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A supposed Gondwanan oviraptorosaur from the Albian of Brazil represents the oldest South American megaraptoran

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ABSTRACT

A specimen composed of a partial sacrum articulated to two anterior caudal vertebrae and an ilium (SMNS 58023) from the Lower Cretaceous (Albian) Santana Formation of Brazil was originally described as an oviraptorosaur, but it is here re-interpreted as the oldest megaraptoran of South America. The phylogenetic relationships of SMNS 58023 were tested quantitatively for the first time including it in the two most comprehensive phylogenetic data sets focused on non-maniraptoran theropods —including megaraptorans. The Brazilian specimen was consistently found as a megaraptoran in both analyses because of the presence of sacral centra longer than tall, absence of a median transverse constriction of sacral centra, and the morphology and position of sacral pleurocoels. SMNS 58023 sheds light on a region of the body that is poorly known in megaraptorans and pulls back the temporal range of the clade in South America. This re-interpretation reinforces the absence of oviraptorosaurs in Gondwana.

1. Introduction

The Cretaceous theropod record of South America is mainly restricted to Argentina and Brazil (Novas, 2009). In particular, the Argentinean record of the group is taxonomically diverse, including ceratosaurids, noasaurids, abelisaurids, carcharodontosaurids, basal coelurosaurs, megaraptorans, alvarezsaurids, basal paravians, and birds (e.g., Novas, 2009; Novas et al., 2013; Ezcurra and Novas, 2016). The theropod Brazilian record is less abundant, but considerably diverse though, including abelisaurids, noasaurids, carcharodontosaurids, spinosaurids, megaraptorans, basal coelurosaurs, and birds (e.g., Kellner and Campos, 2002; Novas, 2009; Bittencourt and Langer, 2011; Lindoso et al., 2012; Martinelli et al., 2013; Carvalho et al., 2015; Brusatte et al., 2017).

Most Brazilian theropod nominal species and the best-known specimens come from the Lower Cretaceous Santana Formation in the northeast of the country (i.e., *Irritator challengeri*, *Angaturama limai*, *Santanaraptor placidus*, *Mirischia asymmetrica*; Kellner and Campos, 1996; Martill et al., 1996; Kellner, 1999; Sues et al., 2002; Naish et al., 2004; Carvalho et al., 2015). However, in recent years a more diverse Late Cretaceous theropod assemblage has been described in other geological units of the country, but still known from mostly fragmentary specimens, including abelisaurids (e.g., *Pycnomemosaurus nevesi*; Kellner and Campos, 2002; Delcourt, 2017; Delcourt and Grillo, 2017), spinosaurids (e.g., *Oxalaia quilombensis*; Kellner et al., 2011), probable carcharodontosaurids (Vilas Bôas et al., 1999; Candeiro et al., 2004, 2006), megaraptorans (Méndez et al., 2012; Martinelli et al., 2013; Sales et al., 2017), and possibly noasaurids (Lindoso et al., 2012) and maniraptorans (Elias

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et al., 2004; Bittencourt and Langer, 2011). As part of the Early Cretaceous theropod record, Frey and Martill (1995) described a partial sacrum articulated to two caudal vertebrae and a partial right ilium (SMNS 58023) from the Albian beds of the Santana Formation. This specimen was interpreted tentatively as an indeterminate oviraptorosaur on the basis of the presence of pleurocoels in the sacral vertebral centra (Frey and Martill, 1995). Subsequently, Kellner (1996) considered that the taxonomic assignment of SMNS 58023 should be considered with caution. Makovicky and Sues (1998) criticized more explicitly the identification of SMNS 58023 as a possible oviraptorosaur and considered it doubtful, stating that sacral pleurocoels are present in some other coelurosaurs (e.g., tyrannosauroids, some dromaeosaurids) and that this specimen differs from oviraptorosaurs in the presence of an arched sacrum in lateral view with much expanded intercentral articulations. This view was followed more recently by Novas (2009), who added that the posterior end of the ilium of SMNS 58023 differs from that of oviraptorosaurs in being transversely broader and possessing a notched posterior margin. As a result, although the identification of SMNS 58023 as an oviraptorosaur was criticized by some previous authors, no alternative hypothesis for its affinities has been proposed.

Two other previous reports of Gondwanan oviraptorosaurs were based on an isolated cervical vertebra from the Maastrichtian Lecho Formation of northern Argentina (Frankfurt and Chiappe, 1999) and a possible surangular bone associated to an isolated dorsal vertebra from the Aptian–Albian of southeastern Australia (Currie et al., 1996). The Argentinean specimen was reinterpreted as belonging to an indeterminate abelisauroid or to *Noasaurus leali* (Agnolín and Martinelli, 2007), and the Australian specimens were reinterpreted as an indeterminate theropod (i.e., possible surangular) (Agnolín et al., 2010) and an indeterminate maniraptoran (i.e., vertebra) (Benson et al., 2012a). As a result, the currently most suggestive evidence for the presence of oviraptosaurs in Gondwana is the specimen from the middle Cretaceous Santana Formation of Brazil. Here we revisit the anatomy and phylogenetic relationships of this specimen because of its potential implications for the palaeobiogeography and evolutionary history of Cretaceous theropods.

1.1. *Institutional abbreviations*

IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

MACN-Pv CH: Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Paleovertebrados (Pv), Colección Chubut (CH), Buenos Aires, Argentina.

MPCA-Pv: Museo Provincial “Carlos Ameghino”, Cipolletti, Río Negro, Argentina.

MUCPv: Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina. SMNS: Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany.

2. Geological setting

The Araripe Basin is a worldwide known sedimentary deposit. It is the most extensive intracratonic basin of northeastern Brazil, covering an area of about 9000 km^2 in the Ceará, Pernambuco, and Piauí states (Fig. 1). It is laid upon the Proterozoic basement that corresponds to the Borborema Tectonic Province. The depositional history was mainly related to the reactivation of faults in the basement during the Late Jurassic–Early Cretaceous, when tectonic movements led to the separation between South America and Africa (Maisey, 1991; Assine, 1992, 2007; Valença et al., 2003; Arai, 2006).

SMNS 58023 lacks field data because it was recovered by nonprofessional collectors. However, Frey and Martill (1995) considered the matrix surrounding the specimen as typical of early diagenetic carbonate concretions of the Araripe Basin. Many of these concretions are fossiliferous and often preserve three-dimensional fossils (e.g., Martill, 1988; Maisey, 1991; Fara et al., 2005); some of them even preserve soft tissues (e.g., Martill, 1988; Kellner, 1996; Martill et al., 2000). The beds bearing these concretions crop out mainly in the slopes of the Chapada do Araripe (=Araripe Plateau) and are characterized by greenish shales and some marls and limestones. Different lithostratigraphic terms have been used for these beds (Fig. 1) (Maisey, 1991; Assine, 1992, 2007; Valença et al., 2003; Fara et al., 2005). For instance, Frey and Martill (1995) regarded them as the Romualdo Member of the Santana Formation; whereas Valença et al. (2003) and Fara et al. (2005) considered them as the Romualdo Formation of the Santana Group –for practical purposes we will follow Frey and Martill (1995) in adopting the Romualdo Member terminology. In any case, both the fossil and sedimentary records are consistent with a depositional environment of calm waters with an anoxic to subanoxic bottom (Martill, 1988; Maisey, 1991; Kellner, 1996; Fara et al., 2005). The water body was likely saline, although some fluvial contribution cannot be ruled out, whereas marine settings are inferred for some layers rich in gastropod and echinoid fossils (Assine, 1992, 2007; Valença et al., 2003).

Regarding its fossil record, the Romualdo Member includes mainly fishes and pterosaurs, but plant remains, invertebrates, and other tetrapods have been also collected from this unit (e.g., Maisey, 1991). These faunal elements indicate a likely Albian age for this unit, although other age estimates are also present in the literature (e.g., Maisey, 1991; Valença et al., 2003; Naish et al., 2004). Despite being rare, all non-avian dinosaur specimens from the Araripe Basin have been discovered within the carbonate concretions of the Romualdo Member. Besides SMNS 58023, they include the holotype of the spinosaurids *Irritator challengeri* and *Angaturama limai*, the possible tyrannosauroid *Santanaraptor placidus*, and the possible compsognathid *Mirischia asymmetrica*, together with other postcranial remains of indeterminate theropods (Maisey, 1991; Kellner, 1996, 1999; Kellner and Campos, 1996; Martill et al., 1996, 2000; Naish et al., 2004; Machado and Kellner, 2007, 2008). This non-avian dinosaur assemblage is unusual because consists only of theropods so far (Naish et al., 2004).

3. Materials and methods

3.1. *Phylogenetic analysis*

In order to test the phylogenetic affinities of SMNS 58023, this specimen was included in two independent data matrixes focused on the higher-level phylogenetic relationships of non-maniraptoran averostrans, namely Carrano et al. (2012) and Porfiri et al. (2014) (following the modifications implemented by Apesteguía et al., [2016] in both data matrixes).

Both data matrixes mainly overlap in the sampling of allosauroid theropods, but the matrix of Carrano et al. (2012) includes a broader sample of megalosauroids and that of Porfiri et al. (2014) possesses a broader sample of basal coelurosaurs. The original results of these data matrixes differ in the position recovered for megaraptorans. Carrano et al. (2012) found megaraptorans as allosauroids, whereas Porfiri et al. (2014) obtained them as deeply nested within Tyrannosauroidea. More recently, Apesteguía et al. (2016) found megaraptorans as allosauroids using the modified data set of Carrano et al. (2012) and as non-tyrannosauroid coelurosaurs (sensu Gauthier, 1986) using the modified data set of Porfiri et al. (2014) Here, both data matrixes were enriched with the

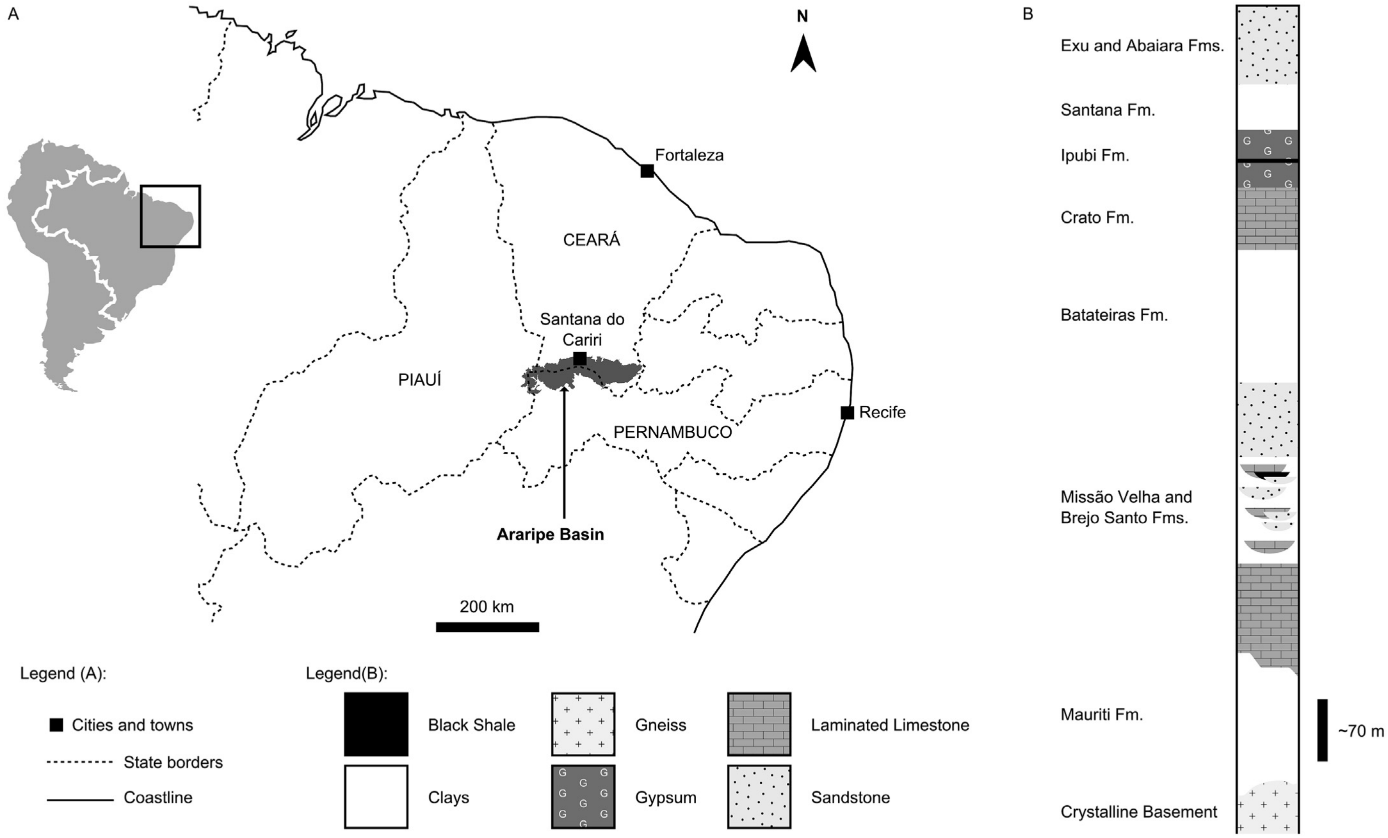

Fig. 1. Geographic location (**A**) and generalized lithological log (**B**) of the Araripe Basin, northeastern Brazil. The concretion-bearing Romualdo Member is part of the Santana Formation after the stratigraphic proposal adopted by Frey and Martill (1995) and Martill et al. (2007). The map and lithological log are modified from Bittencourt and Langer (2011) and Martill et al. (2007), respectively. Abbreviation: **Fm(s)**; Formation(s).

addition of four sacral characters (sacral centra with arched or straight ventral margin in lateral view [Ch. 289:0–1; see SI]; sacral centra longer than tall or taller than long [Ch. 290: 0–1; see SI]; sacral neural spines straight or posteriorly curved [Ch. 291: 0–1; see SI]; and sacral neural spines exceeding the height or at the same level as the iliac blade in lateral view [Ch. 292: 0–1; see SI]). In addition, several scourings of the data matrix originally published by Porfiri et al. (2014) and Carrano et al. (2012) were modified based on new information (see Supplementary Information).

The modified versions of both data matrixes were analysed here under equally-weighted parsimony using TNT 1.5 (Goloboff et al., 2008; Goloboff and Catalano, 2016). In both cases, a heuristic search of 100 replications of Wagner trees followed by TBR branch-swapping algorithm (holding 10 trees per replication) was performed. The best trees obtained at the end of the replications were subjected to a final round of TBR branch swapping. Branches with a maximum possible length of zero among any of the recovered most parsimonious trees were collapsed (rule 3 of Swofford and Begle, 1993; Coddington and Scharff, 1994). Characters 2, 4, 6,13,15,17, 27, 69, 106, 148, 155, 158, 160, 167, 169, 171, 179, 181, 194, 195, 205, 208, 217, 233, 241, 259, 267, 271 were treated as additive (=ordered) for the data matrix of Porfiri et al. (2014) and no additive characters were considered for the data matrix of Carrano et al. (2012), following the original settings of these authors. As a measure of branch support, decay indices (= Bremer support) were calculated (Bremer, 1988, 1994), and as a measure of branch stability, a bootstrap resampling analysis (Felsenstein, 1985) was conducted, performing 10,000 pseudoreplications. Both absolute and GC (i.e., difference between the frequency whereby the original group and the most frequent contradictory group are recovered in the pseudoreplications; Goloboff et al., 2003) bootstrap frequencies are reported. Following the original protocol of Porfiri et al. (2014), a second round of decay indices was calculated for this data matrix after the a posteriori pruning of the fragmentary taxa *Carcharodontosaurus iguidensis*, *Orkoraptor*, *Eotyrannus*, *Chilantaisaurus*, *Kileskus*, and *Santanaraptor*.

4. Systematic palaeontology

Theropoda Marsh, 1881
Tetanurae Gauthier, 1986
Avetheropoda Paul, 1988
Megaraptora Benson et al., 2010

Gen. et sp. indet.

Material. SMNS 58023, last three sacral vertebrae and ribs, two caudal vertebrae, and postacetabular process of the right ilium.
Locality and horizon. Unknown locality, Romualdo Member (Albian) of the Santana Formation, Araripe Basin, northeastern Brazil (Frey and Martill, 1995).

5. Results

5.1. Redescription

5.1.1. Sacral vertebrae

The preserved portion of the sacrum of SMNS 58023 is composed of the last three vertebrae and ribs (Figs. 2–4). The postacetabular process of the ilium is apparently attached to the last two sacral vertebrae (see below), a condition broadly distributed among theropods with five to seven sacral vertebrae (e.g., *Carnotaurus*: Bonaparte et al., 1990; *Tyrannosaurus*: Brochu, 2003; *Shixinggia*: Lü and Zhang, 2005).

The most anteriorly preserved vertebra lacks its anterior region and the broken surface exposes a camellate internal structure (Figs. 2, 3), as in the vertebrae of ceratosaurs, carcharodontosaurids, megaraptorans, and several coelurosaurs (Benson et al., 2010, 2012b). The neural canal is suboval in cross-section where the vertebra is broken off, with a transverse main axis and a more concave dorsal margin than the ventral one. This broken surface also exposes the cross-section of a right zygapophysis, which is interpreted as a postzygapophysis because it possesses a ventrally slanting lateral margin and is placed high in the neural arch, immediately ventral to the base of the neural spine. The postzygapophysis is laterally developed well beyond the level of the centrum.

The right side of the neural arch and dorsal portion of the centrum of the preserved sacral vertebrae are covered by the partial ilium, whereas the left side of these elements is well exposed (Frey and Martill, 1995). The preserved anterior and posterior rims of the sacral centra project ventrally at approximately the same level and the ventral margin of the centra are strongly concave in lateral view, resembling the condition in several other theropods (e.g. *Allosaurus*: Madsen, 1976; *Neovenator*: Brusatte et al., 2008; *Tyrannotitan*: Canale et al., 2015; *Acrocanthosaurus*: Harris, 1998; *Tyrannosaurus*: Brochu, 2003; *Guanlong*: IVPP V14531; Fig. 6). By contrast, the preserved sacral centra of *Megaraptor* are less ventrally concave (MUCPv 595; Fig. 5) and the sacrum of oviraptorosaurs is more dorsally arched and possesses less ventrally concave centra in lateral view (e.g., *Chirostenotes*: Currie and Russell, 1988). The sacral centra of SMNS 58023 are anteroposteriorly longer than tall and more than two times lower than their respective neural arch in lateral view, resembling the condition in the posterior sacral vertebrae of several theropods (e.g., *Carnotaurus*: MACN-Pv CH 894; *Megalosaurus*: Benson, 2010; *Acrocanthosaurus*: Harris, 1998; *Megaraptor*: MUCPv 595;

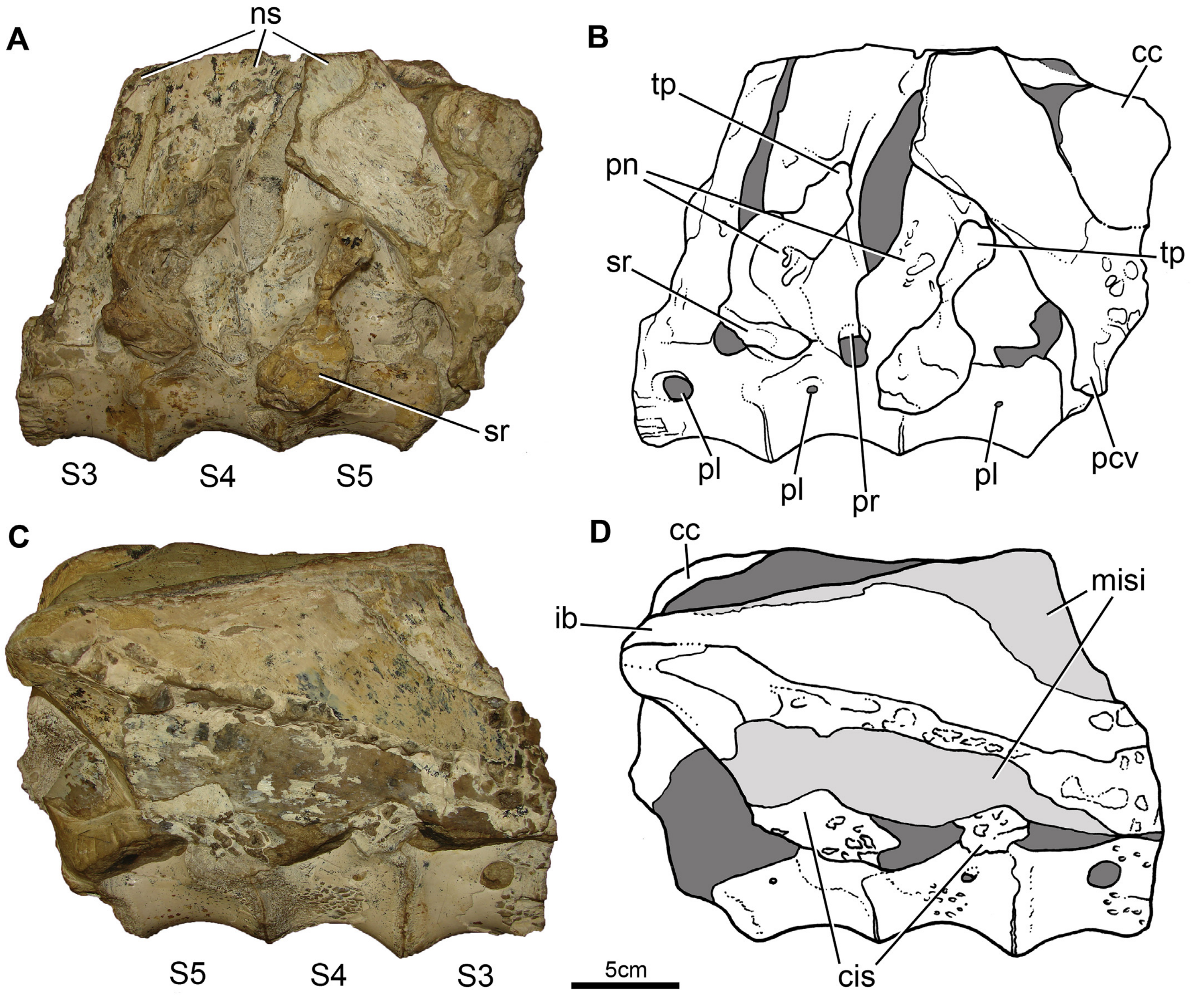

Fig. 2. Specimen SMNS 58023 in left (A, B) and right (C, D) lateral views. Dark grey areas represent matrix and light grey areas are broken surfaces. Abbreviations: cc, caudal centrum; cis, camellate internal structure; ib, iliac blade; misi, mould of the inner surface of the ilium; ns, neural spine; pcv, partial caudal vertebra; pl, pleurocoel; pn, pneumatophore; post, postzygapophysis; sr, sacral rib; tp, transverse process; S3, third sacral; S4, fourth sacral; S5, fifth sacral.

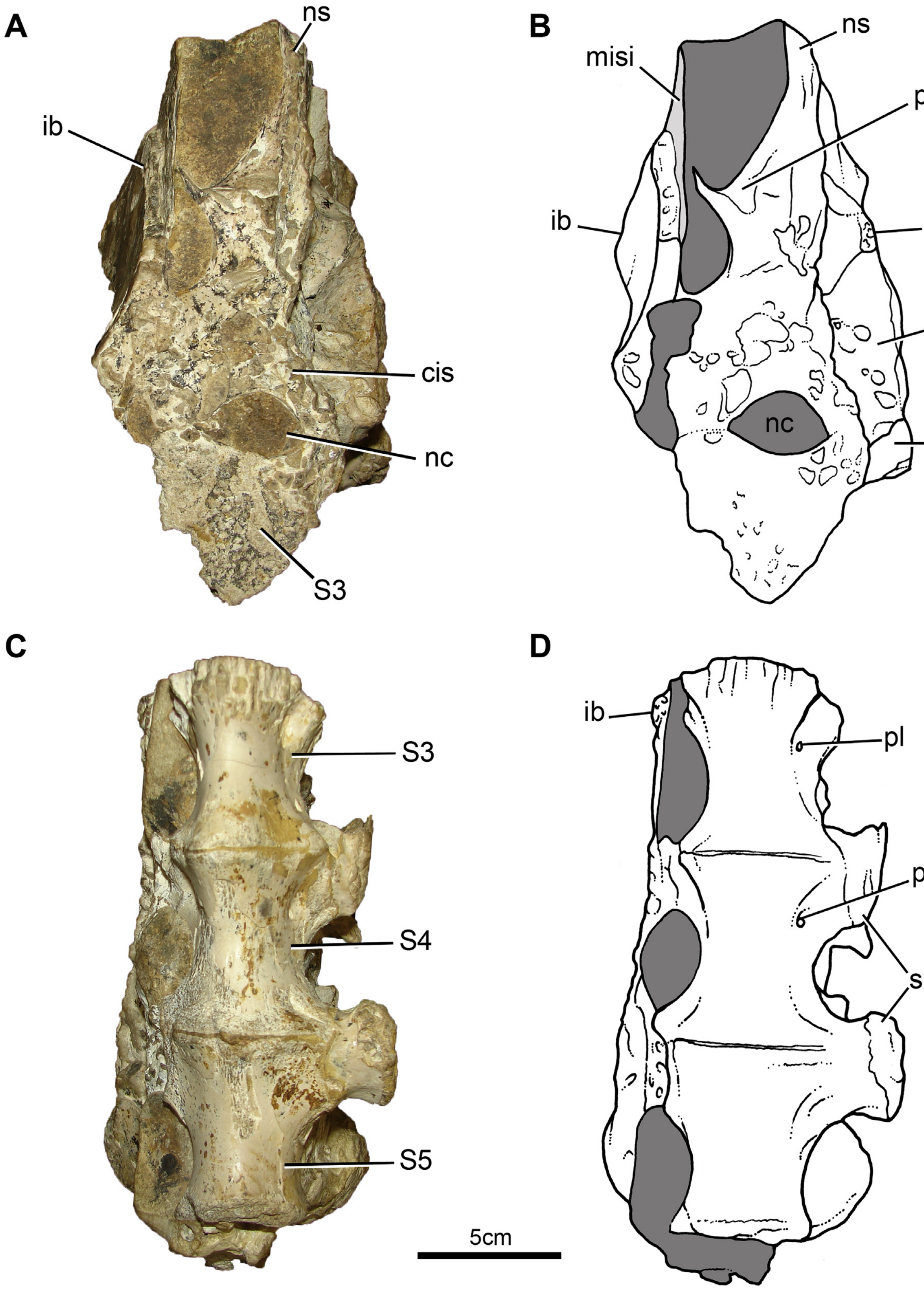

Fig. 3. Specimen SMNS 58023 in anterior (A, B) and ventral (C, D) views. Dark grey areas represent matrix and light grey areas are broken surfaces. Abbreviations: 3sr, third sacral rib; 4sr, fourth sacral rib; cis, camellate internal structure; ib, iliac blade; nc, neural canal; ns, neural spine; misi, mould of the inner surface of the ilium; pl, pleurocoel; pn, pneumatophore; poz, postzygapophysis; sr, sacral rib; tp, transverse process; S3, third sacral vertebra; S4, fourth sacral vertebra; S5, fifth sacral vertebra.

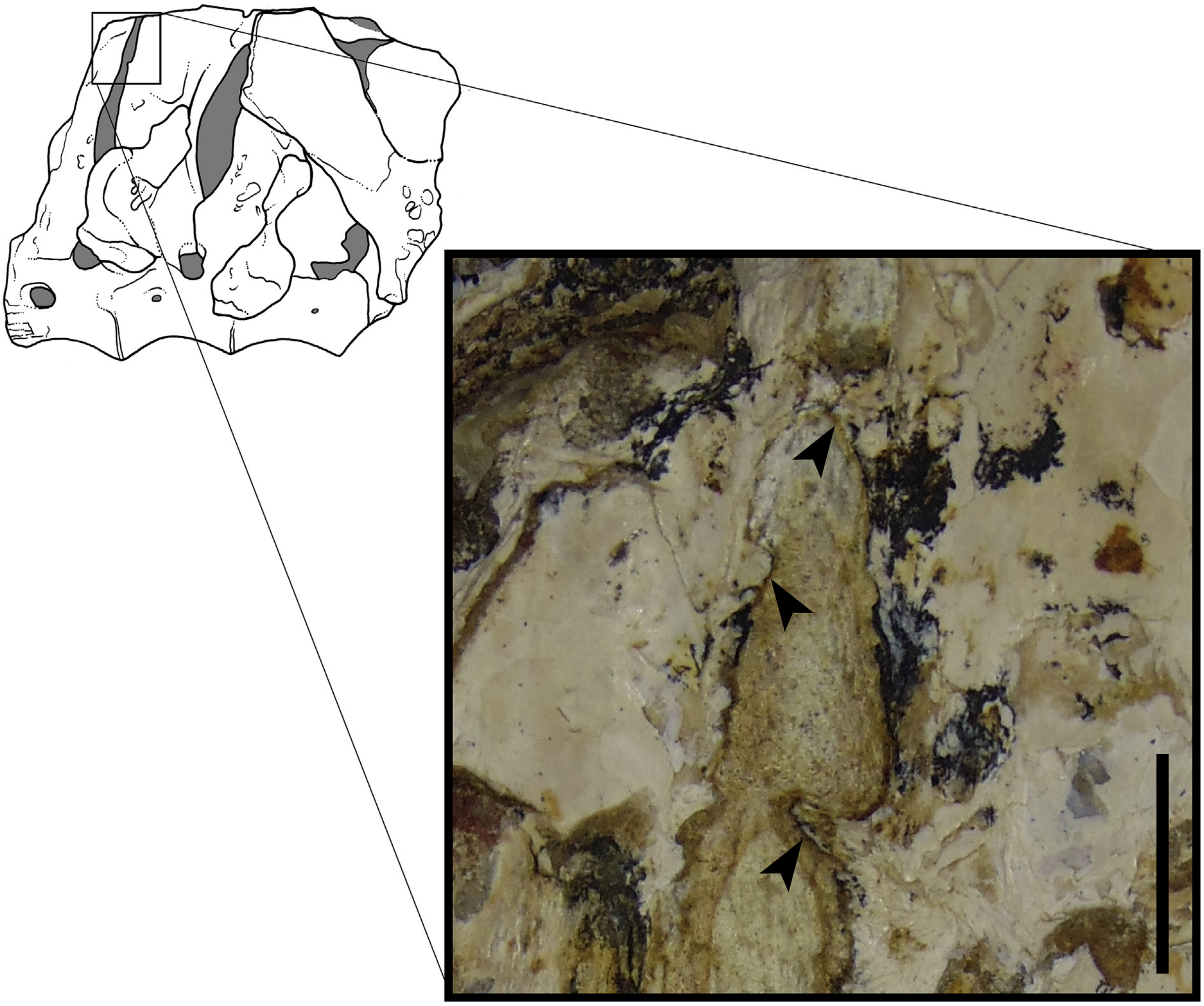

Fig. 4. Close-up of Fig. 2A showing the most distal projections (black arrows) of the posterior and anterior margins of the neural spines of the third and fourth sacral vertebrae of SMNS 58023. Scale bar equals 10 mm.

Tyrannosaurus: Brochu, 2003). Conversely, proportionally lower sacral neural arches in comparison to their respective centrum occur in oviraptorosaurs (e.g., *Chirostenotes*: Currie and Russell, 1988; *Nomingia*: Barsbold et al., 2000) and *Mirischia* (Martill et al., 2000; Naish et al., 2004). The ventral surface of the sacral centra is transversely convex and without a longitudinal keel contrasting with the condition, in at least, some oviraptorosaurs, in which there is a pair of longitudinal ridges on the ventral surface of the sacral centra (e.g., *Chirostenotes*: Currie and Russell, 1988; Osmólska et al., 2004). Each sacral centrum is strongly transversely compressed at mid-length, acquiring a spool-shape in ventral view. The most anteriorly preserved centrum is not distinctly narrower than the posterior ones, thus differing from the rod-like middle sacrals of ceratosaurs (Rauhut, 2003), or the laterally compressed middle sacral vertebrae of derived carcharodontosaurids (Canale et al., 2015).

The lateral surface of each centrum is pierced by a single pleurocoel. In the most anteriorly preserved sacral vertebra the pleurocoel is large and subcircular. The size of the pleurocoel reduces gradually and the opening becomes more dorsoventrally lower towards the caudal series. The presence of sacral pleurocoels has been reported in several theropod clades, such as carcharodontosaurids, oviraptorosaurs, ornithomimosaurs, tyrannosaurids, and megaraptorans (Harris, 1998; Brochu, 2003; Rauhut, 2003; Coria and Currie, 2006; Benson et al., 2012b; Porfiri et al., 2014; Canale et al., 2015; Motta et al., 2016; Coria and Currie, 2016; Fig. 6). The intervertebral foramina are large and subcircular in lateral view and their position indicate that the neural arches overlap half of the centrum of its preceding vertebra, as in other theropods (e.g., *Majungasaurus*: O'Connor, 2007; *Megalosaurus*: Benson, 2010). The lateral surface of the neural arches possesses several foramina of variable size and contour, anterior and posterior to the base of the transverse process (Frey and Martill, 1995). These pneumatic foramina are subdivided by thin laminae in the two most posterior sacral vertebrae.

The posterior third of the neural spine is preserved in the most anterior preserved sacral vertebra, whereas the last two sacral vertebrae have nearly complete neural spines, but only the left side of the spine of the penultimate sacral vertebra is completely exposed. The left side of the neural spine of the last sacral is extensively covered by the displaced neural spine of the first caudal vertebra. In general, the neural spines are very tall (approximately half the total height of the vertebra) and posteriorly bowed in lateral view. The base of the neural spine of, at least, the penultimate sacral vertebra is slightly anteriorly oriented in lateral view. The orientation of the base of the neural spine of the other sacral vertebrae cannot be determined because they are broken or overlapped by the partial caudal centrum and the isolated caudal neural spine. The distal half of the neural spines is anteroposteriorly expanded, in which the posterior margin is more curved than the

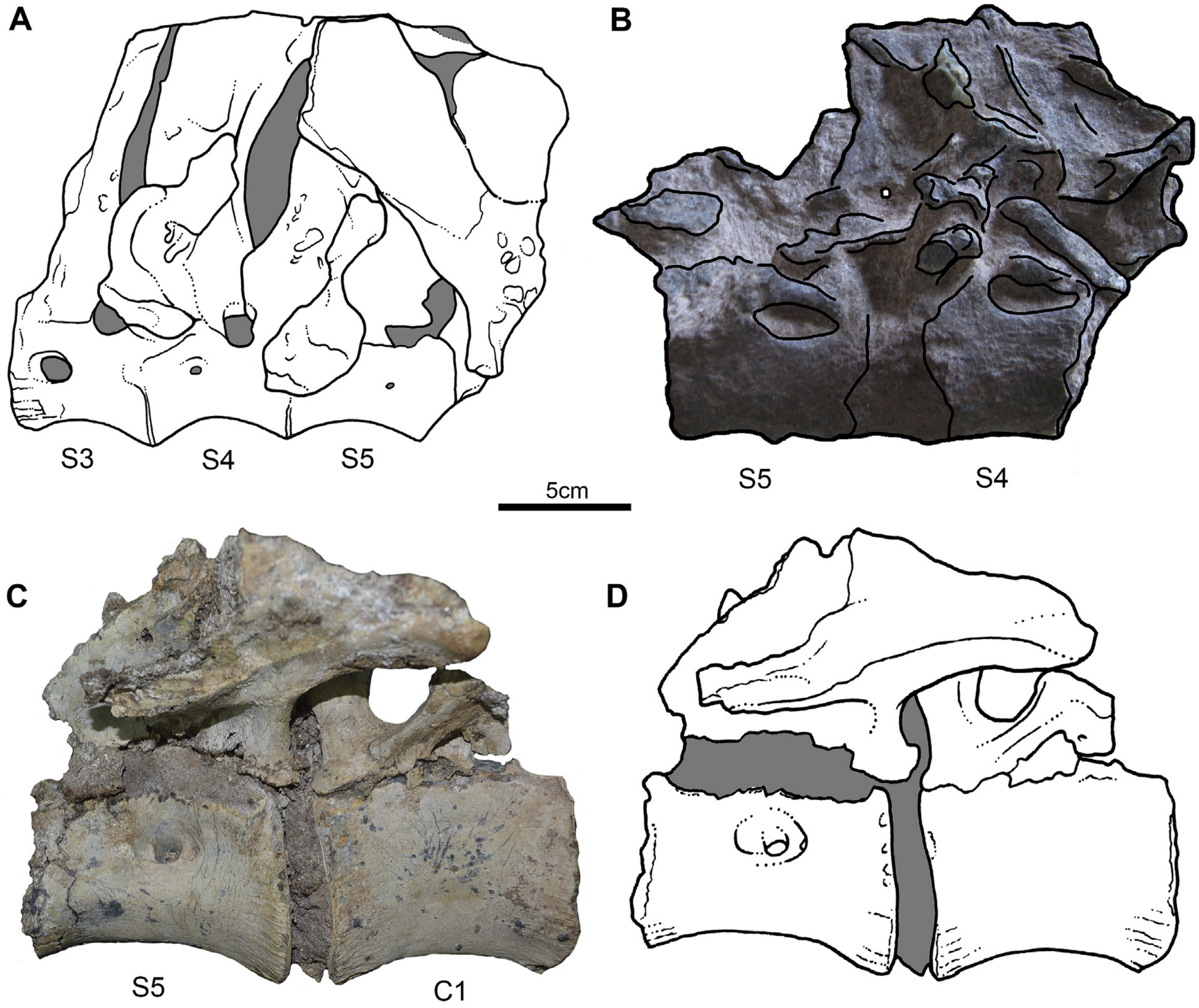

Fig. 5. Comparison of megaraptoran sacral regions in lateral view. SMNS 58023(A). Juvenile specimen of *Megaraptor namunhuaiquii* (MUCPv 595; reversed) (B). *Aoniraptor libertatem* (MPCA-Pv 804) (C, D). Abbreviations: C1, first caudal vertebra; S3, third sacral vertebra; S4, fourth sacral vertebra; S5, fifth sacral vertebra.

anterior one in lateral view. The presence of posteriorly curved and distally anteroposteriorly expanded posterior sacral neural spines also occur in tyrannosaurids (e.g., *Tyrannosaurus*: Brochu, 2003), but contrasts with the absence of such expansion in oviraptorosaurs. None of the sacral neural spines shows any trace of pneumatization. The posterior margin of the neural spines of the first two sacral vertebrae and the anterior margin of the last two sacral vertebrae possess thorn-like, horizontally to obliquely oriented projections (Fig. 4). These projections were called by Frey and Martill (1995) as protuberancia interspinalis, which were considered as comparable to those in dorsal vertebrae of dromaeosaurids and allosauroids (Gilmore, 1920; Stovall and Langston, 1950; Ostrom, 1969). However, the condition in SMNS 58023 more closely resembles that of compsognathids (Peyer, 2006). In large theropods these projections might indeed correspond to metaplasia of interspinous tissues, but in compsognathids and likely SMNS 58023 they seem to be part of the osseous neural spines themselves (Wilson et al., 2016). Although these projections decreased the interspinal space and might have helped to stiffen the column (Wilson et al., 2016), there is no evidence that they represent an early ontogenetic stage of fusion between consecutive neural spines.

The base of the sacral ribs is dorsoventrally elongated and articulates with transverse processes shared by two consecutive vertebrae. The transverse processes extend along the dorsal and ventral halves of the centra and neural arches, respectively. The sacral rib of the penultimate sacral is C-shaped in lateral view, and the last sacral rib is 8-shaped, with an anteroposterior constriction close to its mid-height and a dorsoventrally taller and anteroposteriorly broader ventral portion.

5.1.2. *Caudal vertebrae*

The tail is represented by a partial neural arch of the probable first caudal vertebra and the centrum of an anterior caudal vertebra. The neural spine of the probable first caudal vertebra expands gradually anteroposteriorly towards its tip and curves slightly posteriorly, resembling the condition in the sacral vertebrae. The most distal tip of the spine is broken off. There is no trace of pneumatization on the neural spine, as in the sacral spines. Only the roof of the neural canal is preserved. The broken surfaces of the neural canal show a highly pneumatized, camellate internal structure. The anterior caudal centrum is mostly covered by matrix and, as a consequence, is not very informative. No pneumatic features are observed in this vertebra.

5.1.3. *Ilium*

The partial postacetabular process of the ilium is preserved on the right side of the block, apparently in natural position with the

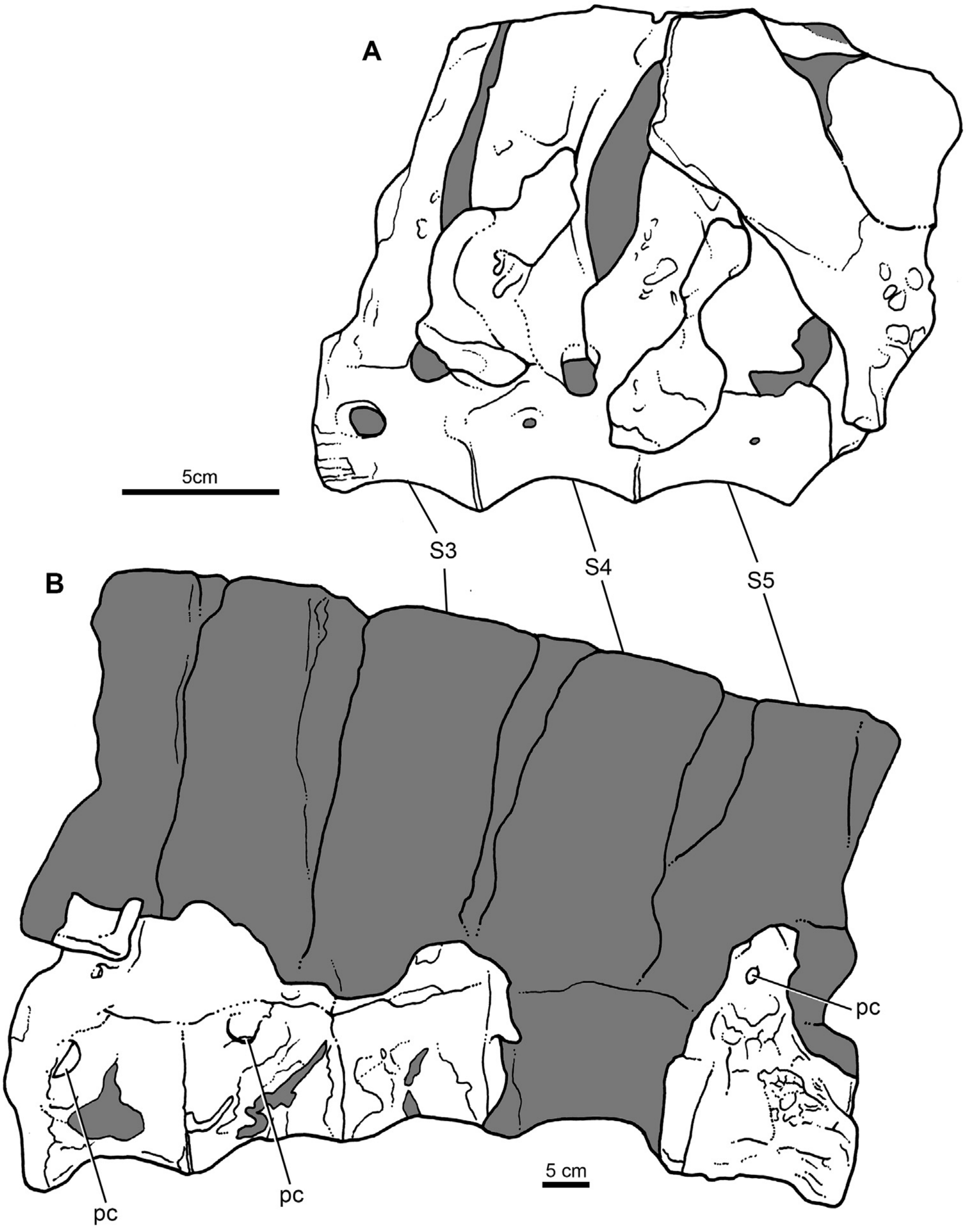

Fig. 6. Comparison of the sacrum of SMNS 58023 (A) and the carcharodontosaurid *Tyrannotitan chubutensis* (B) in left lateral views. Dark grey areas are matrix and reconstructed regions. Abbreviations: pl, pleurocoel; S3, third sacral vertebra; S4, fourth sacral vertebra; S5, fifth sacral vertebra. (B) Redrawn from Canale et al. (2015) and the posterior portion corresponds to the right side reversed for a better understanding of the figure.

sacral vertebrae. The ventral extension of the most anteriorly preserved portion of the ilium below the level of the neurocentral suture of the sacral vertebrae indicates that this broken area should have been very close to or at the postacetabular process-ischiadic peduncle transition. The postacetabular process is severely damaged and, as a result, its overall shape remains unknown. The brevis fossa is exposed in lateral view because the lateroventral portion of the postacetabular process, including the brevis shelf, is broken off. A noteworthy feature of the ilium is the camellate internal structure exposed in most of its broken surfaces. The presence of an extensively pneumatized ilium has been also reported in the megaraptorans *Aerosteon* (Sereno et al., 2008) and *Murusraptor* (Coria and Currie, 2016), the carcharodontosaurid *Mapusaurus* (Coria and Currie, 2006; Bell and Coria, 2013; but see Sereno et al., 2008), an indeterminate abelisaurid from the Upper Cretaceous of Brazil (Brum et al., 2016), and the basal allosauroid *Neovenator* (Brusatte et al., 2008). In other theropods, including oviraptorosaurs, the ilium is apneumatic (Sereno et al., 2008; Benson et al., 2012b).

5.2. Results of the phylogenetic analysis

SMNS 58023 was recovered as a megaraptoran tetanuran in both data matrixes. Megaraptorans are found as basal coelurosaurs in the modified data set of Porfiri et al. (2014) and as carcharodontosaurian allosauroids in the modified data set of Carrano et al. (2012), in agreement with the results recovered in the original analyses of these authors. The analysis of the modified data matrix of Porfiri et al. (2014) found 44 most parsimonious trees (MPTs) of 977 steps, with a consistency index (CI) of 0.3623 and a retention index (RI) of 0.6547, and the best score hit 26 times out of the 100 replications. The topology of the strict consensus tree (SCT) generated from these MPTs is consistent with that recovered by Apesteguía et al. (2016), including a paraphyletic Allosauroidea (carcharodontosaurids are more closely related to coelurosaurs than to *Allosaurus*, *Sinraptor*, and *Monolophosaurus*), and *Neovenator*, *Chilantaisaurus* + *Gualicho*, megaraptorans, and tyrannosauroids as the successive most basal members of Coelurosauria (sensu Gauthier, 1986) (Fig. 7). *Eotyrannus* was not recovered as a megaraptoran, but as a tyrannosauroid (cf. Apesteguía et al., 2016). It should be noted that the position of megaraptorans close to the base of Coelurosauria, being more basal than tyrannosauroids, is similar to the result found by one of the phylogenetic analyses conducted by Novas et al. (2015). SMNS 58023 was recovered in a polytomy with other megaraptorans, namely *Megaraptor*, *Fuikuiraptor*, *Orkoraptor*, *Aerosteon*, and *Australovenator*. The position of the Brazilian specimen as a megaraptoran is supported by the following three synapomorphies: sacral vertebrae with pleurocoels (character 109: 0 → 1), sacrum without ventral keel(s) (character 214: 0 → 1), and ilium with large external foramina and internal pneumatic spaces (character 245: 0 → 1). The Bremer support of Megaraptora is minimal and the absolute and GC bootstrap frequencies are of 35% and 24%, respectively. The lack of resolution within Megaraptora is because SMNS 58023 can acquire all possible positions within the clade. After the a posteriori pruning of SMNS 58023 from the SCT, *Fukuiraptor* is recovered as the sister-taxon of an unresolved Megaraptoridae composed of *Megaraptor*, *Orkoraptor*, *Aerosteon*, and *Australovenator*. Under topologically constrained searches, two additional steps are necessary to force the position of SMNS 58023 as a coelurosaur more derived than megaraptorans (e.g., sister-taxon of *Caudipteryx*, *Compsognathus*, or coelurosaurs more derived than compsognathids), three extra steps to find it as the sister taxon of *Neovenator* (at the base of Coelurosauria), and four additional steps to find it within Carcharodontosauridae.

The analysis of the modified data matrix of Carrano et al. (2012) found 13,365 MPTs of 1126 steps, with a CI of 0.3925 and a RI of 0.6744, and the best score hit 35 times out of the 100 replications. The topology of the SCT generated from these MPTs is congruent with that recovered by Carrano et al. (2012) and Apesteguía et al. (2016) (Fig. 8). Megaraptorans, *Neovenator*, and the clade that includes *Gualicho* and *Deltadromaeus* are recovered within the massive polytomy that includes species usually considered as

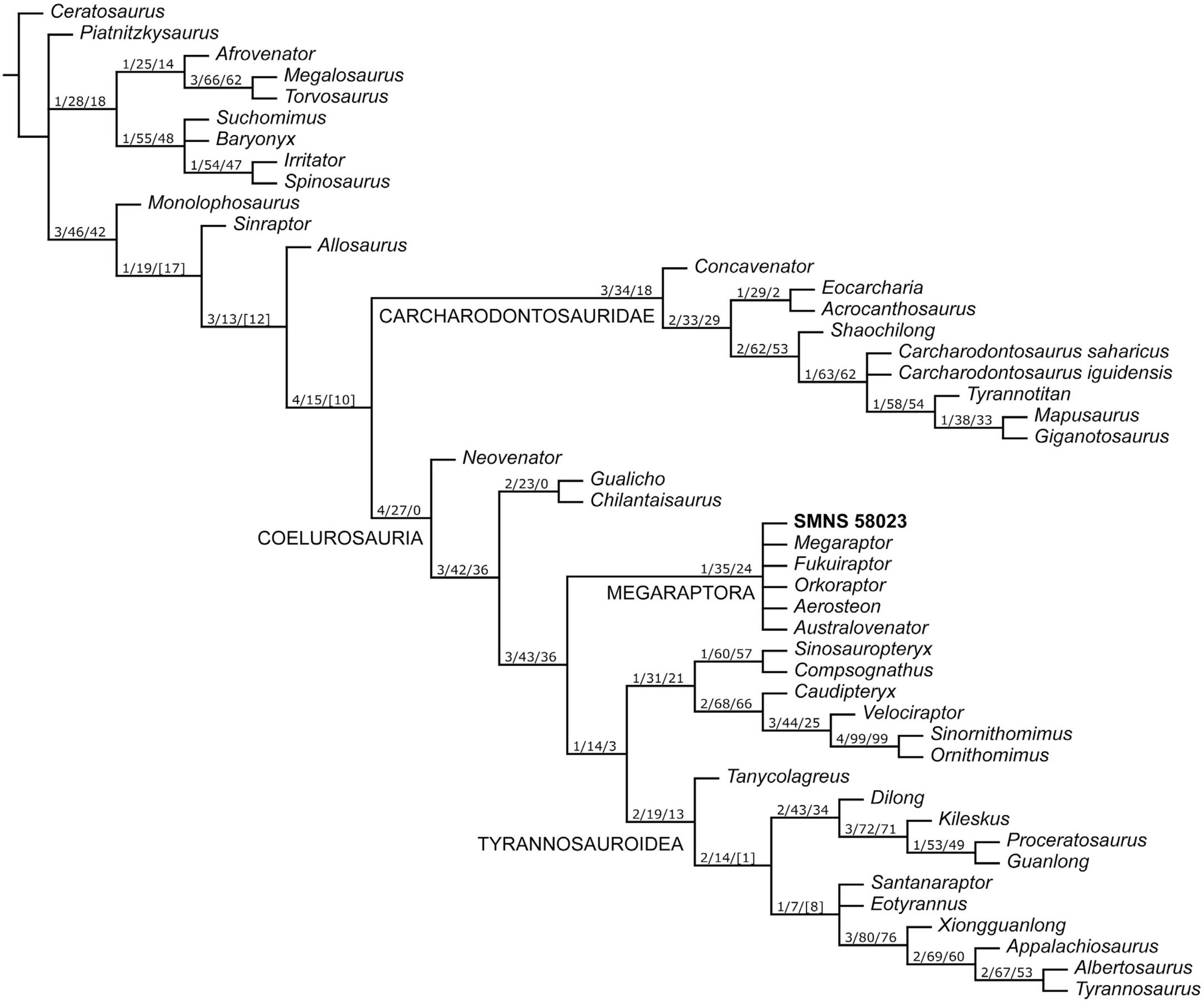

Fig. 7. Strict consensus tree generated from the 44 MPTs recovered after the modified dataset of Porfiri et al. (2014). The values above each node represent Bremer values (left) and bootstrap absolute (centre) and GC (right) frequencies, respectively. Negative values are between brackets.

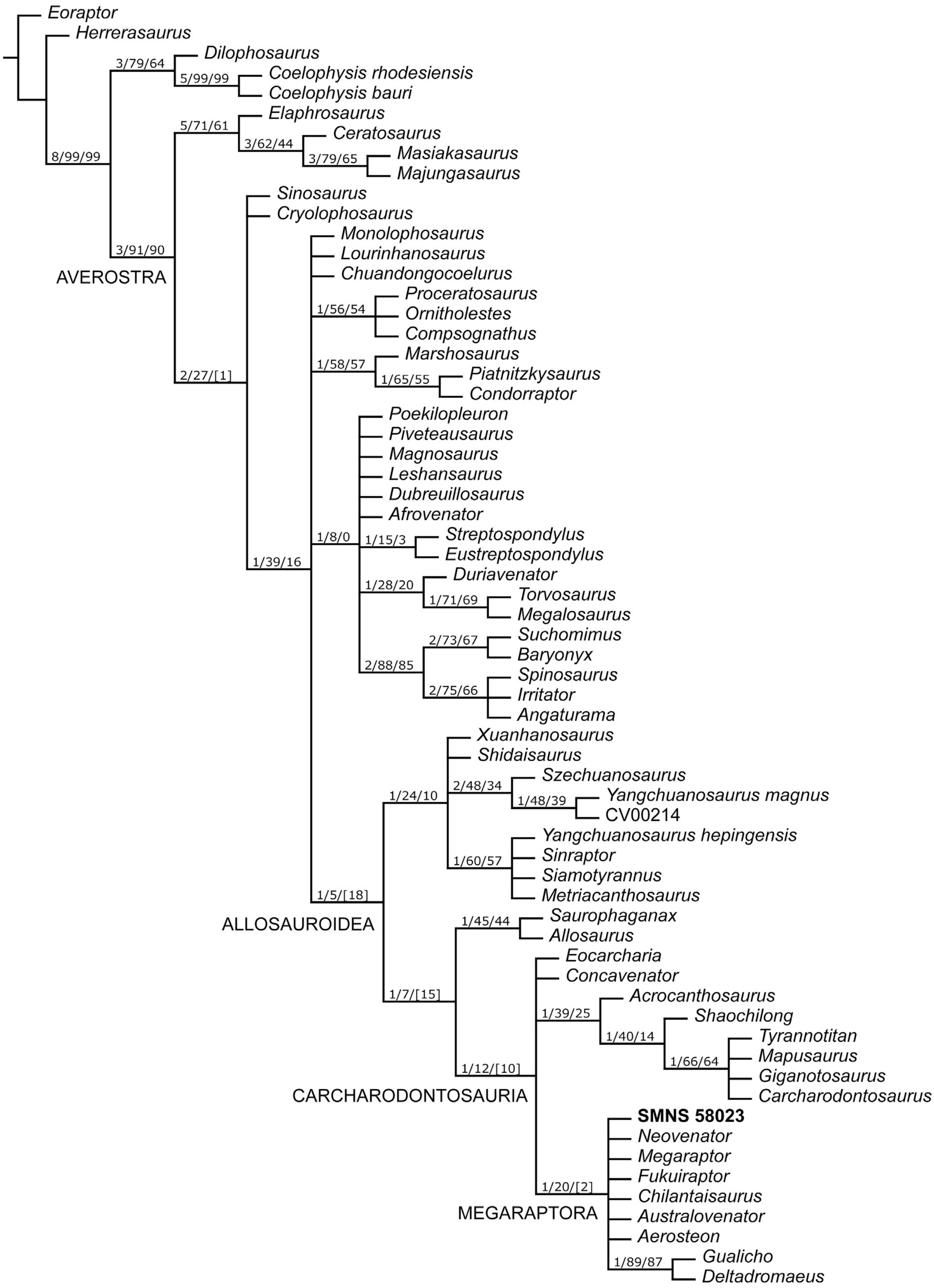

Fig. 8. Strict consensus tree generated from the 13,365 MPTs recovered after the modified data set of Carrano et al. (2012). The values above each node represent Bremer values (left) and bootstrap absolute (centre) and GC (right) frequencies, respectively. Negative values are between brackets.

carcharodontosaurid allosauroids (e.g., *Eocarcharia*, *Carcharodontosaurus*, *Giganotosaurus*). This polytomy is a result of the alternative positions that *Eocarcharia* can acquire within or outside Carcharodontosauridae. The positions of the Brazilian specimen as a megaraptoran in this dataset is supported by the presence of sacral vertebral centra with pneumatic foramina (character 196: 1 → 2). The Bremer support of Carcharodontosauria (= Megaraptora + Carcharodontosauridae; sensu Benson et al., 2010) is minimal and the absolute and GC bootstrap frequencies are of 12% and −10%, respectively. Two additional steps are necessary to force the position of SMNS 58023 as a ceratosaur, a carcharodontosaurid, or a coelurosaur under topologically constrained searches (setting *Eocarcharia*, *Gualicho*, and *Deltadromeus* as floating taxa). Three additional steps allow the placement of SMNS 58023 as the sister-taxon of Carcharodontosauria (with the same combination of floating taxa as above).

6. Concluding remarks

Frey and Martill (1995) assigned, with doubts, SMNS 58023 to Oviraptorosauria on the basis of the presence of pleurocoels in the sacral centra. However, discoveries conducted in the last twenty years have shown that this feature is more widely distributed among theropods and homoplastic than previous thought (e.g., Benson et al., 2010; Novas et al., 2013). By contrast, we found in SMNS 58023 a series of character-states that are not present in oviraptorosaurs and are listed as follows: 1) sacral centra with concave ventral margin in lateral view, whereas the ventral surface of the sacrum is flat in oviraptorosaurs (e.g., *Chirostenotes*, *Microvenator*, *Nomingia*: Currie and Russell, 1988; Makovicky and Sues, 1998; Barsbold et al., 2000). 2) Absence of a pair of ventral longitudinal ridges, which is present in the sacral centra of some oviraptorosaurs (Currie and Russell, 1988; Osmólska et al., 2004). 3) Anteroposteriorly expanded sacral neural spines, which are subrectangular in lateral view in oviraptorosaurs (Currie and Russell, 1988). 4) Posterior margin of sacral neural spines concave and only contacting adjacent neural spines at its distal tip, whereas the posterior margin of the neural spines is straight and contacts the adjacent neural spine through all its length in oviraptorosaurs (Currie and Russell, 1988; Barsbold et al., 2000; Osmólska et al., 2004). 5) Neural arch at least two times higher than its respective centrum, a ratio that is greater than that present in oviraptorosaurs (Currie and Russell, 1988). Finally, 6) a pneumatic ilium, which is a feature absent in all oviraptorosaurs (Sereno et al., 2008). As a consequence, the character-states described above strongly weaken the supposed oviraptorosaur affinities of SMNS 58023.

Among the features listed above, the presence of a pneumatized ilium is a rare character-state among theropod dinosaurs. A highly pneumatized ilium was recovered by Benson et al. (2010) as a synapomorphy of Neovenatoridae, being present in *Neovenator* (Brusatte et al., 2008) and *Aerosteon* (Sereno et al., 2008). In addition, a pneumatic ilium has been also described in the derived carcharodontosaurid *Mapusaurus* (Coria and Currie, 2006; Bell and Coria, 2013). Sereno et al. (2008) stated that the presence of a pneumatized ilium cannot be determined in *Mapusaurus* based on available information and noted that is striking that the passage of the pneumatic diverticulae labelled by Coria and Currie (2006: fig. 26b) is placed on the origin area of the *M. caudofemoralis brevis*. Nevertheless, Bell and Coria (2013) bolstered the original interpretation of Coria and Currie (2006), stating that the ilium of *Mapusaurus* was highly pneumatic. The foramina that occur on the anterior portion of the ventrally facing surface of the brevis fossa of *Mapusaurus* are in a very similar position to the openings placed on the brevis fossa of *Aerosteon*, which were interpreted as the passage of pneumatic diverticulae by Sereno et al. (2008). Thus, we interpret that the openings in *Mapusaurus* should have been also pneumatic in origin, in agreement with Coria and Currie (2006). The presence of a pneumatic ilium is optimized as an apomorphy of Megaraptora in the modified data matrix of Porfiri et al. (2014), whereas the optimization of this character-state is ambiguous at the base of Carcharodontosauria in the modified data set of Carrano et al. (2012).

As discussed above, the South American carcharodontosaurid *Mapusaurus* probably has a pneumatic ilium (but see Sereno et al., 2008) and the preserved sacral centrum possesses a large, anteriorly displaced pleurocoel, as occurs in SMNS 58023. The preserved last sacral centrum of *Mapusaurus* and *Tyrannotitan* are proportionally taller than those of SMNS 58023 (Fig. 6). SMNS 58023 differs from carcharodontosaurids (e.g. *Tyrannotitan* and *Giganotosaurus*; Canale et al., 2015) in the presence of poorly transversely compressed sacral centra in ventral view.

Among megaraptorans, SMNS 58023 resembles *Aerosteon* and *Murusraptor* in the presence of a highly pneumatic ilium, but the latter apparently differ from the former in the presence of a pleurofossa in sacral centra without pleurocoels (following the scourings of Carrano et al., [2012], Coria and Currie, [2016]). By contrast, *Megaraptor* and the supposed basal megaraptoran *Aoniraptor* do have pneumatic openings in the preserved sacral centra (Porfiri et al., 2014; Motta et al., 2016), as occurs in the Brazilian specimen. It should be noted that the pleurocoels of *Aoniraptor* are anteroposteriorly centred in the sacral centrum (MPCA-Pv 804), contrasting with the anteriorly displaced pneumatic openings of SMNS 58023 and *Megaraptor* (MUCPv 595).

In sum, the morphology of SMNS 58023 has a phylogenetic signal that favours its affinities with either derived carcharodontosaurids or megaraptorans. However, we conclude that the phylogenetic position of SMSN 58023 can be constrained as a megaraptoran, because of the proportions of the sacral centra, the absence of a median transverse constriction, and the morphology and position of the pleurocoels. A better knowledge of the anatomy of the sacrum of derived carcharodontosaurids and megaraptorans seems to be necessary to bring more support to the conclusion of this work.

The exclusion of SMNS 58023 from Oviraptorosauria enriches the list of purported Gondwanan oviraptorosaur records (Frey and Martill, 1995; Currie et al., 1996; Frankfurt and Chiappe, 1999) that have been refuted (Agnolín and Martinelli, 2007; Agnolín et al., 2010). As a result, oviraptorosaurs are currently restricted to North America and Asia (Osmólska et al., 2004; Ezcurra and Agnolín, 2012), thus reinforcing the biogeographical dichotomy between Asiamerica and Gondwanan landmasses (Bonaparte and Kielan-Jaworowska, 1987). In addition, the geographic restriction of oviraptorosaurs to Asiamerica is in agreement with the presence of multiple endemic tetrapod clades in the Northern Hemisphere, contrasting with generally more widely distributed clades that were once thought to be restricted to Gondwana (e.g., carcharodontosaurids, megaraptorans, abelisaurids; Ezcurra and Agnolín, 2012). SMNS 58023 represents the oldest South American megaraptoran and one of the oldest worldwide, together with *Fukuiraptor* and *Australovenator* from the Aptian-Albian of Japan and Australia, respectively (Benson et al., 2010).

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.cretres.2017.10.019.

References

Agnolín, F.L., Martinelli, A., 2007. Did oviraptorosaurs (Dinosauria: Theropoda) inhabit Argentina? Cretaceous Research 28, 785–790.

Agnolin, F.L., Ezcurra, M., Pais, D.F., Salisbury, S.W., 2010. A reappraisal of the Cretaceous non-avian dinosaur faunas from Australia and New Zealand: Evidence for their Gondwanan affinities. Journal of Systematic Palaeontology 8, 257–300.

Apesteguía, S., Smith, N.D., Juárez Valieri, R., Makovicky, P.J., 2016. An unusual new theropod with a didactyl manus from the Upper Cretaceous of Patagonia, Argentina. PLoS One 11, 0157793.

Arai, M., 2006. Revisão estratigráfica do Cretáceo Inferior das bacias interiores do Nordeste do Brasil. Geociências 25, 7–15.

Assine, M.L., 1992. Análise estratigráfica da Bacia do Araripe, Nordeste do Brasil. Revista Brasileira de Geociências 22, 289–300.

Assine, M.L., 2007. Bacia do Araripe. Boletim de Geociências da Petrobrás 15, 371–389.

Barsbold, R., Currie, P.J., Myhrvold, N., Osmólska, H., Tsogtbaatar, K., Watabe, M., 2000. The first pygostyle from a non-avian theropod. Nature 403, 155–156.

Bell, P.R., Coria, R.A., 2013. Palaeopathological survey of a population of *Mapusaurus* (Theropoda: Carcharodontosauridae) from the Late Cretaceous Huincul Formation, Argentina. PLoS One 8, e63409.

Benson, R.B.J., 2010. A description of *Megalosaurus bucklandii* (Dinosauria: Theropoda) from the Bathonian of the UK and the relationships of Middle Jurassic theropods. Zoological Journal of the Linnean Society 158, 882–935.

Benson, R.B.J., Carrano, M.T., Brusatte, S.L., 2010. A new clade of archaic large-bodied predatory dinosaurs (Theropoda: Allosauroidea) that survived to the latest Mesozoic. Naturwissenschaften 97, 71–78.

Benson, R.B.J., Rich, T.H., Vickers-Rich, P., Hall, M., 2012a. Theropod fauna from Southern Australia indicates high Polar Diversity and Climate-Driven dinosaur provinciality. PLoS One 7, 37122.

Benson, R.B.J., Butler, R.J., Carrano, M.T., O'connor, P.M., 2012b. Air-filled postcranial bones in theropod dinosaurs: physiological implications and the 'reptile'–bird transition. Biological Reviews 87, 168–193.

Bittencourt, J.S., Langer, M.C., 2011. Mesozoic dinosaurs from Brazil and their biogeographic implications. Anais da Academia Brasileira de Ciências 83, 23–60.

Bremer, K., 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. Evolution 42, 795–803.

Bremer, K., 1994. Branch support and tree stability. Cladistics 10, 295–304.

Bonaparte, J.F., Kielan-Jaworowska, Z., 1987. Late Cretaceous dinosaur and mammal faunas of Laurasia and Gondwana. In: Currie, P.J., Koster, E.H. (Eds.), Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers. Occasional Paper of the Tyrell Museum of Palaeontology, 3, pp. 24–29.

Bonaparte, J.F., Novas, F.E., Coria, R.A., 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnotaur from the middle Cretaceous of Patagonia. Contributions Science Natural History Museum of Los Angeles County 416, 1–42.

Brochu, C.A., 2003. Osteology of *Tyrannosaurus rex*: insights from a nearly complete skeleton and high-resolution computed tomographic analysis of the skull. Society of Vertebrate Paleontology Memoir 7, 1–138.

Brum, A.S., Machado, E.B., Campos, D.A., Kellner, A.W.A., 2016. Morphology and internal structure of two new abelisaurid remains (Theropoda, Dinosauria) from the Adamantina Formation (Turonian-Maastrichtian), Bauru Group, Paraná Basin, Brazil. Cretaceous Research 60, 287–296.

Brusatte, S., Benson, R.B.J., Hutt, S., 2008. The osteology of *Neovenator salerii* (Dinosauria: Theropoda) from the Wealden Group (Barremian) of the Isle of Wight. Palaeontographical Society 162, 1–166.

Brusatte, S.L., Candeiro, C.R., Simbras, F.M., 2017. The last dinosaurs of Brazil: The Bauru Group and its implications for the end-Cretaceous mass extinction. Anais da Academia Brasileira de Ciências 89, 1465–1485.

Canale, J.I., Novas, F.E., Pol, D., 2015. Osteology and phylogenetic relationships of *Tyrannotitan chubutensis* Novas, de Valais, Vickers-Rich and Rich, 2005 (Theropoda: Carcharodontosauridae) from the Lower Cretaceous of Patagonia, Argentina. Historical Biology 27, 1–32.

Candeiro, C.R.A., Abranches, C.T., Abrantes, E.A., Avilla, L.S., Martins, V.C., Moreira, A.L., Torres, S.R., Bergqvist, L.P., 2004. Dinosaurs remains from western São Paulo state, Brazil (Bauru Basin, Adamantina Formation, Upper Cretaceous). Journal of South American Earth Sciences 18, 1–10.

Candeiro, C.R.A., Martinelli, A.G., Avilla, L.S., Rich, T., 2006. Tetrapods from the Upper Cretaceous (Turonian Maastrichtian) Bauru Group of Brazil: a reappraisal. Cretaceous Research 27, 923–946.

Carrano, M.T., Benson, R.B.J., Sampson, S.D., 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). Journal of Systematic Palaeontology 10, 211–300.

Carvalho, I., Novas, F.E., Agnolín, F.L., Isasi, M.P., Freitas, F.I., Andrade, J.A., 2015. A Mesozoic bird from Gondwana preserving feathers. Nature Communications 6, 7141.

Coddington, J.A., Scharff, N., 1994. Problems with zero-length branches. Cladistics 10, 415–423.

Coria, R.A., Currie, P.J., 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. Geodiversitas 28, 71–118.

Coria, R.A., Currie, P.J., 2016. A new megaraptoran dinosaur (Dinosauria, Theropoda, Megaraptoridae) from the Late Cretaceous of Patagonia. PLoS One 11, 0157973.

Currie, P.J., Russell, D.A., 1988. Osteology and relationships of *Chirostenotes pergracilis* (Saurischia, Theropoda) from the Judith River (Oldman) Formation of Alberta, Canada. Canadian Journal of Earth Sciences 25, 972–986.

Currie, P.J., Vickers-Rich, P., Rich, T.H., 1996. Possible oviraptorosaur (Theropoda, Dinosauria) specimen from the Early Cretaceous Otway Group of Dinosaur Cove, Australia. Alcheringa 20, 73–79.

Delcourt, R., 2017. Revised morphology of *Pycnonemosaurus nevesi* Kellner & Campos, 2002 (Theropoda: Abelisauridae) and its phylogenetic relationships. Zootaxa 4276, 1–45.

Delcourt, R., Grillo, O.N., 2017. Carcharodontosaurids remained extinct in the Campanian-Maastrichtian: reassessment of a fragmentary maxilla from Presidente Prudente Formation, Brazil. Cretaceous Research Published Online. https://doi.org/10.1016/j.cretres.2017.09.008.

Elias, F.A., Bertini, R.J., Medeiros, M.A.A., 2004. Velociraptorinae (Maniraptoriformes) teeth from the Coringa Flagstone outcrop, middle Cretaceous of the São Luís-Grajaú Basin, Maranhão State, northern-northeastern Brazil. In: Carvalho, I.S., Cassab, R.C.T., Schwanke, C., Carvalho, M.A., Fernandes, A.C.S., Rodrigues, M.A.C., Carvalho, M.S.S., Arai, M., Oliveira, M.E.Q. (Eds.), Paleontologia: Cenários de Vida, vol. 1. Interciência, Rio de Janeiro, pp. 307–317.

Ezcurra, M.D., Agnolín, F.L., 2012. A new global palaeobiogeographical model for the late Mesozoic and early Tertiary. Systematic Biology 61, 553–566.

Ezcurra, M.D., Novas, F.E., 2016. Theropod dinosaurs from Argentina. In: Historia Evolutiva y Paleobiogeografica de los Vertebrados de América de Sur. Volumen especial de las 30 Jornadas Argentinas de Paleontología de Vertebrados, pp. 139–156.

Fara, E., Saraiva, A.A.F., Campos, D.A., Moreira, J.K.R., Siebra, D.C., Kellner, A.W.A., 2005. Controlled excavations in the Romualdo Member of the Santana Formation (Early Cretaceous, Araripe Basin, northeastern Brazil): stratigraphic, palaeoenvironmental and palaeoecological implications. Palaeogeography, Palaeoclimatology, Palaeoecology 218, 145–160.

Felsenstein, J., 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39, 783–791.

Frankfurt, N.G., Chiappe, L.M., 1999. A possible oviraptorosaur from the Late Cretaceous of northwestern Argentina. Journal of Vertebrate Paleontology 19, 101–105.

Frey, E., Martill, D.M., 1995. A possible oviraptorosaurid theropod from the Santana Formation (Lower Cretaceous? Albian) of Brazil. Neues Jahrbuch für Geologie und Paläontologie 7, 397–412.

Gauthier, J.A., 1986. Saurischian monophyly and the origin of birds. Memoirs of the Californian Academy of Science 8, 1–55.

Gilmore, C.W., 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. Bulletin of the United States National Museum 110, 1–154.

Goloboff, P.A., Catalano, S.A., 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics 32, 221–238.

Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M., Szumik, C.A., 2003. Improvements to resampling measures of group support. Cladistics 19, 324–332.

Goloboff, P.A., Farris, J.S., Nixon, K.C., 2008. TNT, a free program for phylogenetic analysis. Cladistics 24, 774–786.

Harris, J.D., 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and paleobiogeographic implications, based on a new specimen from Texas. New Mexico Museum of Natural History and Science Bulletin 13, 1–75.

Kellner, A.W.A., 1996. Fossilized theropod soft-tissue. Nature 379, 32.

Kellner, A.W.A., 1999. Short note on a new dinosaur (Theropoda, Coelurosauria) from the Santana Formation (Romualdo Member, Albian), Northeastern Brasil. Boletim do Museu Nacional, Geologia 49, 1–8.

Kellner, A.W.A., de Campos, D.A., 1996. First Early Cretaceous theropod dinosaur from Brazil with comments on Spinosauridae. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 199, 151–166.

Kellner, A.W.A., de Campos, D.A., 2002. On a theropod dinosaur (Abelisauria) from the continental Cretaceous of Brazil. Arquivos do Museu Nacional do Rio de Janeiro 60, 163–170.

Kellner, A.W.A., Azevedeo, S.A.K., Machado, E.B., Carvalho, L.B., Henriques, D.D.R., 2011. A new dinosaur (Theropoda, Spinosauridae) from the Cretaceous (Cenomanian) Alcântara Formation, Cajual Island, Brazil. Anais da Academia Brasileira de Ciências 83, 99–108.

Lindoso, R.M., Medeiros, M.A., Carvalho, I.S., Marinho, T.S., 2012. *Masiakasaurus*-like theropod teeth from the Alcântara Formation, São Luís Basin (Cenomanian) northeastern Brazil. Cretaceous Research 36, 119–124.

Lu, J., Zhang, B.K., 2005. A new oviraptorid (Theropoda: Oviraptorosauria) from the Upper Cretaceous of the Nanxiong Basin, Guangdong Province of southern China. Acta Palaeontologica Sinica 44, 412–422.

Machado, E.B., Kellner, A.W.A., 2007. On a supposed ornithischian dinosaur from the Santa Formation, Araripe Basin, Brazil. In: Carvalho, I.S., Cassab, R.C.T., Schwanke, C., Carvalho, M.A., Fernandes, A.C.S., Rodrigues, M.A.C., Carvalho, M.S.S., Arai, M., Oliveira, M.E.Q. (Eds.), Paleontologia: Cenários de Vida, vol. 1. Interciência, Rio de Janeiro, pp. 291–299.

Machado, E.B., Kellner, A.W.A., 2008. An overview of the Spinosauridae (Dinosauria, Theropoda) with comments on the Brazilian material. Journal of Vertebrare Paleontology 28, 109A.

Madsen Jr., J.H., 1976. *Allosaurus fragilis*: a revised osteology. Utah Geological and Mineralogical Survey Bulletin 109, 3–163.

Maisey, J.G., 1991. Santana Fossils: an Illustrated Atlas. T.F.H., Neptune City.

Makovicky, P.J., Sues, H.D., 1998. Anatomy and phylogenetic relationships of the theropod dinosaur *Microvenator celer* from the Lower Cretaceous of Montana. American Museum Novitates 3240, 1–27.

Martill, D.M., 1988. Preservation of fish in the Cretaceous Santana Formation of Brazil. Palaeontology 31, 1–18.

Martill, D.M., Cruickshank, A.R.I., Frey, E., Small, P.G., Clarke, M., 1996. A new crested maniraptoran dinosaur from the Santana Formation (Lower Cretaceous) of Brazil. Journal of the Geological Society of London 153, 5–8.

Martill, D.M., Frey, E., Sues, H.-D., Cruickshank, A.R.I., 2000. Skeletal remains of a small theropod dinosaur with associated soft structures from the Lower Cretaceous Santana Formation of northeastern Brazil. Canadian Journal of Earth Sciences 37, 891–900.

Martill, D.M., Loveridge, R., Heimhofer, U., 2007. Halite pseudomorphs in the Crato Formation (Early Cretaceous, Late Aptian–Early Albian), Araripe Basin, northeast Brazil: further evidence for hypersalinity. Cretaceous Research 28, 613–620.

Martinelli, A.G., Ribeiro, L.C.B., Neto, F.M., Méndez, A.H., Cavellani, C.L., Felix, E., Ferraz, M.L.F., Teixeira, V.P.A., 2013. Insight on the theropod fauna from the Uberaba Formation (Bauru Group), Minas Gerais State: new megaraptoran specimen from the Late Cretaceous of Brazil. Rivista Italiana di Paleontologia e Stratigrafia 119, 205–214.

Marsh, O.C., 1881. A new order of extinct Jurassic reptiles (Coeluria). American Journal of Science, Series 3 21, 339–340.

Méndez, A.H., Novas, F.E., Iori, F.V., 2012. First record of Megaraptora (Theropoda, Neovenatoridae) from Brazil. Comptes Rendus Palevol 11, 251–256.

Motta, M.J., Aranciaga Rolando, A.M., Rozadilla, S., Agnolín, F.E., Chimento, N.R., Brissón Egli, F., Novas, F.E., 2016. New theropod fauna from the Upper Cretaceous (Huincul Formation) of northwestern Patagonia, Argentina. New Mexico Museum of Natural History and Science Bulletin 7, 231–253.

Naish, D., Martill, D.M., Frey, E., 2004. Ecology, systematics and biogeographical relationships of dinosaurs, including a new theropod, from the Santana Formation (Albian, Early Cretaceous) of Brazil. Historical Biology 16, 57–70.

Novas, F.E., 2009. The Age of Dinosaurs in South America. Indiana University Press Bloomington.

Novas, F.E., Agnolín, F.L., Ezcurra, M.D., Porfiri, J., Canale, J.I., 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: the evidence from Patagonia. Cretaceous Research 45, 174–215.

Novas, F.E., Salgado, L., Suárez, M., Agnolín, F.L., Ezcurra, M.D., Chimento, N., de la Cruz, R., Isasi, M.P., Vargas, A., Rubilar-Rogers, D., 2015. An enigmatic plant-eating theropod from the Late Jurassic of Chile. Nature 522, 331–334.

O'Connor, P.M., 2007. The postcranial axial skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. In: Sampson, S.D., Krause, D.W. (Eds.), *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. Society of Vertebrate Paleontology Memoir, 8, pp. 127–162.

Osmólska, H., Currie, P.J., Barsbold, R., 2004. Oviraptorosauria. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria. University of California Press, Berkeley, California, pp. 165–183.

Ostrom, J.H., 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. Bulletin of the Peabody Museum of Natural History, 30. Yale University, pp. 1–165.

Paul, G., 1988. Predatory Dinosaurs of the World: A Complete Illustrated Guide. Simon and Schuster, New York, 464 pp.

Peyer, K., 2006. A reconsideration of *Compsognathus longipes* from the Upper Tithonian of Canjuers, southeastern France. Journal of Vertebrate Paleontology 26, 879–896.

Porfiri, J.D., Novas, F.E., Calvo, J.O., Agnolin, F.L., Ezcurra, M.D., Cerda, I.A., 2014. Juvenile specimen of *Megaraptor* (Dinosauria, Theropoda) sheds light about tyrannosauroid radiation. Cretaceous Research 51, 35–55.

Rauhut, O.W.M., 2003. Interrelationships and evolution of basal theropod dinosaurs. Special Papers in Palaeontology 69, 1–215.

Sales, M.A.F., Martinelli, A.G., Francischini, H., Rubert, R.R., Marconato, L.P., Soares, M.B., Schultz, C.L., 2017. New dinosaur remains and the tetrapod fauna from the Upper Cretaceous of Mato Grosso State, central Brazil. Historical Biology. https://doi.org/10.1080/08912963.2017.1315414.

Sereno, P.C., Martínez, R.N., Wilson, J.A., Varricchio, D.J., Alcober, O.A., 2008. Evidence for avian intrathoracic air sacs in a new predatory dinosaur from Argentina. PLoS One 3, 3303.

Stovall, J.W., Langston Jr., W., 1950. *Acrocanthosaurus atokensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. The American Midland Naturalist 43, 696–728.

Sues, H.-D., Frey, E., Martill, D.M., Scott, D.M., 2002. *Irritator challengeri*, a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. Journal of Vertebrate Paleontology 22, 535–547.

Swofford, D.L., Begle, D.P., 1993. PAUP – Phylogenetic Analysis Using Parsimony, Version 3.1. Laboratory of Molecular Systematics, Smithsonian Institution, Washington DC.

Valença, L.M.M., Neumann, V.H., Mabesoone, J.M., 2003. An overview on Callovian-Cenomanian intracratonic basins of Northeast Brazil: onshore stratigraphic record of the opening of the southern Atlantic. Geologica Acta 1, 261–275.

Vilas Boas, I., Carvalho, I.S., Medeiros, M.A., Pontes, H., 1999. Dentes de *Carcharodontosaurus* (Dinosauria, Tyrannosauridae) do Cenomaniano, Bacia de Sáo Luís (Norte do Brasil). Anais de la Academia Brasileira de Ciéncias 71, 846–847.

Wilson, J.P., Woodruff, D.C., Gardner, J.D., Flora, H.M., Horner, J.R., Organ, C.L., 2016. Vertebral adaptations to large body size in theropod dinosaurs. PLoS One 11, e0158962.