

The first ornithosuchid from Brazil and its macroevolutionary and phylogenetic implications for Late Triassic faunas in Gondwana

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Ornithosuchidae is one of the most enigmatic clades of Triassic pseudosuchians. The group is composed by three carnivorous species that were excavated from Upper Triassic beds of Scotland and Argentina. We describe the first ornithosuchid from the Upper Triassic sediments of Brazil and explore its phylogenetic affinities and implications for the evolution of the group. *Dynamosuchus collisensis* gen. et sp. nov. was found as the sister taxon of the Argentinean form *Venaticosuchus rusconii*. These relationships reject a potential endemic radiation of ornithosuchids from the Ischigualasto-Villa Unión Basin and would better support multiple diversification events. Our findings with ornithosuchids is consistent with the pattern reported for proterochampsid and erpetosuchid archosauriforms from Ischigualasto-Villa Unión and the Paraná basins. In addition, the presence of an ornithosuchid in the Late Triassic of Brazil suggests that ornithosuchids were more widespread than previously thought in the southern hemisphere. The new ornithosuchid further demonstrates a faunistic link between the Argentinean and Brazilian basins during the Carnian. Finally, the discovery of the new species provides the first clue of a putative necrophagous vertebrate from the oldest dinosaur-bearing beds and expands our knowledge regarding the trophic structure of the Late Triassic of Brazil.

Key words: Archosauria, Pseudosuchia, Ornithosuchidae, biogeography, phylogeny, Carnian, Santa Maria Formation, South America.

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Introduction

The radiation of pseudosuchian archosaurs during the Triassic Period is characterized by the origin and extinction of several peculiar and disparate clades, such as Aetosauria (Desojo et al. 2013; Parker 2016), Erpetosuchidae (Benton and Walker 2002; Nesbitt and Butler 2013; Ezcurra et al. 2017; Lacerda et al. 2018), Gracilisuchidae (Butler et al. 2014; Lecuona et al. 2017), and Ornithosuchidae (Walker 1964; Bonaparte 1970; Baczko et al. 2014; Baczko and Desojo 2016; Baczko 2018). The latter is one of the most enig-

matic clades. Coined by Huene in 1908, Ornithosuchidae has a long and controversial taxonomic history. The clade has been found in different phylogenetic positions across Archosauria (e.g., Gauthier 1986; Sereno 1991; Nesbitt 2011; Ezcurra 2016). Nevertheless, most hypotheses following Sereno (1991) converged on a position near the base of Pseudosuchia. Three species form the clade: *Ornithosuchus woodwardi* (Newton, 1894), from the late Carnian–early Norian, the Lossiemouth Sandstone Formation, Scotland (Newton 1894; Walker 1964); *Venaticosuchus rusconii* (Bonaparte, 1970) from the late Carnian of the Ischigualasto Formation, Argentina (Baczko et al. 2014; Baczko 2018);

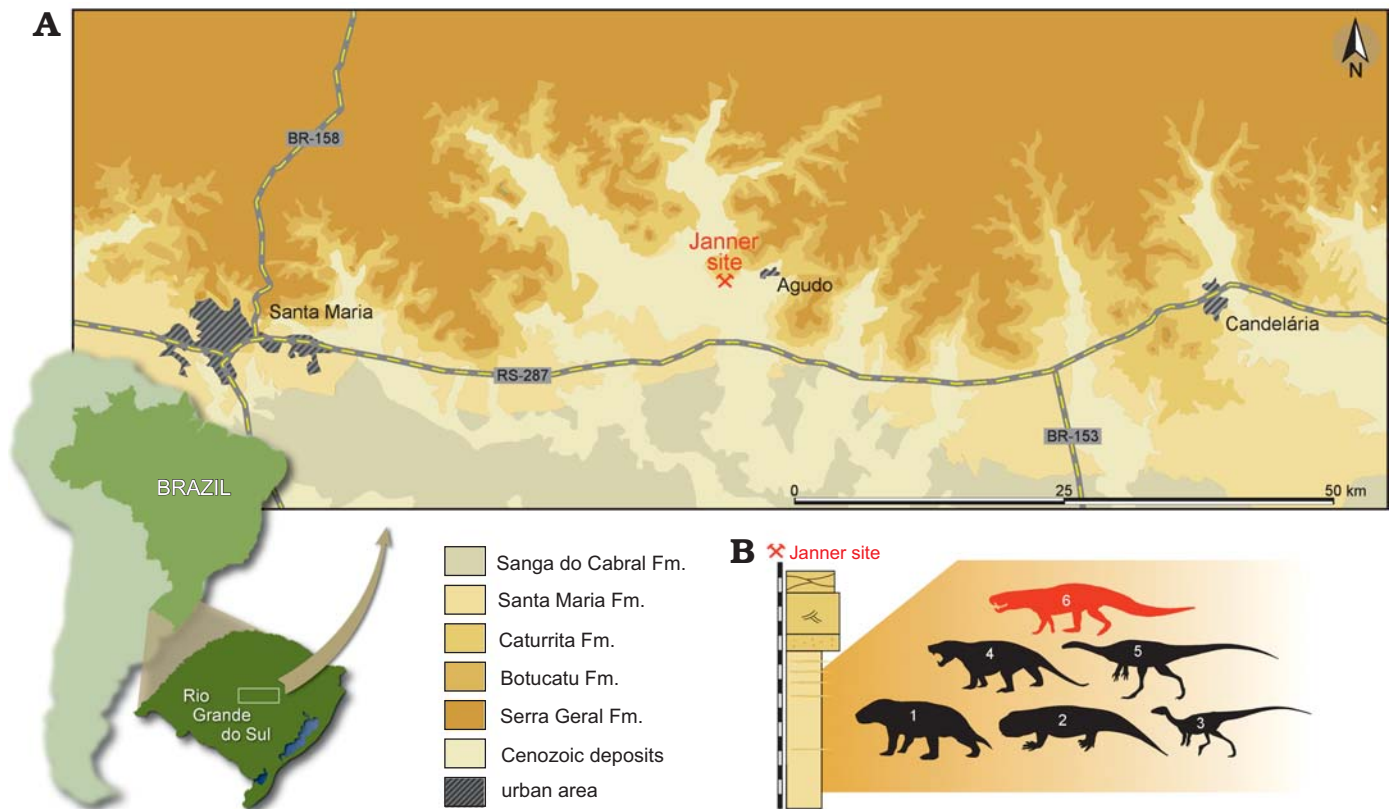


Fig. 1. **A.** Location map of the Janner site and the surface distribution of the geologic units in the area (modified from Müller et al. 2017). **B.** Stratigraphic column of the Janner site (modified from Da-Rosa 2015) depicting its fossiliferous content: 1, *Exaeretodon*; 2, *Hyperodapedon*; 3, *Pampadromaeus*; 4, *Trucidocynodon*; 5, *Bagualosaurus*; and 6, the new ornithosuchid.

and *Riojasuchus tenuisiceps* (Bonaparte, 1967) from the Norian of the Los Colorados Formation, Argentina (Baczko and Desojo 2016; Baczko et al. 2020). All members of this group are carnivorous, putatively scavengers and facultative bipedal during fast gaits (Walker 1964; Baczko and Ezcurra 2013; Baczko 2018). Nevertheless, the fossil record of the group is geographically limited and so far, no remains outside Ischigualasto-Villa Union Basin (Argentina) or the Lossiemouth Sandstone Formation (Scotland) have been identified, thus leaving a large gap in their potential biogeographic distribution. Here, we describe the first partial skeleton of an ornithosuchid from the Upper Triassic sediments of Brazil (Fig. 1) and explore its phylogenetic affinities and implications for the evolution of the group.

Institutional abbreviations.—CAPP/UFMS, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia/ Universidade Federal de Santa Maria, São João do Polêsine, Rio Grande do Sul, Brazil; CRILAR-Pv, Centro Regional de Investigaciones y Transferencia Tecnológica de La Rioja, Paleontología de Vertebrados, Anillaco, La Rioja, Argentina; NHMUK PV, Natural History Museum, London, UK; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; PIMUZ, Paläontologisches Institut und Museum der Universität Zurich, Switzerland; PULR, Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; PVL, Paleontología de Vertebrados,

Instituto Miguel Lillo, Tucumán, Argentina; PVSJ, División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; TTUP, Museum of Texas Tech University, Lubbock, Texas, USA; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil.

Nomenclatural acts.—This published work and the nomenclatural acts it contains, have been registered in ZooBank: [urn:lsid:zoobank.org:pub:A90DC693-B65F-472D-AA40-3C608C00B8D5](https://www.zoobank.org/pub:A90DC693-B65F-472D-AA40-3C608C00B8D5)

Material and methods

In order to test its phylogenetic affinities and potential implications for the understanding of pseudosuchian evolution, the new taxon was scored in the data matrix of Ezcurra et al. (2017). This data matrix was employed because of the large sample of erpetosuchids included, whose importance is crucial for this study because they were proposed as sister group of ornithosuchids (Ezcurra et al. 2017; Lacerda et al. 2018). The Brazilian erpetosuchid *Pagosvenator candelariensis* (Lacerda et al. 2018) which was published after Ezcurra et al. (2017) was also included here. Therefore, the

final data matrix includes 676 characters and 109 terminal taxa. Our data matrix was subjected to an equally weighted parsimony analysis in TNT v. 1.1 (Goloboff et al. 2008). The characters treated by Ezcurra et al. (2017) as additive (1, 2, 7, 10, 17, 19, 20, 21, 28, 29, 36, 40, 42, 50, 54, 66, 71, 75, 76, 122, 127, 146, 153, 156, 157, 171, 176, 177, 187, 202, 221, 227, 263, 266, 279, 283, 324, 327, 331, 337, 345, 351, 352, 354, 361, 365, 370, 377, 379, 398, 410, 424, 430, 435, 446, 448, 454, 458, 460, 463, 472, 478, 482, 483, 489, 490, 504, 510, 516, 529, 537, 546, 552, 556, 557, 567, 569, 571, 574, 581, 582, 588, 648, 652, and 662) were also treated as such in our analysis. *Petrolacosaurus kansensis* was used to root the most parsimonious trees (MPTs), which were recovered with a “Traditional search” (random addition sequence + tree bisection reconnection) with 1000 replicates of Wagner trees (with random seed = 0), and using tree bisection reconnection and branch swapping (holding 10 trees save per replicate).

Systematic palaeontology

Archosauria Cope, 1869

(sensu Gauthier and Padian 1985)

Pseudosuchia Zittel, 1887–1890

(sensu Gauthier and Padian 1985)

Ornithosuchidae Huene, 1908

(sensu Sereno 1991)

Genus *Dynamosuchus* nov.

ZooBank LSID: urn:lsid:zoobank.org:act:B3DA19CB-0750-466F-A6C1-97A14114A41B

Type species: *Dynamosuchus collisensis* gen. et sp. nov., monotypic, see below.

Etymology: From Greek (transliterated) *dynamis*, power and *soukhos*, crocodile, referring to the strong bite force inferred to ornithosuchids.

Diagnosis.—Same as for the only known species.

Dynamosuchus collisensis sp. nov.

Fig. 2.

ZooBank LSID: urn:lsid:zoobank.org:act:4B1FFAFB-6287-4448-9E34-B7976D307C80

Etymology: From Latin *collis*, hill, reflecting the fact that the holotype was collected from the Janner site, which is located at the base of the Agudo Hill (Morro Agudo in Portuguese).

Holotype: CAPP/UFMS 0248, a partial skeleton including the premaxillae, left maxilla, frontals, right postfrontal, right parietal, squamosals, quadratojugals, quadrates, parabasisphenoid, both hemimandibles, some cervical, dorsal, sacral and caudal vertebrae, several ribs, gastralia, osteoderms, left scapula, both forelimbs, left ilium, right pubis, left femur, right tibia, and left fibula.

Type locality: Janner site (29°39'10.89" S, 53°17'34.20" W), Agudo, Rio Grande do Sul, Brazil (Fig. 1).

Type horizon: Santa Maria Formation; Candelária Sequence, Paraná Basin. The presence of the genus *Hyperodapedon* and *Exaeretodon* at the Janner site (Langer et al. 2007) supports a Carnian age based on

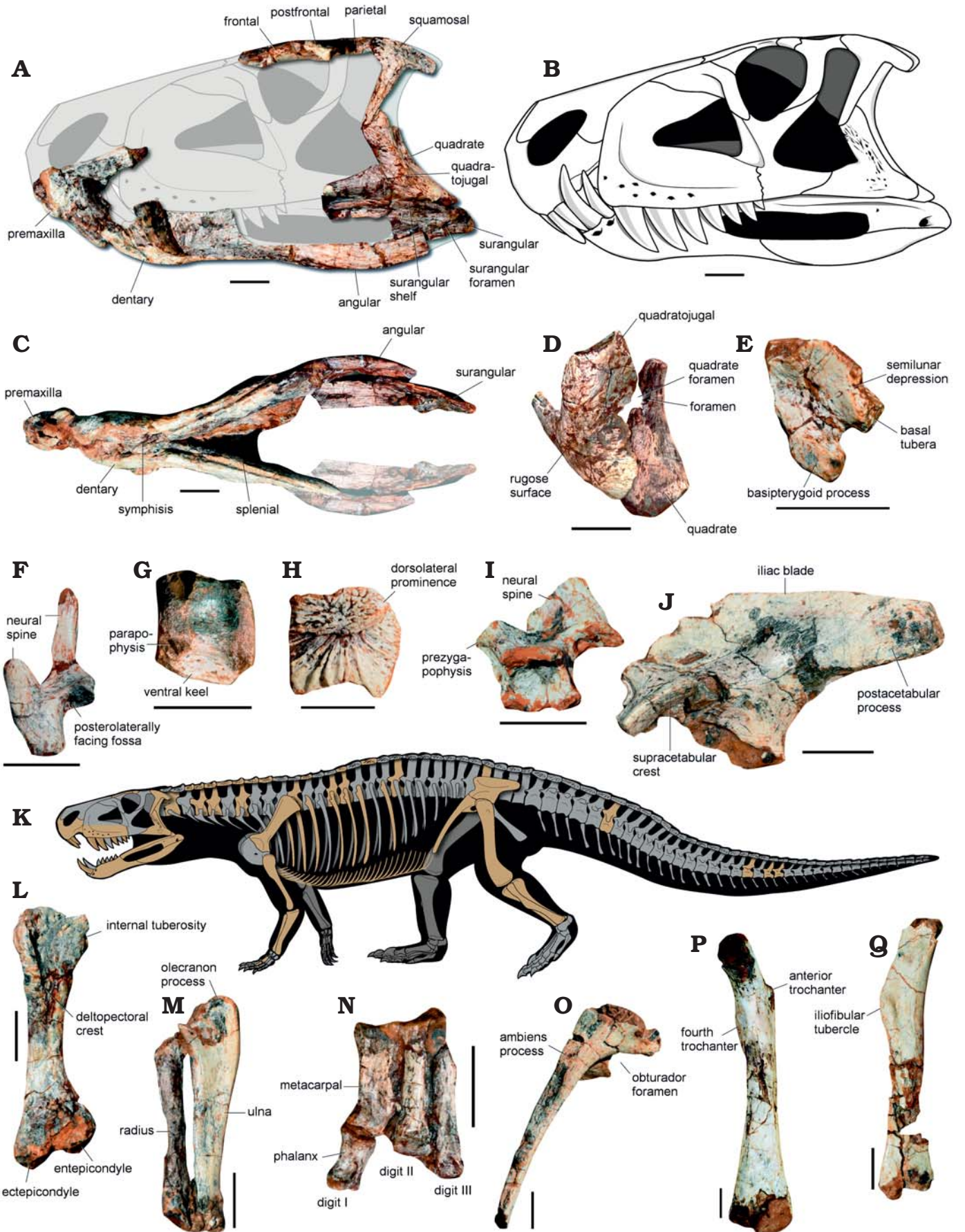
correlation with radioisotope dating of another Brazilian site (Langer et al. 2018) and Argentine beds from the La Peña Member of the Ischigualasto Formation (Martínez et al. 2011) with the same taxa.

Diagnosis.—*Dynamosuchus collisensis* differs from all other known ornithosuchids based on a unique combination of character states (* autapomorphy): dorsal process of the quadratojugal mostly dorsally oriented and with the lateral surface densely covered by rugosities; additional foramen on the medial wall of the quadrate foramen*; parabasisphenoid component of the basal tubera ventrally separated from the basiptyergoid process by a slight notch at the midline; main axis of the parabasisphenoid process posteroventrally directed; surangular with a conspicuous lateral shelf and an anteroposteriorly wide surangular foramen; anterior dorsal vertebrae with anterior and posterior centrodiaepophyseal laminae and without prezygodiaepophyseal and postzygodiaepophyseal laminae; dorsal body osteoderms with an external pattern of dense crests and grooves; and iliofibularis tubercle of the fibula located within the proximal half of the bone.

Ornithosuchus woodwardi differs from *Dynamosuchus collisensis* in that *O. woodwardi* has (for comparative illustrations see the SOM, Supplementary Online Material available at http://app.pan.pl/SOM/app65-Muller_etal_SOM.pdf): dorsal process of the quadratojugal is more anteriorly projected (*O. woodwardi*, 45°; *D. collisensis*, 90°); no additional foramen on the medial wall of the quadrate foramen; the lateral surface of the angular has ornamentation; less laterally extended surangular shelf; presence of prezygodiaepophyseal and postzygodiaepophyseal lamina in the anterior dorsal vertebrae; presence of a fossa ventral to the neurocentral suture on the lateral side of the dorsal centra; presence of an accessory process on the anterior margin of the neural arch of the middle caudal vertebrae; and a less expanded distal end of the radius.

Venaticosuchus rusconii differs from *D. collisensis* in that *V. rusconii* has: absence of foramina on the lateral surface of the maxilla; no additional foramen on the medial wall of the quadrate foramen; parabasisphenoid component of the basal tubera ventrally separated from the basiptyergoid process by a notch that forms an acute angle; basiptyergoid processes more transversely separated from each other in comparison to *D. collisensis*; basiptyergoid processes are ventrally directed with a semicircular shape in lateral view; and absence of the surangular foramen (autapomorphy of *V. rusconii*; Baczko et al. 2014).

Riojasuchus tenuisiceps differs from *D. collisensis* in that *R. tenuisiceps* has: absence of foramina on the lateral surface of the maxilla; anterior and ventral margins of the antorbital fossa almost meet with the anterior and ventral edges of the maxilla; lateral surface of the quadratojugal is smooth; dorsal process of the quadratojugal is more anteriorly projected (c. 45°); no additional foramen on the medial wall of the quadrate foramen; ventral process of the squamosal anteroposteriorly larger proportionally; absence of a semilunar depression on the posterolateral surface of



the parabasisphenoid; absence of the anterior and posterior centrodiapophyseal laminae of the anterior dorsal vertebrae; osteoderms with smooth ornamentation; internal tuberosity of the humerus is more pronounced; postacetabular process of the ilium is proportionally anteroposteriorly longer; iliac blade with a concave dorsal margin in lateral view; and iliofibularis tubercle of the fibula more distally located.

Description.—The body of the premaxilla of *Dynamosuchus collisensis* is ventrally deflected at the anterior portion (= downturned) and bears three teeth, as typical of ornithosuchids (Baczko and Ezcurra 2013), and the anterior tip of the premaxilla extends further anteriorly than the anterior tip of the dentary (Fig. 2A–C). The elongated palatal process of the premaxilla of *D. collisensis* bears a ridge at its ventral margin, like in *Venaticosuchus rusconii* (PVL 2578; Baczko et al. 2014). There is a lateral edentulous constriction at the posterior process of the premaxilla, where two caniniform teeth from the dentary fit. The lateral surface of the maxilla is pierced by several foramina (see the Supplementary Online Material for additional figures), which are not recognized in *V. rusconii* (PVL 2578; Baczko et al. 2014) and *R. tenuisiceps* (PVL 3827, PVL 3828; Baczko and Desojo 2016), but present in *Ornithosuchus woodwardi* (NHMUK PV R 3143; Walker 1964). The anterior and ventral portions of the antorbital fossa do not coincide with the anterior and ventral edges of the maxilla in *D. collisensis*, whereas in *R. tenuisiceps* (PVL 3827, PVL 3828) these margins almost coincide with each other (Baczko and Desojo 2016). There are six tooth positions preserved; however, the total number of maxillary teeth of *D. collisensis* is uncertain, but probably does not exceed seven or eight teeth based on the preserved length of the maxilla, the length of the hemimandible, and through comparisons with other ornithosuchids.

The right frontal, postfrontal, and anterior portion of the parietal were preserved in articulation showing a markedly constricted interorbital area and delimiting the medial half of the supratemporal fenestra (SOM: fig. S2). A depression for the olfactory bulbs occurs on the ventral surface of the anterior half of the frontal. Like in *R. tenuisiceps* (PVL 3827), the supratemporal fenestra is anteroposteriorly short, approximately half of the orbit, whereas in *Saurosuchus galilei* (PVSJ 32; Alcober 2000), *Prestosuchus chiniquensis* (UFRGS-PV-0629-T; Mastrantonio et al. 2019), *Tarjadia ruthae* (CRILAR-Pv 495; Ezcurra et al. 2017) and in aetosaurs (e.g. *Neoaetosauroides engaeus*; PVL 5698; Desojo and Báez 2007), the supratemporal fenestra is equivalent to the length of the orbit. The ventral process of the squamosal of *D. collisensis* is elongated and slender (Fig. 2A),

resembling that of *O. woodwardi* (NHMUK PV R 2409, NHMUK PV R 3562), whereas in *R. tenuisiceps* (PVL 3827) it is proportionally wider anteroposteriorly. There is a longitudinally oriented sulcus bounded medially by a sharp crest on the dorsal surface of the squamosal of *D. collisensis*. The general morphology of the quadratojugal of *D. collisensis* resembles that of *V. rusconii* (PVL 2578), where the dorsal process is less anteriorly inclined than in *R. tenuisiceps* (PVL 3827). Like in *O. woodwardi* (NHMUK PV R 3142), the lateral surface of the quadratojugal of *D. collisensis* bears a strongly rugose surface (Fig. 2D), whereas in other ornithosuchids the homologous surface is smooth (Baczko et al. 2018). The quadrate foramen lies between the medial margin of the quadratojugal and the lateral margin of the quadrate. In addition, there is a foramen piercing the wall that forms the medial margin of the quadrate foramen in the quadrate (Fig. 2D). Although present in some archosauriforms (e.g., *Sarmatosuchus otschevi*; PIN 2865/68; Ezcurra 2016), this trait was not reported previously for ornithosuchids.

There is a shallow semilunar depression on the posterolateral surface of the parabasisphenoid of *D. collisensis* (Fig. 2E), a trait shared with *V. rusconii* (PVL 2578; Baczko et al. 2014). Like in *R. tenuisiceps* (PVL 3827), in lateral view, the parabasisphenoid component of the basal tubera of *D. collisensis* is ventrally separated from the basiptyergoid process by a gentle notch, as in most of the pseudosuchians (Fig. 2E). On the other hand, in *V. rusconii* (PVL 2578) there is a more acute angle (about to 40°) formed by the main axis of the basal tubera and the basiptyergoid process in lateral view, whereas in *D. collisensis* the angle is wider (about to 60°). The basiptyergoid processes of *V. rusconii* (PVL 2578) are more transversely separated from each other when compared to *D. collisensis*. Moreover, in *V. rusconii* (PVL 2578) the basiptyergoid processes are ventrally directed with a semicircular shape in lateral view (Baczko et al. 2014), whereas in *D. collisensis*, the processes lie posteroventrally, which results in a more elongated ventral margin in comparison. The basiptyergoid recess of *D. collisensis* is well-excavated differing from the shallower recess seen in *R. tenuisiceps* (PVL 3827) and in aetosaurs (e.g., *Neoaetosauroides engaeus* PVL 5698, *Desmotosuchus spurensis* TTUP 9024).

The lower jaws of *D. collisensis* are anteroposteriorly shorter than the skull (Fig. 2A–C). The symphysis is approximately 35% of the mandible length (synapomorphic character state of ornithosuchids; Sereno 1991) and the external mandibular fenestra is also anteroposteriorly longer than tall in comparison with other ornithosuchids. The dorsal margin of the anterior portion of the dentary is elevated relative to the more posterior portion. The splenial forms most of

← Fig. 2. Representative skeletal elements of ornithosuchid archosaur *Dynamosuchus collisensis* gen. et sp. nov. (CAPP/UFMS 0248) from Janner outcrop, Carnian, Late Triassic. **A.** Selected skull bones in left lateral view. **B.** Reconstruction of the skull. **C.** Skull in ventral view. **D.** Left quadrate and quadratojugal in posterodorsal view. **E.** Parabasisphenoid in left lateral view. **F.** Neural arch of an anterior cervical vertebra in anterior view. **G.** Centrum of a cervical vertebra in left lateral view. **H.** Right osteoderm in dorsal view. **I.** Neural arch of an anterior dorsal vertebra in left lateral view. **J.** Left ilium in lateral view. **L.** Right humerus in anterior view. **M.** Right forearm in medial view. **N.** Left manus in dorsal view. **O.** Right (reversed) pubis in lateral view. **P.** Left femur in anterior view. **Q.** Left fibula in lateral view. Some unpreserved portions are modified from Baczko et al. in press, for the reconstruction of the skeleton of CAPP/UFMS 0248 (preserved elements indicated in orange) (**K**). Scale bars 20 mm.

the medial portion of the lower jaw and lacks any foramen. The dorsoventrally slender angular is anteroposteriorly elongated, and delimits the posterior $\frac{3}{4}$ of the ventral margin of the external mandibular fenestra. Posteriorly, the angular meets the surangular, which delimits the posterodorsal and dorsal margin of the fenestra. There is a wide surangular foramen dorsal to the contact with the angular (Fig. 2A). Such structure occurs in the other ornithosuchids, except in *V. rusconii* (PVL 2578; Baczkó et al. 2014). *Dynamosuchus collisensis* bears a well-developed surangular shelf, which resembles the sharp shelf of *R. tenuisiceps* (PVL 3827; Baczkó and Desojo 2016) and *V. rusconii* (PVL 2578; Baczkó 2018), whereas in *O. woodwardi* (NHMUK PV R 2409) the shelf is less pronounced. This shelf is also present in proterochampsids, erpetosuchids, and gracilisuchids (Ezcurra 2016; Ezcurra et al. 2017).

The axial neural spine is anteroposteriorly longer than the neural spine of the other preserved post-axial cervical vertebrae. At the ventral surface of the postzygapophysis of the cervical vertebrae there is a posterolaterally facing fossa (Fig. 2F), a trait unusual in pseudosuchians, except by *Gracilisuchus stipanicorum* (PULR 08; Ezcurra 2016). The cervical neural spines are tall relative to the neural arch, straight, and possess transverse expansions at their dorsal end, forming “spine tables”. The cervical centra have a strongly developed ventral keel that extends longitudinally and project ventral to the margin of the centra (Fig. 2G). This condition is uncommon within pseudosuchians being present only in *R. tenuisiceps* (PVL 3827), *Erpetosuchus granti* (NHMUK PV 3139), *Stagonolepis robertsoni* (NHMUK PV 4784), and *Batrachotomus kupferzellensis* (SMNS 80284). The anterior dorsal vertebrae (Fig. 2I) of *D. collisensis* have an anterior and posterior centrodiaepophyseal lamina, absent in *R. tenuisiceps* (PVL 3827) and unknown in *V. rusconii*, but lack prezygodiaepophyseal and postzygodiaepophyseal lamina. The dorsal vertebrae of *D. collisensis* lack hyposphene-hypantrum accessory intervertebral articulation similar to *R. tenuisiceps* (PVL 3827). The condition is uncertain in other ornithosuchids. The centra of *D. collisensis* lack a fossa just ventral to the neurocentral suture like in *R. tenuisiceps* (PVL 3827), whereas a poorly rimmed fossa occurs in *O. woodwardi* (NHMUK PV R 3916; Walker 1964). The preserved dorsal vertebrae *D. collisensis* do not preserve the distal tip of the neural spine. The neural spine of the caudal vertebra is posterodorsally directed and bears a pointed posterior projection. *Dynamosuchus collisensis* lacks an accessory laminar process on the anterior margin of the caudal vertebrae, differing from *O. woodwardi* (NHMUK PV R 3561).

The preserved paramedian osteoderms are square in dorsal view and strongly ornamented by radial ridges and elongated grooves (Fig. 2H), like in *O. woodwardi* (NHMUK PV R 3916; Walker 1964) whereas the same surface of the osteoderms of *R. tenuisiceps* (PVL 3827) bear a gentle radial pattern (Baczkó et al. 2020). Nevertheless, *D. collisensis* shares with the other ornithosuchids the presence of a

prominence on the dorsolateral surface of the osteoderms. In *D. collisensis*, this dorsolateral prominence is marked by a rugose surface and, in some elements, it has a pointed dorsal tip. The dorsolateral prominence becomes less developed progressively in posterior osteoderms of the cervical and dorsal series. A longitudinally oriented ridge is absent on the dorsal surface of the osteoderms, such as in other ornithosuchids. The anterior margin of the osteoderms is straight and lacks an anterior process or an unornamented anterior articular lamina. The posterior margin is concave in dorsal view (Fig. 2H). The ventral surface is smooth and ventrally convex in anterior view. The length of the osteoderms indicate that there is a pair of osteoderms per vertebra, forming two paramedian rows along the dorsal surface of the body (unknown for the tail).

The acromion process of the scapula gently rises from the anterior margin of the scapular blade at an angle of approximately 120°, resembling the condition of *O. woodwardi* (NHMUK PV R 3916). In contrast, *D. collisensis* has a well-developed acromion process, which is nearly flat in *O. woodwardi* (NHMUK PV R 3916); the condition of *D. collisensis* resembles that of *R. tenuisiceps* (PVL 3828). The humerus (Fig. 2L) is robust, about 0.6 times the total length of the femur (0.65–0.75 in *R. tenuisiceps*), similar to the ratio in some aetosaurs and *Ticinosuchus ferox* (PIMUZ 2817), among pseudosuchians (Ezcurra 2016). The proximal end of the humerus is widely expanded with a moderately developed internal tuberosity, which is less pronounced in *D. collisensis* than in *R. tenuisiceps* (PVL 3826). The deltopectoral crest of *D. collisensis* is well-developed and restricted to the proximal third of the bone. *Dynamosuchus collisensis* lacks an ectepicondylar flange or it is poorly developed. The ulna (Fig. 2M) bears a moderately developed olecranon process and tappers towards its distal end, whereas the radius expands distally. Metacarpal I is the widest, whereas the metacarpal III is the longest of the metacarpals preserved (Fig. 2N).

Most of the preacetabular process of the ilium is not preserved (Fig. 2J). Nevertheless, it is evident that the ilium of *D. collisensis* lacks a lateral crest dorsal to the supraacetabular crest, as in other ornithosuchids and many pseudosuchians (e.g., *G. stipanicorum* PVL 4597; *T. ruthae* CRILAR-Pv 478; Ezcurra et al. 2017). As in *O. woodwardi* (NHMUK PV R 3561), the dorsal margin of the iliac blade of *D. collisensis* is straight to convex, whereas the homologous area in *R. tenuisiceps* (PVL 3828) is concave. The supraacetabular crest merges into the main body of the bone approximately at the mid-length of the acetabulum in *D. collisensis*. The postacetabular process is proportionally shorter than in *R. tenuisiceps* (PVL 3828) and lacks any evidence of a brevis fossa on the ventral surface. There are three articular surfaces for the sacral ribs on the medial surface of the ilium, as in other ornithosuchids and poposauroids, differing from the rest of pseudosuchians, which typically possess two sacral vertebrae. Although the distal end of the pubis is not preserved, the length of the pubis is estimated to be mark-

edly elongated (~0.68 times the total length of the femur) compared to other pseudosuchians (Fig. 2O). The pubis is anteroventrally projected, but gently arched ventrally along its length. It has a large obturator foramen and a well-developed pubic apron present along the shaft. The distal end is not preserved and it is not possible to determine whether it has a pubic boot or any expansion.

The hindlimb is estimated to be about 1.6 times longer than the forelimb. The femur (Fig. 2P) is sigmoidal with both ends expanded relative to the shaft. The proximal end preserves a well-developed posteromedial tuber, however, the anterolateral and anteromedial tubers as well as the greater trochanter have been eroded. There is a proximodistally oriented anterior trochanter at the proximal portion of the bone and a mound-like fourth trochanter more ventrally located at the opposite surface of the shaft. The presence of an anterior trochanter is a condition only registered in the ornithosuchids *R. tenuisiceps* (PVL 3828) and *O. woodwardi* (NHMUK PV R 2410, NHMUK PV R 3561, NHMUK PV R 3916) within pseudosuchians (unknown in *V. rusconii*). The fourth trochanter of *D. collisensis* is less pronounced than in *R. tenuisiceps* (PVL 3828), resembling the condition of *O. woodwardi* (NHMUK PV R 2410). The anterior surface of the distal end of *D. collisensis* is gently concave and the popliteal fossa, at the opposite surface, is proximodistally short. The distal condyles were eroded. The tibia is about 0.7 times of the length of the femur. The cnemial crest is poorly expanded from the shaft and has a straight anterior surface. The posterior edge of the proximal end is strongly projected. The fibula (Fig. 2Q) has an elliptical proximal end with an expanded posterior portion. There is a well-developed tubercle for the attachment of the iliofibularis muscle at the proximal half of the bone. In *R. tenuisiceps* (PVL 3827), this tubercle is more distally located (Baczko and Ezcurra 2013). The specimen preserves slender gastralia (diameter 1.7 mm).

Geographic and stratigraphic range.—Type locality and horizon only.

Phylogenetic analysis

The phylogenetic analysis recovered 18 most parsimonious trees (MPTs) of 3356 steps each, with a consistency index of 0.261 and a retention index of 0.626. In all the MPTs, *Dynamosuchus collisensis* nests within Ornithosuchidae (Fig 3A). *Ornithosuchus woodwardi* lies as the basal-most member of Ornithosuchidae. The clade is supported by 19 synapomorphies (the complete list of synapomorphies is in Fig 3A), such as the alveolar margin of the premaxilla not reaching the contact with the maxilla [26 (0→1)], three premaxillary teeth [42 (2→3)], mandibular symphysis present along one-third of the lower jaw [265 (0→1)], three sacral vertebrae [370 (0→1)], perforated acetabulum [455 (0→1)], and presence of the anterior trochanter on the femur [502 (0→1)]. *Dynamosuchus collisensis* was found as the sister taxon of

Venaticosuchus rusconii and this is supported by the semilunar depression on the posterolateral surface of the parabasisphenoid [238 (1)] and ascending process of the quadratojugal moderately anterodorsally to posteroventrally oriented in an angle higher than 40° [636 (0)]. The clade including both taxa is the sister group of *Riojasuchus tenuisiceps*. This arrangement relies in the strongly downturned main body of the premaxilla [29 (2)] and the strongly anteroposteriorly expanded distal end of the radius [437 (1)]. Similar to the results of Ezcurra et al. (2017), Ornithosuchidae is found as the sister taxon of Erpetosuchidae, whereas this clade is found as the sister taxon of Aetosauria.

Discussion

Ornithosuchids, first described at the end of the 19th century (Newton 1894; see Baczko and Ezcurra 2016 for additional details), were important for deciphering the relationships among basal archosaurs because of their controversial anatomical features (Gauthier 1986; Sereno 1991; Nesbitt 2011; Ezcurra et al. 2017). However, no other ornithosuchids have been found since *Venaticosuchus rusconii* was discovered in Argentina almost a half century ago (Bonaparte 1970). Furthermore, *Dynamosuchus collisensis* is the first unambiguous Ornithosuchidae from Brazil.

The presence of ornithosuchids in Upper Triassic beds from Brazil is not a surprise, as the group is recorded in coeval strata of Argentina (i.e., *V. rusconii*). The age of the strata that yielded *D. collisensis* is similar to that of the levels in which *Ornithosuchus woodwardi* from Scotland and *V. rusconii* from Argentina were found, as these strata have also yielded remains of the rhynchosaur *Hyperodapedon*, which is extensively adopted as index fossil of Carnian age (Langer et al. 2007, 2018; Martínez et al. 2011; Desojo et al. 2018). The other known ornithosuchid, *Riojasuchus tenuisiceps*, was exhumed from the Los Colorados Formation, Argentina, which is Norian in age (Kent et al. 2014). Therefore, *D. collisensis* falls within the stratigraphic range of the oldest known ornithosuchids (Fig. 3B).

The close relationship between *Venaticosuchus rusconii* and *D. collisensis* reinforces the previous proposed biostratigraphic hypotheses (Langer et al. 2007), indicating a similar faunal assemblage in both contemporaneous Paraná and Ischigualasto-Villa Unión basins. Moreover, the sister taxon affinity between *V. rusconii* and *D. collisensis* rejects a potential endemic radiation of ornithosuchids from the Ischigualasto-Villa Unión Basin and would better support multiple diversification events, at least at the Carnian. Indeed, according to Ezcurra et al. (2015, 2017), the phylogenetic affinities of proterochampsid archosauriforms and erpetosuchids would also suggest multiple dispersal events between the Ischigualasto-Villa Unión and the Paraná basins with the simultaneous appearance of several closely-related species in both basins (i.e., the Argentinean proterochampsids *Proterochampsia barrionuevoi* and *Pseudochampsia is-*

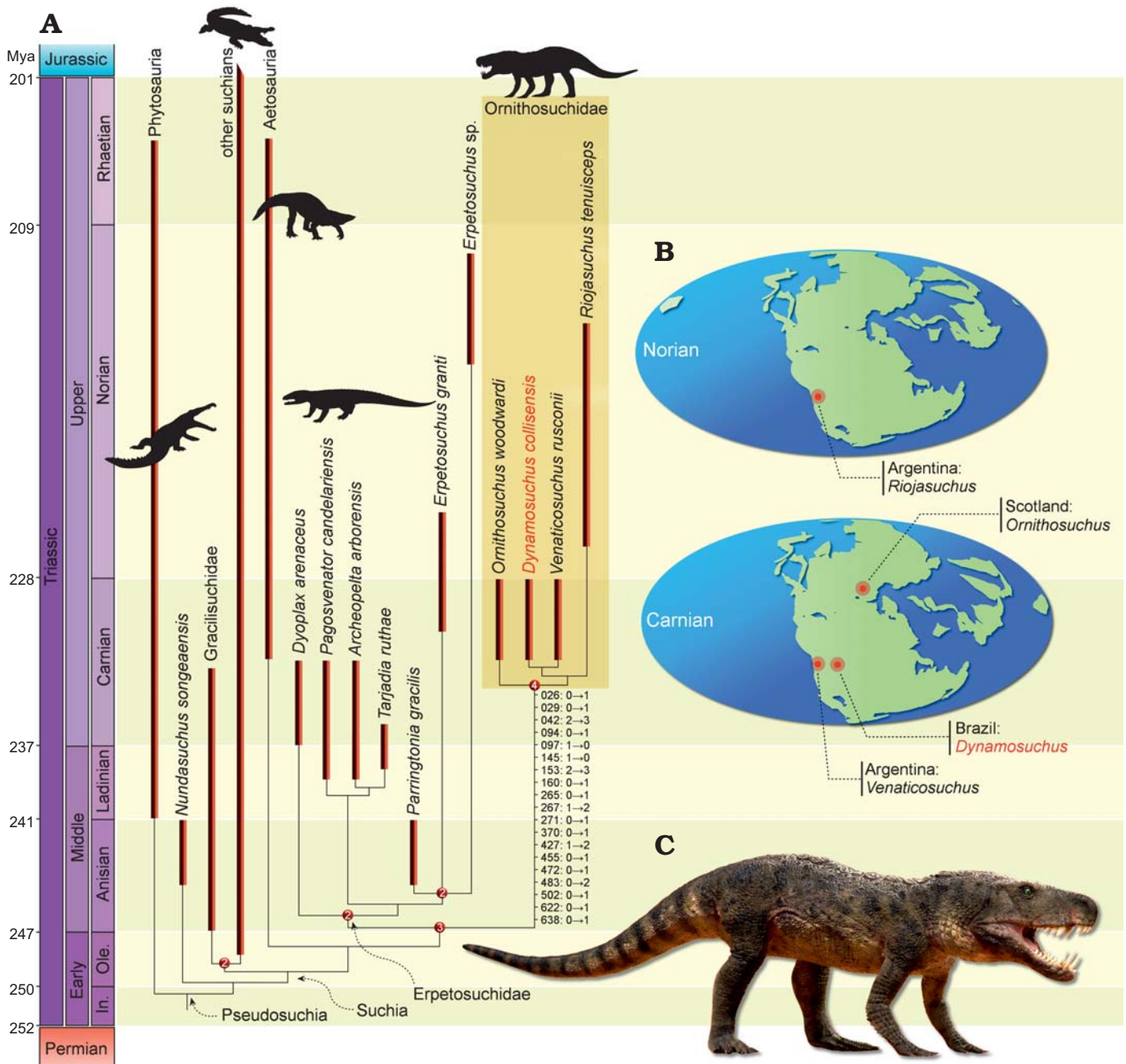


Fig. 3. Macroevolutionary patterns of Ornithosuchidae. **A**. Time-calibrated reduced strict consensus tree depicting the phylogenetic position of *Dynamosuchus collisensis* gen. et sp. nov. Numbers on nodes represent Bremer support values higher than one. Numbers associated with the ornithosuchid branch represent the characters and states that support the clade. **B**. Geographical distribution of ornithosuchids across the time. **C**. Life reconstruction of *Dynamosuchus collisensis* gen. et sp. nov. by Márcio L. Castro.

chigualastensis, and the Brazilian *Rhadinosuchus gracilis* and *Proterochampsia nodosa*; the Brazilian erpetosuchids *Archeopelta arborensis* and *Pagosvenator candelariensis* and the Argentinean *Tarjadia ruthae*). In addition, the presence of an ornithosuchid in Brazil expands the longitudinal distribution of the group, suggesting that ornithosuchids were more widespread than previously thought in the southern hemisphere. No records of the group have been found in lower latitudes close to the Paleo-Equator (Baczko and Ezcurra 2013), however, age equivalent formations or local-

ities are very scarce (Irmis et al. 2011). Therefore, ornithosuchids are still restricted to higher latitudes of northern and southern Pangea.

The discovery of *D. collisensis* (Fig. 3C) in the Paraná Basin also provides novel paleoecological implications for this type locality (i.e., Janner site). Strictly carnivorous reptiles were previously absent from this site, as the early saurpodomorph *Pampadromaeus barberenai* (Cabreira et al. 2011) was more likely to be an omnivorous animal according to a recent ecomorphological analysis (Müller and Garcia

2019). On the other hand, *Bagualosaurus agudoensis* (Pretto et al. 2018) is more related to post-Carnian sauropodomorphs, which are considered herbivorous or omnivorous. Therefore, strictly carnivorous animals are solely represented in the site through the record of ecteniniid cynodonts (Oliveira et al. 2010; Stefanello et al. 2018). Indeed, ornithosuchids have been considered as top tier predators (Walker 1964). However, recently the feeding behavior of these animals have been explored through more rigorous techniques (i.e., quantitative approaches), indicating that ornithosuchids likely adopted scavenging feeding habits or preyed only on small vertebrates (Baczko 2018). Such statement relies on the elevated bite force together with the low bite speed and the morphology of their constricted snouts. Therefore, the discovery of *D. collisensis* provides the first clue of a putative necrophagous vertebrate from the Janner site and expands our knowledge regarding the trophic chain of Late Triassic of Brazil. This is particularly interesting because necrophagous animals are an important part of the extant terrestrial ecosystems, interacting with the carcasses before its incorporation within the lithosphere. Therefore, identifying the animals that played such role in ancient environments is crucial for the reconstruction of reliable pictures of these. Indeed, the Janner site has yielded evidences of osteophagic behavior by insects (Paes et al. 2016) and the putative action of necrophagous animals that produced an accumulation with predominance of cranial elements (Müller et al. 2015).

Conclusions

Dynamosuchus collisensis is the first unambiguous member of Ornithosuchidae from Brazil, and was recovered as sister taxa of the Argentinean taxon *Venaticosuchus rusconii*. This sister taxon relationship would support multiple radiation events between Paraná and Ischigualasto-Villa Unión basins in agreement with previous hypothesis based on other archosauriforms that are shared across these basins. The discovery of an ornithosuchid in Carnian continental outcrops of Brazil provides a new shared faunal component between the basins. The Carnian archosauromorph communities of Argentina and Brazil would therefore consist of rynchosaurs, proterochampsids, ornithosuchids, aetosaurs, rauisuchians, erpetosuchids, sauropodomorphs, and theropods. In addition, the discovery *Dynamosuchus collisensis* provides the first clue of a putative necrophagous vertebrate from the oldest dinosaur-bearing beds and expands our knowledge regarding the trophic structure of the Late Triassic of Brazil.

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