yes	?	No	Yates et al. (2012)
<i>Haplocanthosaurus</i> (CM879)	Kimmeridgian	Yes	Yes	Yes	Yes	Yes	Yes	Wedel (2009)
<i>Saltasaurus</i> (PVL 4017–214, 47, 192)	Maastrichtian	Yes	Yes	Yes	Yes	Yes	Yes	(Cerda, Salgado, & Powell, 2012); Zurriaguz and Powell (2015)

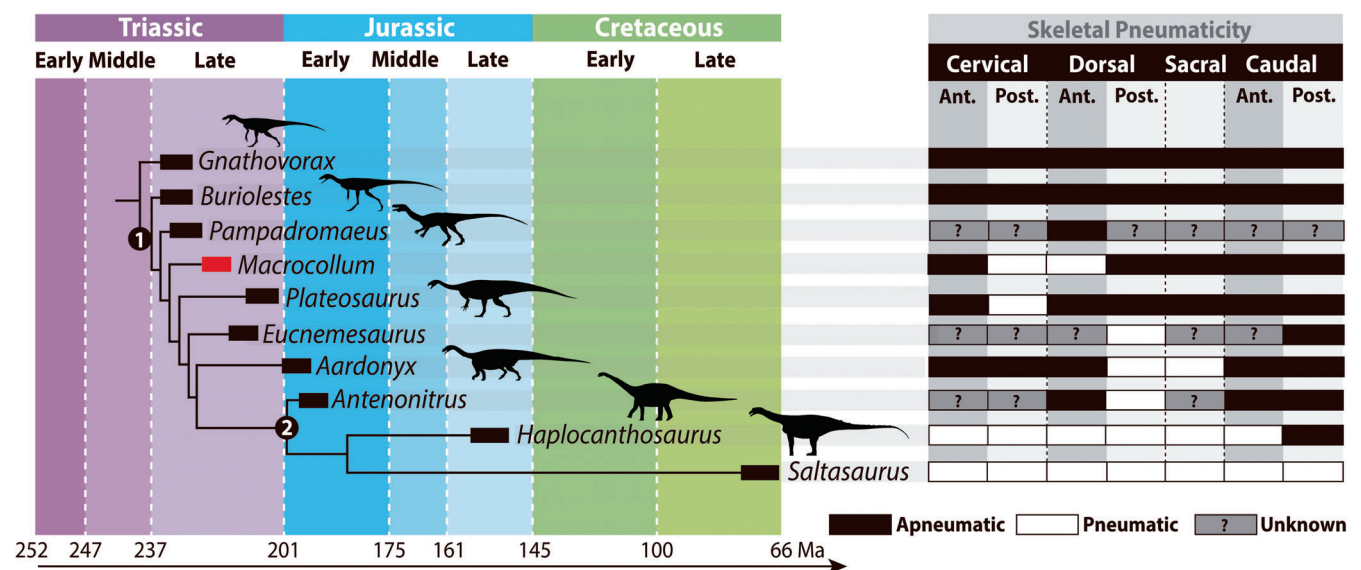


FIGURE 4 Chronological and phylogenetic evolution of postcranial skeletal pneumaticity in sauropodomorph dinosaurs, and the herrerasaurid *Gnathovorax* as an outgroup. 1, Sauropodomorpha. 2, Sauropoda. Based on the topology by Yates et al. (2012) and Müller, Langer, and Dias-da-Silva (2018). Silhouettes are from [Phylopic.org](https://www.phylopic.org) by Bruno Navarro, Mathew Wedel, Ryan Soledade, and Scott Hartman.

chambers. These chambers are neither camerate nor camellate, but a new type of tissue with an intermediate texture. We propose the term “protocamerate chambers” (ptc) for these structures which are not large enough to be considered camerae, but also present a camellate array internally. The μ CT scan of the anterior dorsal vertebra (Figure 3), on the other hand, shows only chaotic apneumatic trabeculae in the centrum with no lateral pneumatic foramina. Only the neural arch is pneumatized, encompassing well-defined laminae connecting with the internal protocamerate tissue (ptc) throughout the fossae (cdf, pocdf, and prcdf). The protocamerate tissue also expands ventrodorsally to the interior base of the spinal arch.

4 | DISCUSSION

An evaluation of the herrerasaurid *Gnathovorax* and the early sauropodomorphs *Buriolestes* and *Pampadromaeus* found evidence suggesting the absence of PSP in early saurischians during the Carnian (Aureliano et al., 2022). We analyzed the unaysaurid *Macrocollum* from the early Norian of South Brazil. The presence of well-developed fossae connected with internal chambers throughout foramina is the definitive evidence of unambiguous PSP (O'Connor, 2006). Consequently, this find represents the oldest evidence of an invasive air sac system in Sauropodomorpha.

Previously, Yates et al. (2012) analyzed the patterns of pneumatization in Rhaetian and Early Jurassic sauropodomorphs, finding PSP to be restricted to the posterior dorsal elements, as in *Eucnemesaurus*, *Aardonyx*, and *Antenonitrus* (Yates et al., 2012). This evidence led the authors to suggest that the pneumatization process in early forms was influenced directly and solely by the abdominal air sac system, a term defined in previous studies on extant birds (McLelland, 1989). According to their hypothesis, only in eusauropods would the cervical air sac system develop with phyletic consistency, and not sporadically as in non-gravisaurian taxa. The presence of pneumatic foramina invading the centrum in a posterior cervical vertebra and not in an anterior dorsal element in *Macrocollum* is intriguing and so far unique in early sauropodomorphs (see Table 1). The neural arches of *Macrocollum* also showed many connections between the interior pneumatic architecture and the outer fossae (cdf, cprf, cporf; see Figures 2 and 3). Some *Plateosaurus* specimens were also interpreted as showing limited and restricted cervical pneumatization (e.g., AMNH 6810) and were thus considered exceptions in the evolution of the group (Yates et al., 2012). *Pantydraco* could potentially be another exception (Yates et al., 2012) but the absence of almost the entire sacral and dorsal series precludes unequivocal determination of PSP features in this taxon for the time being.

The presence of both cervical and anterior dorsal pneumatization in *Macrocollum* is unique within non-gravisaurians, and could suggest the influence of both cervical and lung air sac systems invading the vertebral series. However, the absence of pneumatic foramina in the dorsal centra might be indicative that lung and abdominal diverticula were not invading the skeleton. The absence of evidence of PSP in posterior dorsal elements in chronologically and phylogenetically earlier forms prior to *Eucnemesaurus* contrasts with the pattern of pneumatization observed in later forms, specially anchisaurians (see Table 1 and Figure 4). The evidence of unambiguous PSP in *Macrocollum*, *Pantydraco*, and *Plateosaurus*, when compared with the apneumatic skeleton of *Buriolestes*, *Pampadromaeus*, *Thecodontosaurus*, *Efraasia*, and *Massospondylus*, demonstrates that the initial evolution of diverticular ventilation systems did not follow a pronounced pattern (at least at our current phylogenetic resolution).

Macrocollum also presented a new type of pneumatic tissue, showing properties of both camerae and camellae as defined by Wedel et al. (2000). We named this tissue “protocamerae” (see ptc in Figures 2 and 3). This evidence supports a previous hypothesis from Aureliano et al. (2022) in which the pneumatic tissues would not have evolved as camerae in the Jurassic and then camellae in the Cretaceous but actually derived from delicate camellate-like trabeculae. The structural change from the apneumatic pseudo-polycamerate tissue in *Pampadromaeus* during the Carnian (Aureliano et al., 2022) to the protocamerae in *Macrocollum* demonstrates the possible developmental trajectory of PSP during the earliest evolution of sauropodomorph dinosaurs. Additionally, Yates et al. (2012) observed that the pneumatization throughout the infradiapophyseal fossae appears later in neosauropods due to the presence of camellate tissue, which would increase the volume and the rigidity of the neural arch, allowing the invasion of the diverticula. The invasion of air sacs throughout the cdf, cprf and cporf in *Macrocollum* could have been facilitated by the presence of this protocamerate tissue, with a similar structural consequence.

5 | CONCLUSIONS

The evidence of unambiguous postcranial pneumaticity in the unaysaurid *Macrocollum itaquii* from the early Norian of Southern Brazil resulted in several insights into the evolution of the air sac systems. Some of the highlights are listed below:

- The chronologically oldest and phylogenetically earliest evidence described to date of an invasive air sac system in a dinosaur.

- The pattern of pneumatization seen in the posterior cervical and anterior dorsal vertebrae of *Macrocollum* is unique in non-sauropod sauropodomorphs. Our data support previous hypotheses that this clade did not develop a consistent and extensive pattern of PSP until the evolution of eusauropods in the Jurassic.
- We described a new type of pneumatic tissue, the protocameræ, showing properties of both camellate and cameræ tissues found later in the Mesozoic. This changes the previous hypothesis which stated that the pneumatization of the skeleton first evolved into cameræ, and only later derived into delicate trabecular camellæ. The protocameræ tissue is evidence of delicate thin tissue forming larger chambers.

Macrocollum is an example of gradual evolution of both morphology and histology, with the skeletal tissues adapting to the invasion of the air sac diverticula. We suggest that the great number of new taxa and specimens of Late Triassic sauropodomorphs described in the recent decade should be also sampled since they have the potential to provide a high-resolution understanding of the evolution of the Respiratory System in dinosaurs. Finally, the usage of microtomography coupled with histological thin sections should be encouraged in future approaches to achieve this goal.

AUTHOR CONTRIBUTIONS

Tito Aureliano: Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; software; formal analysis; project administration; data curation. **Aline M. Ghilardi:** Conceptualization; investigation; methodology; validation; software; formal analysis; data curation; supervision. **Rodrigo T. Müller:** Writing – original draft; writing – review and editing; data curation; supervision; resources; validation. **Leonardo Kerber:** Investigation; validation; writing – review and editing; project administration; supervision; data curation; resources. **Marcelo A. Fernandes:** Supervision; data curation; resources; writing – review and editing; validation; project administration. **Fresia Ricardi-Branco:** Funding acquisition; writing – original draft; writing – review and editing; validation; formal analysis; project administration; supervision; data curation; resources. **Mathew J. Wedel:** Conceptualization; investigation; funding acquisition; writing – original draft; writing – review and editing; validation; methodology; formal analysis; supervision; data curation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

All fossils are housed in a public research institution and can be accessed upon request and addressed to the collection's curator. Microtomography data and specimen photographs are available in a Morphobank project linked to this article.

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