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Sacral co-ossification in dinosaurs: The oldest record of fused sacral vertebrae in Dinosauria and the diversity of sacral co-ossification patterns in the group

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Abstract

The fusion of the sacrum occurs in the major dinosaur lineages, i.e. ornithischians, theropods, and sauropodomorphs, but it is unclear if this trait is a common ancestral condition, or if it evolved independently in each lineage, or even how or if it is related to ontogeny. In addition, the order in which the different structures of the sacrum are fused, as well as the causes that lead to this co-ossification, are poorly understood. Herein, we described the oldest record of fused sacral vertebrae within dinosaurs, based on two primordial sacral vertebrae from the Late Triassic of Candelária Sequence, southern Brazil. We used computed microtomography (micro-CT) to analyze the extent of vertebral fusion, which revealed that it occurred only between the centra. We also assessed the occurrence of sacral fusion in Dinosauria and close relatives. The degree of fusion observed in representatives of the major dinosaur lineages suggested that there may be a sequential pattern of fusion of the elements of the sacrum, more clearly observed in Sauropodomorpha. Our analyses suggest that primordial sacral vertebrae fuse earlier in the lineage (as seen in Norian sauropodomorphs). Intervertebral fusion is observed to encompass progressively more vertebral units as sauropodomorphs evolve, reaching up to five or more fully fused sacrals in Neosauropoda. Furthermore, the new specimen described here indicates that the fusion of sacral elements occurred early in the evolution of dinosaurs. Factors such as ontogeny and the increase in body size, combined with the incorporation of vertebrae to the sacrum may have a significant role in the process and in the variation of sacral fusion observed.

KEYWORDS

Candelária Sequence, Carnian, co-ossification, Dinosauria, sacrum, Triassic

1 | INTRODUCTION

The sacral region has structural, functional, and phylogenetic importance in the evolution of dinosaurs, mainly due to the variation in the number of vertebrae incorporated to the sacrum, which was historically used to diagnose certain groups and even served as one of the anatomical bases for the first definition of the clade Dinosauria (Owen, 1842). However, the order in which the osteological units of the sacrum successively fuse is poorly understood (Wilson, 2011), both phylogenetically and ontogenetically. The fusion of the sacral elements may have impacted on the stabilization of the dinosaur pelvis, as suggested by Colbert (1989), and is likely interconnected to different processes and causes, such as pathologies (Butler et al., 2013; Xing et al., 2015), ontogeny (Griffin, 2018; Hone et al., 2016), and gigantism (Klein et al., 2011; Sander et al., 2011; Wilson, 2011), among other aspects.

The sacrum is a transitory structure between the trunk and caudal series, with recognizable morphological changes that allow it to be distinguished from other vertebral series. The sacral vertebrae are composed of the centra and neural arches associated with sacral ribs, the latter promoting articulation with the ilium (Nesbitt, 2011; Wilson, 2011). The presence of only two sacral vertebrae (S1 and S2) is considered to be a plesiomorphic feature for Archosauria (Nesbitt, 2011). Because of this, they are considered the primordial sacral vertebrae, being identified mainly through the morphology of their sacral ribs and transverse processes (which together form a robust structure referred to as lateral process). The shape of their articular surfaces for attachment to the ilium is also diagnostic in the phylogenetic context (Langer, 2003; Nesbitt, 2011; Romer, 1956). In Dinosauria, the joint area of the lateral process of S1 generally is "C"-shaped in left lateral view, whereas the S2, has a much larger articular facet in its lateral process, sometimes assuming the shape of an "S" (Langer & Benton, 2006, fig. 7C).

Previous studies have highlighted that morphological aspects of the sacrum, variation in the number of sacral vertebrae, as well as other modifications present in the axial skeleton of vertebrates are at least in part controlled by the expression of the *Hox* genes (Casaca et al., 2013; Scheyer et al., 2019; Wellik & Capecchi, 2003). In Dinosauria, for example, an increase in the number of sacral vertebrae is observed during the evolution of all three major lineages, varying from two, in the early members, to more than five vertebrae. This increase in the sacral count is probably achieved by the incorporation of dorsal and/or caudal vertebrae to the primordial series, thus being recognized as dorsosacrals and caudosacrals (Langer & Benton, 2006; Romer, 1956), although Nesbitt (2011) proposed that new vertebrae could also arise between the primordial series in some archosaurs, including dinosaurs.

Besides the increase in the number of sacral vertebrae among dinosaur lineages, a variation in the pattern of intervertebral fusion is also observed, which may occur between the vertebral centra, zygapophyses, and neural spines. Nesbitt (2011) emphasized that fusion of the sacral centra is common in Archosauria, including dinosaurs, being observed in Ornithischia, some Sauropodomorpha, and all Neotheropoda. However, there is no consensus whether the fusion of the sacral elements in Ornithischia, Theropoda, and Sauropodomorpha is an ancestral condition of these clades (consequently being common to all Dinosauria, ancestrally) or emerged independently in each of the lineages. Assessment of this question is hampered by a scarcity of data, especially from dinosaurs of the early-diverging strains of each group. Thus, data from Late Triassic early dinosaurs can help to understand how sacral fusion processes initially took place.

The oldest dinosaur fossils have been recorded in Upper Triassic beds, and stratigraphic data suggest that the beginning of the group diversification occurred in the Upper Triassic (Carnian) mainly from Argentina (Ischigualasto Formation) and southern Brazil (Candelária Sequence) (Bonaparte, 1982; Brusatte et al., 2010; Cabreira et al., 2016; Irmis, 2011; Langer et al., 1999, 2010; Sereno et al., 1993; Sereno & Novas, 1992). In this study, we describe the first record of fused sacral vertebrae in a dinosaur from one of the oldest dinosaur-bearing units worldwide and provide a comparative review of the distribution of sacral fusion in Dinosauria and close relatives.

1.1 | Institutional abbreviations

AMNH, American Museum of Natural History, New York, NY, USA; CAPPA/UFSM, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia, São João do Polêsine, Rio Grande do Sul, Brazil; CM, Carnegie Museum of Natural History, Pittsburgh, PA, USA; CMNH, Cleveland Museum of Natural History, Cleveland, OH, USA; CXMVZA, Chuxiong Museum, Chuxiong, China; FMNH, Field Museum of Natural History, Chicago, IL, USA; GCP, Grupo Cultural Paleontológico de Elche, Spain; GR, Ghost Ranch Ruth Hall Museum of Paleontology, Abiquiu, NM, USA; HMN, Museum für Naturkunde, Humboldt Universität, Berlin, German; ISIR, India Statistical Institute, Kolkata, India; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LACM, Dinosaur Institute of the Natural History Museum of Los Angeles, California, USA; LCM, Leicester City Museums, Leicester; LFGT, Bureau of Land and Resources of Lufeng Country, Lufeng, Yunnan, China; LPRP/USP, Laboratório de Paleontologia de Ribeirão Preto, Ribeirão Preto, Brazil; MACN-CH, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Colección Chubut; MB, Musseum für Naturkunde Berlin, Germany; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica, Porto Alegre, Brazil; MCZ, Museum of Comparative zoology, Harvard University, Cambridge, MA, USA; MLP, Museo de La Plata, La Plata, Argentina; MNA, Museum of Northern Arizona, Arizona, USA; MPEF-PV, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; NGMJ, Nanjing Geological Museum, Nanjing, China; NHMUK, Natural History Museum, London, UK; NMMNH, New Mexico Museum of Natural History and Science, Alburquerque, NM, USA; NMT, National Museum of Tanzania, Dar es Salaan, Tanzania; OUMNH, Oxford University Museum of Natural History, Oxford, UK; PULR, Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Fundación "Miguel Lillo", San Miguel de Tucumán; PVSJ, Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, Argentina; QG, Queen Victoria Museum, Department of Paleontology, Harare, Zimbabwe; S.A.M, South African Museum, Africa; SAM-PK-K, Iziko South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; UCM, University of Colorado Museum of Natural History, Boulder, CO, USA; UCMP, University of California Museum of Paleontolog, Berkeley, CA, USA; UFRGS-PV, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil; ULBRA-PVT, Universidade Luterana do Brazil, Canoas, Brazil; YPM, Yale Peabody Museum of Natural History, New Haven, USA; ZDM, Zigong Dinosaur Museum, China; ZMNH, Zhejiang Museum of

Natural History, China; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

2 | MATERIALS AND METHODS

2.1 | Material

CAPPA/UFSM 0228, comprises two primordial sacral vertebrae. The specimen comes from the Buriol outcrop (29°39′34.2″ S; 53°25′47.4″ W), municipality of São João do Polêsine, Rio Grande do Sul, Brazil (Figure S2). It was collected from the same stratigraphic level of the holotype of *Buriolestes schultzi* (ULBRA-PVT280; Cabreira et al., 2016), approximately five meters from the holotype (Figure S3). The outcrop belongs to the lower portion of the Candelária Sequence (Horn et al., 2014) part of the Santa Maria Supersequence (Zerfass et al., 2003), dated as mid-Carnian (ca 233.23 ± 0.73; Langer et al., 2019). This is mainly established by the co-occurrence of hyperodapedontid rhynchosaurs at the outcrop, which allows us to refer it to the *Hyperodapedon* Assemblage Zone (see Supplementary File for an extended discussion and Schultz et al., 2020 for a comprehensive review).

2.2 | CT-scanning

Tomography and microtomography data were used to analyze the extent of fusion between elements of the sacrum of CAPPA/UFSM 0228 and CAPPA/UFSM 0035 (a partial skeleton referred to *Buriolestes schultzi*; Müller, Langer, Bronzati et al. 2018). Specimen CAPPA/UFSM 0228 was scanned with a µCT scan Skyscan^{TM} 1173 at Laboratório de Sedimentologia e Petrologia of the Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), Porto Alegre, Brazil, using 115 kV and 61 µA. The scan resulted in 2,631 tomographic slices, with a pixel size of 29.98 µm. Specimen CAPPA/UFSM 0035 was scanned using a Philips Brilliance 64-Slice CT Scanner (located at Santa Maria city), using 120 kV and 150.52 mAs. The analysis generated 332 slices with a 0.67 mm thickness, increment of 0.33 mm, and pixel size of 0.553 mm. The reconstructed images were imported in 3D Slicer 3.10, in order to observe the vertebrae in section and to create three-dimensional models of the specimens. The 3D models of both specimens are available in a digital repository (see Appendix) and were published by Moro et al. (2020).

2.3 | Phylogenetic analysis

In order to assess the phylogenetic relationships of CAPPA/UFSM 0228, it was scored in a modified version of the data matrix of Cabreira et al. (2016), also modified by Pacheco et al. (2019). The modified data matrix has 259 morphological characters and 52 operational taxonomic units (OTUs). Apart from the scoring of the new specimen, two characters not present in the original analysis were added (260—sacral vertebrae, fusion between neural spines: 0, absent; 1, present; 261—sacral vertebrae, prezygapophyses, and complementary postzygapophyses: 0, free; 1, co-ossified). For character 98 (sacral centra: 0, separated; 1 co-ossified at the ventral border) it was changed from 0 to 0&1 in *Silesaurus opolensis* (Dzik, 2003; Piechowski & Dzik, 2010) and *Plateosaurus engelhardti* (Moser, 2003); 0 to 1 in *Lesothosaurus diagnosticus* (Baron et al., 2016), and *Dilophosaurus wetherelli* (Griffin, 2018; Weishampel et al., 1990)? for 1 in *Lilensternus liliensterni* (Galton, 1999). All characters received the same weight and characters 3, 4, 6, 11, 36, 60, 62, 64, 83, 115, 123, 39, 147, 148, 157, 160, 171, 173, 175, 178, 179, 182, 195, 200, 201, 202, 202, 205, 216, 222, 240, and 248 were treated as ordered following the study of Cabreira et al. (2016). The analysis was conducted in TNT v.1.5 (Goloboff & Catalano, 2016; Goloboff et al., 2008), with the most parsimonious trees (MPTs) recovered via 'Traditional search' (RAS + TBR), random seed = 0; 5000 replicates; hold = 10. Two analyses were performed. Firstly, CAPPA/UFSM 0228 was coded as a distinct operational taxonomic unit (OTU). In the second analysis, data from CAPPA/UFSM 0228 and *Buriolestes schultzi* (ULBRA-PVT280 + CAPPA/UFSM 0035) were merged into a single OTU, keeping the computational parameters. The scores for the three specimens were combined in this merged OTU. Therefore, the character state 98 has been changed from '0' to '0/1', in this analysis. The second analysis was done considering the proximity between the collection site of *Buriolestes* specimens with CAPPA/UFSM 0228 and their overall similarity (other than the fusion). The analysis was conducted in order to test if variability in the sacral fusion would impact the phylogenetic positioning of *Buriolestes*.

2.4 | Source of comparative data

The review of data concerning morphology and sacral fusion in Dinosauria was carried out through first-hand observation and/or bibliographic research at a specimen level (see supplementary file).

3 | RESULTS AND DISCUSSION

3.1 | Systematic palaeontology

Archosauria Cope, 1869.
    Dinosauria Owen, 1842.
    Saurischia Seeley, 1887.

3.2 | Description

CAPPA/UFSM 0228 is composed of two partially fused sacral vertebrae (Figure 1). The elements show no signs of compression, but some structures, such as the tips of the neural spines, were broken away by recent weathering. Overall, the second sacral vertebra is better preserved than the first one. Both centra are recognized as

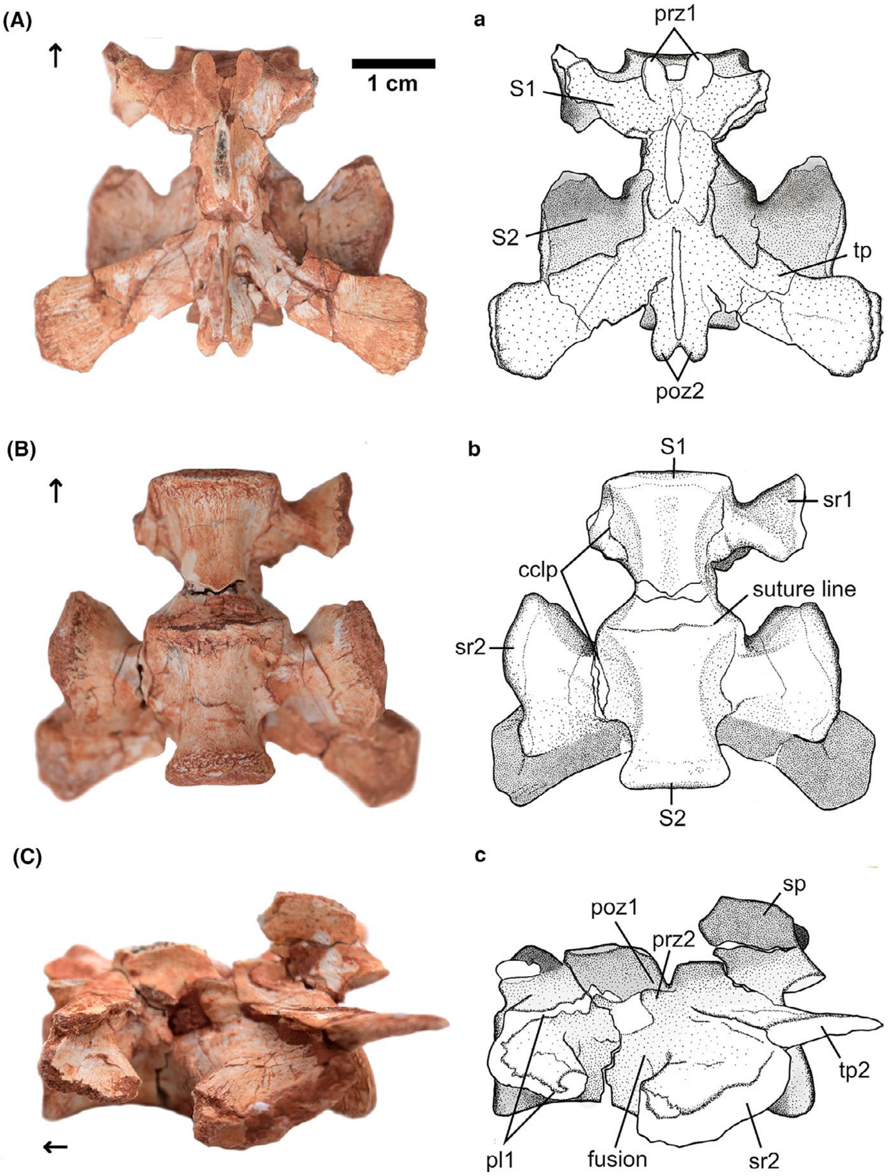

FIGURE 1 CAPPA/UFSM 0228 from the Late Triassic Buriol outcrop, southern Brazil. Photographs (A–C) and schematic drawings (a–c) in dorsal (A), ventral (B), and left lateral (C) views. Abbreviations: sc, sacral centra, cclp, contact between centra and respective lateral processes; lp, lateral process; poz, postzygapophysis; prz, prezygapophysis; S1, first primordial sacral vertebra; S2, second primordial sacral vertebra; sp, neural spine; sr, sacral rib; tp, transverse process. Arrow indicates cranial direction

the primordial sacral S1 and S2, according to the morphology of the articular surfaces that contacted the ilia, composed by both the transverse process and the rib (see below).

The vertebrae have elongated centra (craniocaudally longer than their dorsoventral height) which are slightly slenderer in their middle portion (i.e. spool shape; Figure 1B), with expanded articular facets, resembling other dinosauromorphs except for Herrerasauridae (Alcober & Martinez, 2010; Novas, 1993; Pacheco et al., 2019), which generally have craniocaudally shorter centra in the last dorsals, as well as in the sacrum. The centra of S1 and S2 have approximately the same length (S1 = 17 mm, S2 = 17.5 mm). The sacral elements of CAPPA/UFSM 0228 are only slightly smaller (91% and 94% for each primordial centrum length) than those of CAPPA/UFSM 0035, referred to *Buriolestes schultzi* (Müller, Langer, Bronzati et al., 2018). The first primordial sacral is slightly slender than the second sacral (S1 = 7 mm, S2 = 8.5 mm, both measured at the minimum lateral width of the centrum). Both centra have a height of 10 mm. The subequal size of both sacral centra in CAPPA/UFSM 0228 differs from the condition originally described for *Guaibasaurus candelariensis*, which presents the first sacral centrum notably larger than the second (MCN-PV 2355, Bonaparte et al., 2007, but see Langer et al., 2011). The cranial articular facet of the centrum of S1 is elliptical, as well as its medullary canal, whereas the caudal articular facet of S2 is circular, similar to that observed in *Pampadromaeus barberenai* (Langer et al., 2019). The exposed articular surfaces of both centra are slightly concave. In lateral view (Figure 1B), the centra of S1 and S2 are completely fused, though in ventral view a suture line still superficially marks the point where the two centra contact each other (Figure 1C).

S1 is missing the distal portion of both lateral processes, hampering the inference of the nature of their contact with the ilium (Figure 1A). From the preserved portions of both right and left sides of the vertebra, it is possible to infer that originally the lateral process had a 'C- shape' in lateral view, with two parallel horizontal shelves, bounded by a cranial vertical bar, as observed in most early saurischians. Both the vertical bar and the ventral horizontal shelf, which are more robust, correspond to the sacral rib, as in *Saturnalia tupiniquim* (Langer, 2003), whereas the dorsal horizontal shelf, more delicate, represents the transverse process. Both the rib and transverse processes are fused to one another, constituting a single lateral process, which is fused to the centrum, though a faint line of contact can still be seen in ventral view (Figure 1B).

The prezygapophyses have articular facets in the form of lobes and their postzygapophyses are tightly associated with the prezygapophyses of S2, with a thin line separating each other (Figure 1C). Most of the neural spine was also worn away, but its base indicates that it was transversely narrow and craniocaudally elongated (Figure 1C), distinct from the transversely expanded neural spine of herrerasaurids (Novas, 1993; Pacheco et al., 2019).

In lateral view, the transverse processes of S2 are dorsoventrally thin sheets of bone that expand caudally, being oriented horizontally, as in *Bu. schultzi* (Figure S4), *Bagualosaurus agudoensis* (Pretto et al., 2019) and *S. tupiniquim*. In some specimens, such as the holotype of *P. barberenai* (Langer et al., 2019), the paratype of *S.tupiniquim* (MCP 3845-PV), and the unnamed sauropodomorph UFPel 014 (Bittencourt et al., 2013) present a more dorsally inclined orientation of the transverse processes, when compared to CAPPA/UFSM 0228. In a ventral view, the S2 sacral rib has a fan-shape (Figure 1B), as well as in *H.ischigualastensis* (Novas, 1993), *G.candelariensis* (Langer et al., 2011), *P.barberenai* (Langer et al., 2019), *E.lunensis* (Sereno et al., 2012), and *Bu. schultzi* (Figure S4). In lateral view, the sacral rib of S2 extends from the point of contact of both centra, at the cranioventral corner of the centrum of S2, trending caudally and dorsally to meet the transverse process, thus forming a very robust diagonal shelf. Both rib and transverse processes also fused together, forming a robust lateral process that contacts the ilium (Figure 1A). Like in S1, the lateral processes are fused to the centrum, leaving a faint line reminiscent of their previous limits (Figure 1B).

The neural spine is partially preserved in S2. In dorsal view, it is transversally narrower than in S1 (Figure 1C). The lateromedially slender condition of the neural spines of CAPPA/UFSM 0228 resembles most coeval dinosauromorphs, but is strikingly distinct from the robust neural spines seen in herrerasaurids (Alcober & Martinez, 2010; Bittencourt & Kellner, 2009; Novas, 1993). The total height of the neural spines of both sacrals cannot be assessed due to fragmentation. Despite their incompleteness there is no sign of fusion between the neural spines.

The internal morphology of the fusion between the centra of CAPPA/UFSM 0228 was analyzed in the tomograms (Figure 2). This allowed recognizing that the centra are fused to each other along

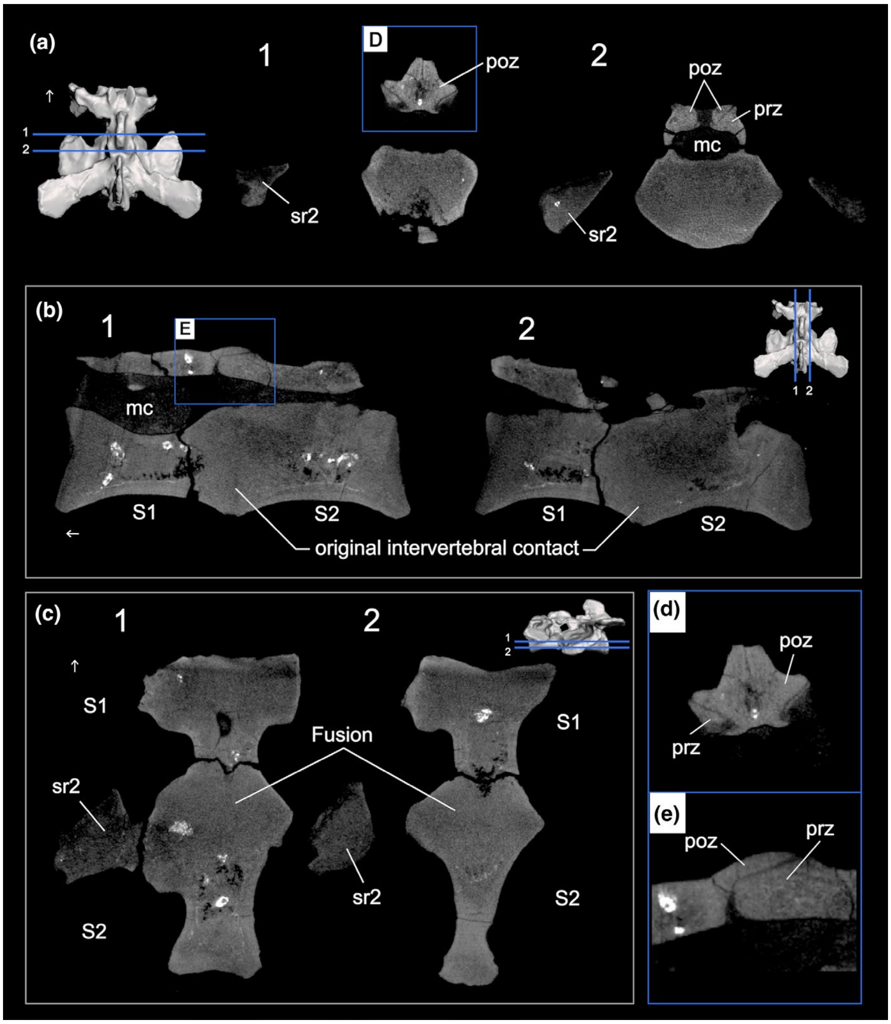

FIGURE 2 CAPPA/UFSM 0228, µCT scan of fused sacral primordial vertebrae. (a) 1. Transverse sections of the contact between S1 and S2 showing the unfused between zygapophyses. 2 Transverse section of the S2 showing details of the medullary canal, sacral ribs, and contact of postzygapophyses and prezygapophyses. (b) Sagittal sections along the midline of S1 and S2 showing the fusion between the centra of the vertebrae. Repair the slightly less dense co-ossification close to the ventral margin of the centra. (c) Coronal sections showing the fusion between the primordial sacral centra. (d and e) Details of the unfused contact between the pre- and postzygapophyses of S1 and S2 in transverse section and sagittal section respectively. Abbreviations: mc, medullary canal; poz, postzygapophysis; prz, prezygapophysis; S1, first primordial sacral vertebra; S2, second primordial sacral vertebra; sr, sacral rib. Arrow indicates cranial direction

their entire contact (Figure 2b and c). Closer to their ventral portion, the fusion is less dense than the neighboring bone, allowing to locally identify the original contact between both vertebrae as a faint darker band in the reconstructed images (Figure 2b). As recognized, though firmly associated with each other, the articulated zygapophyses of S1 and S2 are not fused, because a clear line of contact is visible between them (Figure 2d and e). The analysis of the tomograms showed that fusion between vertebrae does not indicate pathology,

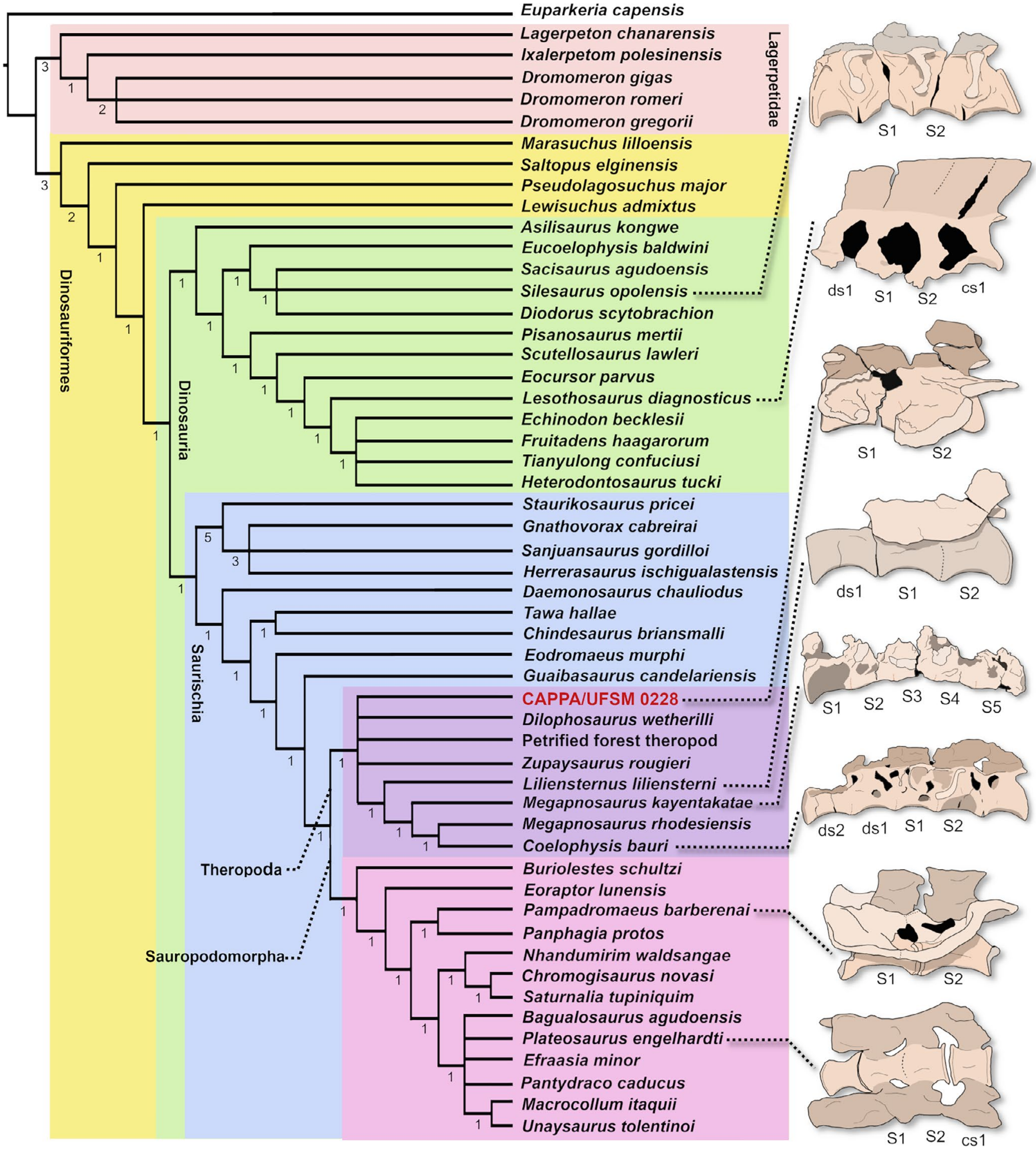

FIGURE 3 Strict consensus tree showing the phylogenetic position of CAPPA/UFSM 0228 and schematic morphology of the sacrum of taxa that present sacral fusion. *Silesaurus opolensis* (ZPAL Ab III/401/1 - reversed); *Lesothosaurus diagnosticus* (SAM-PK-K1107—reversed); *Lilientesnus liliensterni* (HMN); *Syntarsus kayentakatae* (TR 97/12); coelophysoid sacrum (NMMNH P-31661); *Pampadromaeus barberenai* (ULBRA-PVT016—reversed); *Plateosaurus engelhardti* (SMNS 13200—reversed). Abbreviations: S1, first sacral vertebra; S2, second sacral vertebra; ds, dorsosacral; cs, caudosacral

as there are no bone irregularities (i.e. bone reshuffle) in contact between vertebral centra, as well as changes in shape, rough, or porous texture on their bone surface, often observed in vertebrae fused by pathology in vertebrates (e.g. Haridy et al., 2019; Witzmann et al., 2014; Xing et al., 2015).

3.3 | Phylogenetic analysis

Our first phylogenetic analysis recovered 90 MPTs of 894 steps (CI = 0.336; RI = 0.664). In the strict consensus, CAPPA/UFSM 0228 is found in a polytomy at the base of Theropoda (Figure 3), together with *Dilophosaurus wetherilli*, the 'Petrified Forest theropod', and *Zupaysaurus rougieri*. The characters that support CAPPA/UFSM 0228 as a theropod are the presence of fusion at the ventral edge of the centra (character 98, state 1) and articular surface of the lateral process of primordial sacral vertebra, C-shaped in lateral view (character 103, state 1). Although the optimization of these characters nests the specimen as a theropod, these character states are also supportive of other taxa, showing a homoplasic distribution. However, fusion between centra is also identified in sauropodomorphs starting in Norian records (e.g. *Plateosaurus engelhardti*, *Melanorosaurus readi*, and *Riojasaurus incertus*). Likewise, the C-shaped articular surface of the first lateral process is widespread in Saurischia, including the earliest sauropodomorphs (e.g. *Buriolestes schultzi*, *Bagualosaurus agudoensis*, *Saturnalia tupiniquim*, and *Pampadromaeus barberenai*).

Our second analysis recovered 20 MPTs of 894 steps (CI = 0.336; RI = 0.664). The strict consensus (Figure S7) shows that the combination of CAPPA/UFSM 0228 with *Buriolestes schultzi*, even with the modification in the state of character 98 did not affect the topology presented in previous studies, where the taxon nests as the sister-taxon to all other sauropodomorphs (e.g. Cabreira et al., 2016; Müller, Langer, Bronzati et al., 2018; Pacheco et al., 2019).

3.4 | Variation in the occurrence of co-ossification of sacral elements

3.4.1 | Non-dinosaurian Dinosauromorpha

Among Archosauria, sacral fusion is not exclusive to Dinosauromorpha. It occurs also in some pseudosuchians, being notably common in members of Poposauroidea (Alcober & Parrish, 1997; Nesbitt, 2005; Nesbitt, 2007; Weinbaum & Hungerbühler, 2007) and aetosaurs (Parker, 2008). Among Ornithodira, many Pterosauria also shows intervertebral fusion not only in the sacrum but also in the dorsal sequence (i.e. notarium; Aires et al., 2020), possibly as a strategy of stabilizing the axial skeleton during the flight (Hyder et al., 2014).

Nevertheless, sacral morphology is important in Dinosauromorpha and has received more attention, especially in phylogenetic studies (e.g. Gauthier, 1986; Langer & Benton, 2006; Nesbitt, 2011; Novas, 1996). The ancestral condition in Dinosauromorpha is the presence of two only primordial sacral vertebrae, without evidence of fusion between the centra, as observed in *Lagerpeton chanarensis* (Sereno & Arcucci, 1993) and *Ixalerpeton polesinensis* (Cabreira et al., 2016). Conversely, the distal portions of the lateral processes of *Ixalerpeton polesinensis* (ULBRA-PVT059) are fused to each other. Moreover, Sereno and Arcucci (1994) point out that the two sacral vertebrae of *Lagosuchus talampayensis* (sensu Agnolin & Ezcurra, 2019) might be so closely associated that they could have been fused, but the authors do not go into depth about the subject, and their sacral vertebrae are therefore considered as unfused.

Among non-dinosaurian dinosauromorphs, the most evident exception to the ancestral condition occurs in *Silesaurus opolensis* (Dzik, 2003). Although the sacrum is not commonly preserved in specimens of Silesauridae (Langer et al., 2013), it is notable that in *Asilisaurus kongwe*, the sacrum appears to follow the original pattern of Dinosauromorpha (Nesbitt, Irmis et al., 2009, 2019) in having two unfused sacrals. *Silesaurus*, however, had extensive fusion between the sacral centra (Dzik, 2003; Dzik & Sulej, 2007; Piechowski & Dzik, 2010), in addition to the incorporation of extra vertebrae into the sacrum (Langer et al., 2013; Nesbitt, 2011). In fact, the sacrum of specimens such as ZPAL Ab III/404/3 appears to have up to four fused vertebrae.

3.4.2 | Ornithischia

Romer (1956) pointed out a tendency for the sacral series to expand and merge in Ornithischia, even more than in Saurischia. However, the Triassic record of the group is extremely rare (Agnolín & Rozadilla, 2018; Baron, 2019; Irmis et al., 2007), which makes it difficult to trace the sequence of incorporation of sacral vertebrae, and the time when they begin to fuse in the lineage. The putative ornithischian *Pisanosaurus mertii* was supposed to have data from its sacrum preserved only in the form of a natural cast (Bonaparte, 1976), but questions were raised as to the identity of these vertebrae (Irmis et al., 2007), as well as the taxonomic position of *Pisanosaurus* (Agnolín & Rozadilla, 2018; Desojo et al., 2020; Müller & Garcia, 2020). Agnolín and Rozadilla (2018) maintain that *Pisanosaurus* would have four sacral vertebrae, which was corroborated in the study of Desojo et al. (2020), but the fusion relationship between their centra would be impossible to evaluate. For Agnolín and Rozadilla (2018**)**, *Pisanosaurus* would not be an ornithischian, but a silesaurid, which was contested in the study of Desojo et al. (2020). Furthermore, Müller and Garcia (2020) suggested that 'silesaurids' nest in low-diversity clades representing successive outgroups leading to core ornithischians. Hence, *Pisanosaurus* is regarded as an intermediate form between 'silesaurids' and typical ornithischians. The composite cladogram in Figure 4, however, shows the traditional hypothesis, with silesaurids being nested separated from Dinosauria.

Among Heterodontosauridae, however, an increase in sacral number is observed, as well as extensive fusion, are seen early in

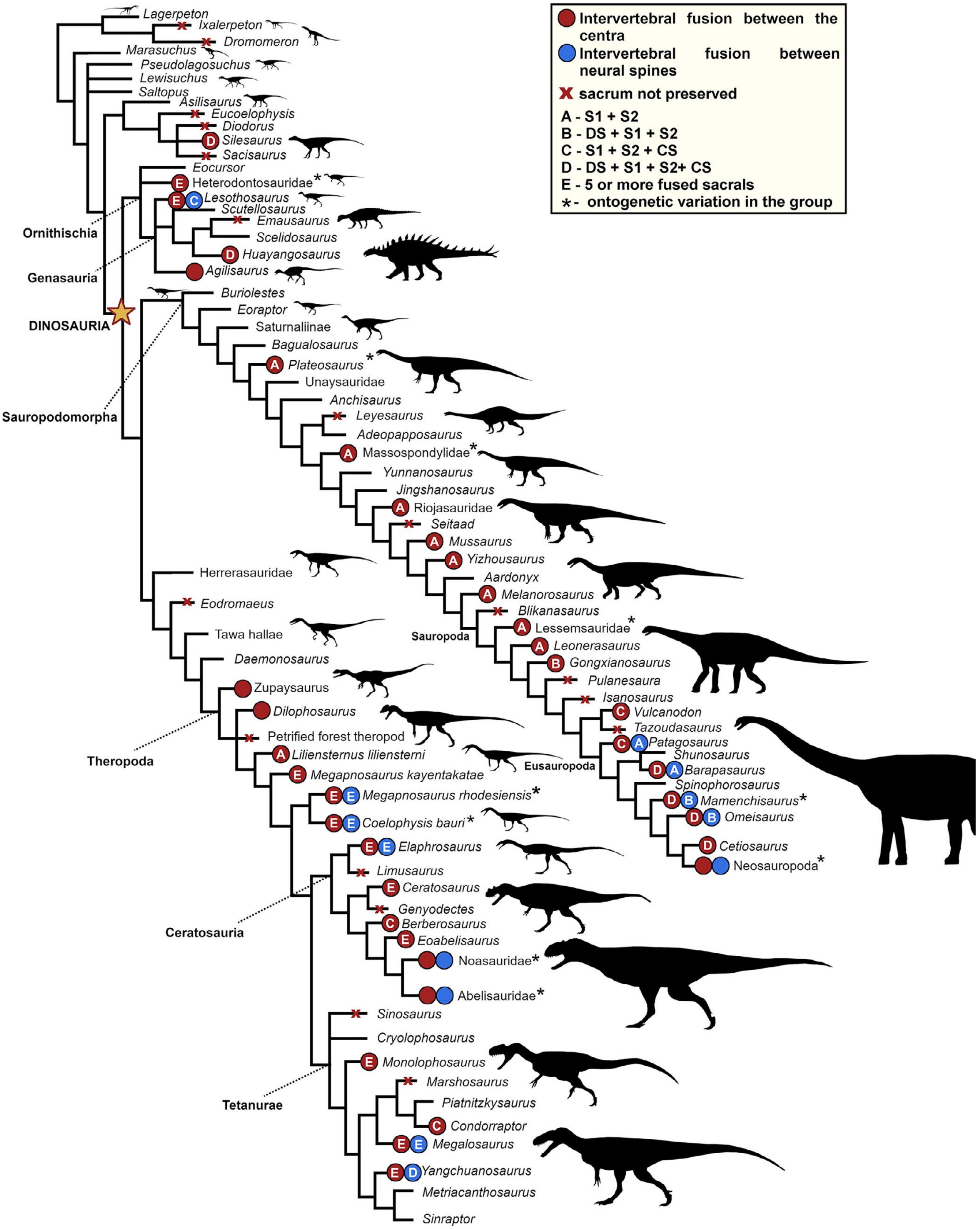

FIGURE 4 - Cladogram showing the occurrence and pattern of sacral fusion in early dinosauromorphs and dinosaurs. The tree topology follows the results of the cladistic analyses obtained by Irmis (2011) (adapted) for Dinosauromorpha and Dinosauriformes, Han et al. (2018) for Ornithischia, Müller (2020) for Sauropodomorpha, and Hendrickx et al. (2015) for Theropoda. Silhouettes based on the artwork by Scott Hartman and Márcio L. Castro

that lineage (Figure 4). The sacrum of *Heterodontosaurus tucki* (Santa Luca, 1980) consists of six vertebrae, with fused centra (Hailu & Dodson, 2004). In *Manidens condorensis* (Pol, Rauhut et al., 2011), the sacrum is also composed of six vertebrae, but their spines are fused in such a way that they form a single continuous bone bar. *Lesothosaurus diagnosticus* (SAM-PK-K1107), also presents fused centra, but the fusion between the spines occurs between the second and third sacrals only. Butler (2005) suggested that this specimen represented a separate taxon, *Stormbergia dangershoeki*, but Baron et al. (2016) and Knoll et al. (2010) argued that the specimen should be included in *Lesothosaurus diagnosticus*, representing an ontogenetically older individual. Thus, the extent of sacral fusion in the taxon could be an effect of ontogeny.

The sacral series of the *Eocursor parvus* holotype (Butler, 2010) does not appear to have a fusion between its elements, but the structure of the sacrum is not very well-preserved in the specimen. In the thyreophorans *Scutellosaurus lawleri* and *Scelidosaurus harrisonii*, the sacral elements are completely free, but it is probably related to the skeletally immature of the known specimens (Colbert, 1981; Norman et al., 2004; Owen, 1861). However, extensive fusion of centra and sacral spines is the typical condition in both Stegosauria (Galton & Upchurch, 2004) and Ankylosauria (Vickaryous et al., 2004). In the latter, fusion often extends to the last dorsal vertebrae, and the sacrum itself can fuse even in sub-adult individuals, such as in *Pinacosaurus*, for example (Coombs, 1986). The tendency to incorporate vertebrae to an extensively fused sacral series is also maintained in Ornithopoda (Norman et al., 2004). In Hadrosauridae the condition is extreme, reaching up to 12 sacral elements (Horner et al., 2004), which is also observed in Ceratopsia (Hailu & Dodson, 2004).

3.4.3 | Theropoda

Similar to Ornithischia, Theropoda presents both an increase in the number of sacral elements and a high degree of fusion between these elements early in the lineage (Figure 4). Nesbitt (2011) pointed out that fusion between sacral centra is a potential synapomorphy of Neotheropoda. It is interesting to note that Herrerasauridae, occasionally treated out as basal theropods (Nesbitt, Smith et al., 2009; Novas, 1993; Sereno, 1999; Sereno & Novas, 1992), but also as basal members of Saurischia (Alcober & Martinez, 2010; Baron et al., 2016; Cabreira et al., 2016; Langer & Benton, 2006), do not present any trace of fusion between their sacral vertebrae (Bittencourt & Kellner, 2009; Novas, 1993; Pacheco et al., 2019).

According to Griffin (2018), *Coelophysis* and *Megapnosaurus* present variation in intervertebral sacral fusion, but most individuals of larger size present a total of five fused centra. The author reports that it is relatively common, however, for the last sacral of the series to be non-fused, or in some cases, the last two. Concerning the neural spines, *Coelophysis* and *Megapnosaurus* also present considerable variation, with specimens showing free spines (Spielmann et al., 2007), and others with the five spines forming a single fused bar, as in some Ornithischia (Griffin, 2018). Although some authors (Colbert, 1989; Rinehart et al., 2009) suggested that variation in the degree of sacral spines fusion may be evidence of sexual dimorphism, the presence of intermediate stages reinforces at least some ontogenetic control (Griffin, 2018; Griffin & Nesbitt, 2016; Raath, 1990).

Arcucci and Coria (2003) reported two incomplete sacral vertebrae, with evidence of fusion among them for *Zupaysaurus rougieri*, however, other works considered the number of sacral vertebrae and fusion as still undetermined characteristics (Ezcurra & Brusatte, 2011; Ezcurra & Novas, 2007; Langer et al., 2017; Nesbitt & Ezcurra, 2015; Nesbitt, Smith et al., 2009). Although Welles (1984) and Marsh and Rowe (2020) reported that the sacrum of *Dilophosaurus wetherilli* is composed of four non-fused elements, this may be related to ontogeny, because it presents signs of immaturity, such as the absence of neurocentral fusion in the dorsal vertebrae (Weishampel et al., 1990; Welles, 1984). Griffin (2018) suggests that a larger specimen of *D. wetherilli* (UCMP 77270) has partial fusion between the sacral centra, but Marsh and Rowe (2020) highlight that the specimen has only a pair of ossified discs between the sacral vertebrae, and though the transverse processes of these vertebrae are fused to the ilia, there is no fusion between neighboring sacral centra. According to Tykoski and Rowe (2004), *Liliensternus lilensterni* (Huene, 1934), presents three sacral vertebrae (the second and third being fused), and *Lophostropheus airelensis*, has four free sacral vertebrae (Cuny & Galton, 1993; Ezcurra & Cuny, 2007; Huene, 1934).

Averostrans in general maintain both the increase in sacral count and the broad fusion of sacral elements that were already observed in Coelophysoidea (Figure 4). Ceratosaurians, such as *Ceratosaurus* and *Elaphrosaurus*, have a sacrum composed of six fused vertebrae, a count that increases to seven in *Carnotaurus* (Bonaparte et al., 1990; Rauhut & Carrano, 2016; Tykoski & Rowe, 2004). Tetanurae (Holtz et al., 2004), as observed for example in *Megalosaurus bucklandii* (Benson, 2010), shows a sacrum composed of five vertebrae with fused centra and neural spines.

3.4.4 | Sauropodomorpha

The records of the sacrum in Sauropodomorpha show that, although the presence of extensive sacral fusion is common in Sauropoda, it is relatively unusual in its earliest members (Figure 4). In a similar fashion, the increase in sacral numbers occurs not as abruptly in tree topologies (compared to Theropoda and Ornithischia), and sacral fusion gradually incorporates more elements from early members toward Neosauropoda. In this sense, the typical early sauropodomorph sacrum comprises three vertebrae, and additional vertebrae are incorporated along the lineage. Especially in Carnian sauropodomorphs, such as *Buriolestes schultzi* (Cabreira et al., 2016; Müller, Langer, Bronzati et al. 2018), *Eoraptor lunensis* (Sereno et al., 2012), *Panphagia protos* (Martinez & Alcober, 2009), *Saturnalia tupiniquim* (Langer, 2003), and *Bagualosaurus agudoensis* (Pretto et al., 2019), the vertebrae of the sacrum always occur as independent structures, without fusion. The only exception may be in *Pampadromaeus barberenai*, whose sacrum has reported signs of fusion in the zygapophyses of the primordial sacrals (Langer et al., 2019). However, their vertebral centra and neural spines are, at least superficially, free.

Arising during the Norian, the fusion of elements of the sacrum begins to be reported sparsely in some specimens of *Plateosaurus engelhardti* (Moser, 2003), *Melanorosaurus readi* (Heerden & Galton, 1997), and *Riojasaurus incertus* (Bonaparte, 1971; Galton, 1999). However, as evidenced by specimens assigned to *Efraasia minor* (Yates, 2003) and *Macrocollum itaquii* (Müller, Langer & Dias da Silva, 2018), which present free sacrals, as well as in most individuals of the other aforementioned taxa, sacral fusion is scarce in Norian sauropodomorphs.

Specimens of *Plateosaurus* have the sacrum composed of three sacral vertebrae. When fusion occurs, it usually occurs between the centra of the primordial sacral vertebrae (Moser, 2003). Exceptionally, fusion may occur between all (primary and additional) sacral vertebrae, such as the lectotype of *Plateosaurus engelhardti* (UEN 552), which presents the centra of its primordial sacral and caudosacral fused (pl.5, Moser, 2003). In *Riojasaurus incertus*, the primordial sacral centra of PVL3808 are fused (Bonaparte, 1971; Galton, 1999). Although the taxon still has a dorsosacral (Novas, 1996), there is no evidence of fusion of this element to the rest of the sacrum.

The condition in Massospondylidae is variable. In the case of *Massospondylus carinatus* (QG115; BP/1/4934), although the sacral vertebrae (two primordial and one dorsosacral) form a firmly associated set (Barrett et al., 2019; Cooper, 1981), the contacts between the centra are severely damaged, making it impossible to determine for certain the possibility of fusion (Barrett et al., 2019). In the closely related *Adeopapposaurus mognai* (Martinez & Alcober, 2009), all sacral vertebrae are free.

In *Yunnanosaurus huangi* and *Yunnanosaurus youngi* (Lu et al., 2007; Young, 1942), the sacrum is also composed of three sacral vertebrae. The ribs and transverse processes may be fused, forming a "sacrocostal yoke", but the fusion between the centra is not reported in any of those taxa. *Yunnanosaurus robustus* (Sekiya et al., 2014), on the other hand, does not present a fused sacrum, not even in its ribs. However, this is probably due to the immaturity of the specimen, as evidenced by the separation of its neurocentral sutures.

The sauropodiform *Xingxiulong chengi* has four sacral vertebrae (LFGT-D0002; Wang et al., 2017), the first being a dorsosacral, followed by two fused primordials, plus a caudosacral. Besides the fusion between the primordial sacral vertebrae, the authors report a partial fusion between the dorsosacral and the first primordial sacral. In fact, at this point of the lineage, the fusion between the centra of primordial sacral is common among Sauropodiformes. This occurs for example in *Yizhosaurus sunae* (LFGT-ZLJ0033), whose sacrum is composed of three elements: dorsosacral, and two strongly fused primordial sacral centra (Zhang et al., 2018).

The sacrum of *Mussaurus patagonicus* is best preserved in MLP68-II-27-1 and MLP 61-III-20-23, being composed of three vertebrae, with the additional vertebra interpreted as a dorsosacral. Otero and Pol (2013), however, discuss the possibility of a caudosacral being present in MLP 61-III-20-23. The authors point out the strong fusion between the primary sacral centra of MLP 61-III-20-23, to the point of obscuring the contact between them. *Leonerasaurus taquetrensis* also shows similar fusion between S1 and S2 (Pol, Garrido et al., 2011).

Melanorosaurus readi (NMR1551, Heerden & Galton, 1997) follows the same pattern as *Leonerasaurus taquetrensis*, with the sacrum having four sacral vertebrae (one dorsosacral, two primordials fused by the centra, and one caudosacral). Yates (2007), however, suggests that the sacrum of NMR1551 would be composed of two dorsosacrals followed by the two primordials. If so, the resulting fused vertebrae would be the second dorsosacral and the first primordial sacral, and thus *Melanorosaurus* would not fit the pattern otherwise observed in closely related taxa.

Unfortunately, most records of Lessemsauridae did not preserve the sacrum, or at best they are very fragmentary (Apaldetti et al., 2018; McPhee et al., 2014; Pol & Powell, 2007). The best record is that of *Ledumahadi mafube* (BP/1/7120), which the sacrals are recognized as a fused set of primordial sacrals (McPhee et al., 2018). However, there are no remains of the rest of the sacrum of the specimen.

Concerning Sauropoda, the fusion between sacral vertebrae is widely distributed (Figure 4). In fact, intervertebral fusion, together with the increase in the number of sacral vertebrae, are pointed out as a typical attribute of Sauropoda, or sauropodiforms phylogenetically close to Sauropoda (Romer, 1956; Weishampel et al., 2004; Wilson, 2011). This advent would possibly be related to increased abdominal volume and mass (Otero & Pol, 2013; Pol, Garrido et al., 2011; Wilson & Sereno, 1998). Indeed, the number of vertebrae fused into the sacrum of sauropods has historically been treated as a diagnostic feature for the group (e.g. Marsh, 1878, 1881). Osborn (1898) and Williston (1898), however, pointed out that the sacral fusion varies according to the ontogenetic stage, or among taxa. Sacral fusion of sauropod elements is fully accomplished with skeletal maturity, but the complexity of the form of this structure and timing of fusion are matters that historically received little attention (Wilson, 2011).

Even so, the extent of sacral fusion varies along the lineage. Whereas sauropodiforms closer to Sauropoda fuse only the centra of their primary sacral vertebrae, despite they present a sacrum with up to four vertebrae (e.g. *Leonerasaurus*, *Melanorosaurus*), sauropods fuse additional vertebrae, in addition to the two primary sacral vertebrae, such as the dorsosacral of *Gongxianosaurus shibeiensis* (He et al., 1998) and the caudosacral of *Vulcanodon karibaensis* (fig. 12A, Cooper, 1984; Moser, 2003). Although *Spinophorosaurus nigerensis* apparently has the dorsosacral free from the rest of the sacrum, Remes et al. (2009) also point out that the holotype, which preserves the sacrum, represents a subadult individual, so that an ontogenetic component may be responsible for this separation from the dorsosacral.

In Eusauropoda it is remarkable that fusion is no longer limited only to the centra of the sacral vertebrae, but extends to the neural arches, including neural spines (Figure S1). For example, Bonaparte

(1986) described the sacrum of the holotype of *Patagosaurus fariasi* (PVL 4170) as having five sacral vertebrae, the first four being fused by the centra. The second and third sacral vertebrae, however, extend the fusion to the apex of the neural spines. They probably correspond to the primary sacral vertebrae, since Bonaparte (1986) recognizes the last two vertebrae of the series as having characteristics of caudal (or caudosacral) vertebrae. In *Barapasaurus tagorei* (ISIR 50), a specimen with four sacral vertebrae fused in their centra, and similar to *Patagosaurus*, bearing a fusion of the neural spines of the second and third sacral vertebrae (Bandyopadhyay et al., 2010; Jain et al., 1975). The sacrum of *Omeisaurus junghsiensis* has four fused sacral vertebrae, and the first three of the series have coalesced spines, a condition also reported for *Mamenchisaurus hochuanensis* (Young & Zhao, 1972) and *Mamenchisaurus jingyanensis* (Zhang et al., 1998).

In Neosauropoda, intervertebral fusion commonly encompasses all or most of the sacral centra. In addition, the fusion between the zygapophyses and neural spines includes progressively more dorsosacrals and/or caudosacrals, although the number of vertebrae in which fusion of zygapophyses and neural spines is observed varies among taxa. Taxa like *Haplocanthosaurus* show five sacral vertebrae fused by all centra, neural arches, and neural spines (McIntosh & Williams, 1988), although in at least one specimen (CM572), the neural spines of the fourth and fifth sacral (caudosacrals) are incompletely fused. *Camarasaurus* shows a similar pattern of five fused sacrals, though an extensive variation may be observed, and fusion can even extend beyond the sacrum (Ikejiri, 2004; McIntosh et al., 1996; Tidwell et al., 2005). Similar condition is observed in other macronarians, such as *Brachiosaurus altithorax* and *Giraffatitan brancai* (Riggs, 1903; Taylor, 2009), as well as *Opisthocoelicaudia skarzynkii* (Borsuk-Białynicka, 1977) and *Saltasaurus loricatus* (Powell, 1992). Species referred to *Diplodocus* generally, show five sacrals fused by the centra, the fusion extending to the spines of the first three sacrals, often recognized as “true sacrals” (Hatcher, 1901; Wilson & Sereno, 1998). A notable exception occurs in *Diplodocus hallorum* (NMMNH 3690), in which the neural spines of the second, third, and fourth sacral are firmly fused, while the first and fifth sacral are apparently free, or fused, if at all, only at their apex (Gillette, 1991; Herne & Lucas, 2006; Lucas et al., 2006; Tschopp et al., 2015). The sacral fusion in specimens of *Apatosaurus* is similar to *Diplodocus*, (Gilmore, 1936; Upchurch et al., 2004) but the three more commonly fused neural spines are from the second to the fourth sacral, as in NSMT-PV 20375 (Upchurch et al., 2004). *Brontosaurus parvus* (UW 15556), is similar to *Apatosaurus* in this regard (Hatcher, 1903; Tschopp et al., 2015), and some examples of ontogenetic variations can be seen in the taxon. The preserved sacrals of CM 556, for instance, which is a juvenile now referred to *Brontosaurus parvus* (Peterson & Gilmore, 1902), are free from each other, perhaps due to the ontogenetic immaturity of the specimen (Peterson & Gilmore, 1902; Tschopp et al., 2015).

Indeed, ontogeny is a factor that may explain the intraspecific variation in sacral fusion patterns, especially in Neosauropoda, where morphology seems to be more plastic (Wilson, 2011). However, it is also worth noting that other factors may be associated with the process of sacral fusion along sauropodomorph lineages, notably the increase in body size combined with the incorporation of vertebrae into the sacrum. Because the sacrum supports a good portion of the body mass, besides suffering mechanical stress due to locomotion, the increase in the number of sacral vertebrae might confer better stability to the sacral complex (Sander et al., 2011; Weishampel et al., 2004), and the same might be true to intervertebral fusion.

Through a detailed analysis of ontogenetic processes is still hampered by incomplete fossil sampling in many sauropodomorphs, the comparative analysis of sacral structure among adult specimens of different sauropodomorph taxa (Figure 5) suggests that throughout the evolution of the group, fusion begins from the centra of the two primordial sacrals (as observed in non-sauropod sauropodomorphs). This occurs with a certain frequency, for example, in specimens of the Triassic taxon *Plateosaurus* (Moser, 2003), and becomes common especially in Early Jurassic Sauropodiformes (e.g. *Leonerasaurus*). The fusion spreads later in the lineage to the additional sacral centra (Figure 5). At the same time, the fusion seems to begin in the zygapophyses and finally reaches the neural spines. Though this stage shows increasing variability in the vertebrae effectively involved in the fusion process (especially within Sauropoda), it is evident that the vertebral centra fuse to each other before the fusion extends to the zygapophyses and spines (Figure 5). Also, the process of fusion, especially observable in the neural spines, seems to begin in the primordial sacrals (e.g., *Patagosaurus*, *Barapasaurus*) and then propagates to additional sacral vertebrae. Supposedly, late fusion in adjacent vertebrae may be more strongly related to the time of incorporation of dorsosacrals and caudosacrals, in addition to the variation in fusion related to ontogeny as widely observed in Neosauropoda, for example.

According to Pol, Garrido et al. (2011), the fusion of the centra of the primordial sacral elements is one of the criteria that has a significant role in the identification of these elements on sacral structure. This criterion is generally applicable to basal sauropodomorphs, for as one progresses in the lineage, a confident assessment of the identities of the sacral elements becomes more difficult, due to the high degree of fusion, as reported by Filippini et al. (2016). In this sense, the recognition that fusion of the neural spines follows a similar pace as the observed in the centra (Figure 5) may help in the identification of the primordial sacral elements, especially in taxa with extensively fused sacral vertebrae.

3.5 | On the taxonomic status of CAPPA/UFSM 0228

Despite the fragmentary condition of the specimen, it preserved character states that allow some degree of low-level taxonomic identification. Particularly, the morphology of the first lateral process, observable in CAPPA/UFSM 0228 is C-shaped in lateral view (character 103, state 1), is widespread among Saurischia, being supported by the analysis as a synapomorphy for the group (see also Langer

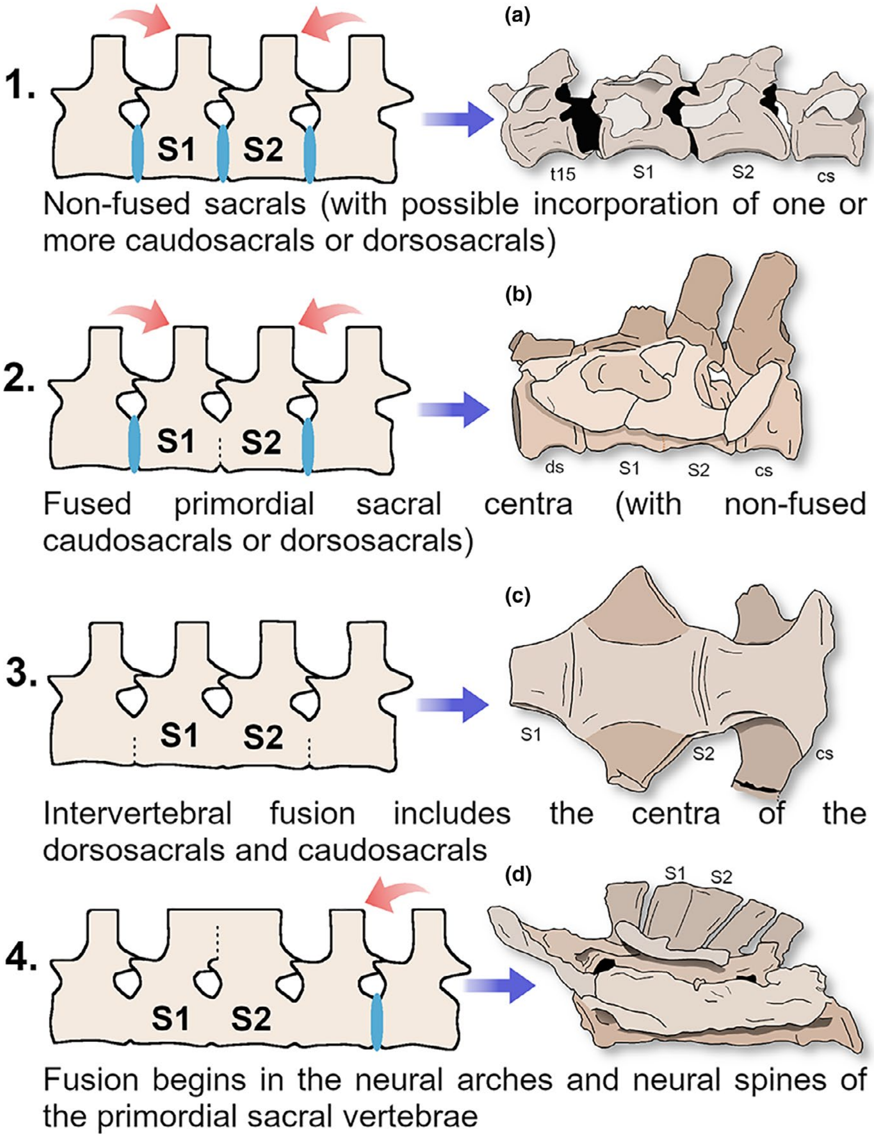

FIGURE 5 Schematics depicting the variation of the sacral fusion patterns along the lineage in Sauropodomorpha. (a) *Bagualosaurus agudoensis* (UFRGS-PV-1099-T). (b) *Melanorosaurus readi* (NMR1551). (c) *Vulcanodon karibaensis* (QG 24). (d) *Brachiosaurus altihorax* (FMNH P 25107 - reversed)

& Benton, 2006). The state of this character in basal Ornithischia is somewhat obscure, due to the lack of specimens that preserve a sacrum free from the ilium, but Nesbitt (2011) pointed out that the articular facet of the first primordial sacral of *Eocursor* and *Lesothosaurus* is circular, similar to that of non-dinosaur dinosauromorphs, such as *Ixalerpeton*, *Lagosuchus*, *Lewisuchus*, and *Silesaurus*, for example (Cabreira et al., 2016; Dzik, 2003; Langer et al., 2011; Nesbitt, 2011). Nesbitt et al. (2019) pointed out that *Asilisaurus kongwe*, considered an early diverging silesaurid, might have a condition similar to Saurischia (with a C-shaped articular facet). Even so, the morphology of the second sacral vertebra is remarkably different from that of CAPPA/UFSM 0228, mainly due to the amplitude of the articular facet with the ilium, which in *Asilisaurus* is restricted to the ventral portion of the sacral rib (Nesbitt et al., 2019). Thus, the shape of the first sacral lateral process confidently supports CAPPA/UFSM 0228 as a saurischian dinosaur.

Our first phylogenetic analysis nested the specimen, within Saurischia, as a member of Theropoda (Figure 3). The only feature preserved in CAPPA/UFSM 0228 that allows such assignation is the sacral fusion at least along the ventral margin of the sacral centra (character 98, state 1). Although such a condition occurs extensively among theropods, it is not exclusive of the clade. Indeed, its distribution is quite wide within Dinosauriformes, with significant variation and many homoplasies, as summarized in the previous section. Nevertheless, the intercentral fusion pattern observed in CAPPA/UFSM 0228 is remarkably similar to that observed in basal Sauropodomorpha (see above), such as *Plateosaurus*, *Massospondylus*, and *Leonerasaurus* (Figures 4 and 5), in which only the vertebral centra of S1 and S2 fuse. The earliest records of sacral fusion in both ornithischians and theropods encompass more vertebrae than just the primordial sacrals, and both groups show fusion of the neural spines early in the lineage, differing from CAPPA/UFSM 0228. Nevertheless, although the fusion pattern observed in the specimen is similar to that observed in Sauropodomorpha, such affiliation is not supported by phylogenetic analysis. It is very likely that the incompleteness of CAPPA/UFSM 0228 artificially affects the topology, similar to the situation faced by Müller et al. (2017). Indeed, a constrained analysis forcing the nesting of CAPPA/UFSM

0228 shows that such topology requires a single extra step (895, versus 894 steps in the unconstrained analysis). This indicates that the assignation of the specimen within Theropoda is weakly supported by the dataset employed in our analysis. Additional analyses (see Supplementary Information) show that the exclusion of the character 98 (char #97 in TNT) deeply affects the positioning of CAPPA/UFSM 0228, but has no significant impact in the topology for other OTUs.

CAPPA/UFSM 0228 was collected at the same stratigraphic level as the sauropodomorph *Buriolestes schultzi*, this being the only dinosaur taxon yet collected at the site. However, *Buriolestes* specimens lack any kind of sacral fusion, like other Carnian sauropodomorphs (see above). Though an assignation of CAPPA/UFSM 0228 to *Buriolestes* is tentative at best, an experimental analysis merging phylogenetic data of both OTUs does not change the placement of *Buriolestes* as a sauropodomorph. Indeed, the MPTs recovered from that analysis have the same number of steps (895) of the first analysis. Therefore, both are equally parsimonious.

In summary, the two most plausible hypotheses for the taxonomic identity CAPPA/UFSM 0228 are: (i) the specimen is a theropod dinosaur, as indicated by the first phylogenetic analysis, but its fusion pattern is unique in the group, resembling the early fusion patterns observed in Sauropodomorpha. This would be one of the earliest theropod records worldwide, but the character state that supports such statement is highly homoplasic and widespread in other close taxa; (ii) the specimen is a sauropodomorph (possibly *Buriolestes*, since it comes from the same strata and the same locality) and its fusion pattern corresponds to that observed in the first sauropodomorphs to exhibit such attribute. Furthermore, according to the second hypothesis, the occurrence of sacral fusion in CAPPA/UFSM 0228 is the oldest recorded for Sauropodomorpha. If CAPPA/UFSM 0228 represents a new specimen of *Buriolestes*, this also implies that the condition in the taxon is variable, because both the holotype and CAPPA/UFSM 0035 (Figure S4) present free sacrals. Regardless of the taxonomic ascription, CAPPA/UFSM 0228 comprises the oldest unequivocal record of fused sacral elements for Dinosauria, indicating that this condition occurred in the early evolution of the clade.

4 | CONCLUSION

Although fragmentary, the new specimen expands the fossil record of dinosaurs from the Candelária Sequence and contributes to the knowledge of Carnian dinosaurs. It also extends the record of sacral fusion to the oldest strata to yield dinosaur fossils. Comparative analysis suggests that sacral fusion followed a pattern, at least in Sauropodomorpha, starting from the primordial centra, followed by fusion of additional sacral centra, and then encompassing zygapophyses and neural spines, again starting in the primordial sacrals and spreading to the additional sacrals. Recognition of a pattern in Theropoda and Ornithischia is still hampered by the lack of early well-preserved and unambiguous representatives of those groups.

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AUTHOR CONTRIBUTIONS

D.M and F.A.P conducted the research. Computed tomography and microtomography data were generated by L.K. The manuscript was written by D.M, F.A.P, R.T.M, and L.K. The figures were prepared by D.M and reviewed by F.A.P, R.T.M, and L.K. All authors approved the submission of this work.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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APPENDIX

Digital models of CAPPA/UFSM 0035

http://morphomuseum.com/Specimenfiles/sendFile/705/578f5a

Digital models of CAPPA/UFSM 0228 http://morphomuseum.com/Specimenfiles/sendFile/706/cf10b8