RESEARCH PAPER

The oldest rhynchosaur from Argentina: a Middle Triassic rhynchosaurid from the Chañares Formation (Ischigualasto–Villa Unión Basin, La Rioja Province)

Martín D. Ezcurra · M. Jimena Trotteyn · Lucas E. Fiorelli ·
M. Belén von Baczko · Jeremías R. A. Taborda ·
Maximiliano Iberlucea · Julia B. Desojo

Abstract Rhynchosaurs first appear in the Early Triassic fossil record and flourished during the late Carnian as the dominant members of several assemblages worldwide. In Argentina, the rhynchosaur record is currently restricted to the Ischigualasto Formation of late Carnian–earliest Norian age. Recent fieldwork in the new locality of Brazo del Puma, in the lowermost levels of the Chañares Formation, yielded three rhynchosaur tooth-bearing bones, which were collected five metres above the contact with the underlying Tarjados Formation. The most complete specimen is the posterior end of the alveolar region of a left dentary. The dentary possesses densely packed tooth rows on the lingual surface and medial half of the occlusal surface, showing longitudinal *Zahnreihen*. The teeth of the occlusal surface are worn flat and those of the lingual surface are organized in multiple rows, supporting the referral of the specimen to Rhynchosauridae. In addition, the dentary teeth are conical to mesiodistally compressed, resembling the condition observed in hyperodapedontines. The rhynchosaur remains reported here are the oldest collected in Argentina and among the oldest in South America, together with an unnamed form from Brazil. The new rhynchosaur specimens come from levels in which dicynodonts are numerically dominant, whereas cynodonts are considerably less abundant. Accordingly, the specimens reported here bolster faunal differences within the Chañares Formation and add a new faunal component to this already diverse vertebrate assemblage.

Keywords Archosauromorpha · Rhynchosauria · Rhynchosauridae · South America · Los Chañares local fauna

M. D. Ezcurra (✉)
School of Geography, Earth and Environmental Sciences,
University of Birmingham, Birmingham, UK
e-mail: martindezcurra@yahoo.com.ar

M. D. Ezcurra
GeoBio-Center, Ludwig-Maximilian-Universität München,
Richard-Wagner-Str. 10, 80333 Munich, Germany

M. J. Trotteyn
INGEO, Facultad de Ciencias Exactas, Universidad de San Juan,
San Juan, Argentina

M. J. Trotteyn · L. E. Fiorelli · M. B. von Baczko ·
J. R. A. Taborda · M. Iberlucea · J. B. Desojo
CONICET, Consejo Nacional de Investigaciones Científicas y
Técnicas, Buenos Aires, Argentina

L. E. Fiorelli
CRILAR-CONICET, Entre Ríos y Mendoza s/n, Anillaco,
La Rioja, Argentina

M. B. von Baczko · J. R. A. Taborda · M. Iberlucea ·
J. B. Desojo
Sección Paleontología de Vertebrados, Museo Argentino de
Ciencias Naturales "Bernardino Rivadavia", Av. Ángel Gallardo
470, C1405DJR Buenos Aires, Argentina

Kurzfassung Rhynchosaurier sind erstmals für die Untere Trias im Fossilbericht nachgewiesen und erlebten ihre Blüte im Oberen Karnium, als eine dominierende Gruppe in merheren Fossilgesellschaften weltweit. In Argentinien sind Rhynchosauier bislang nur für die Ischigualasto Formation (Oberes Karnium-Unteres Norium) belegt. Kürzliche Grabungen in einer neuen Lokalität in Brazo del Puma, im untersten Niveau der Chañares Formation, ergaben drei zahntragende Knochen von Rhynchosaurierern. Die Knochen wurden ungefähr fünf Meter über unterliegenden Tarjados Formation gefunden. Der vollständigste Knochen repräsentiert das posteriore Ende der Zahnregion in der linken Dentale. Die Dentale besitzt dichtgepackte Zahnreihen auf der

lingualen Seite und längslaufenden Zahnreihen auf der medialen Hälfte der okklusalen Seite. Die abgeflachten Zähne der okklusalen Seite sowie die mehrreihige Anordnung der Zähne auf der lingualen Seite erlaubt eine Zuordnung zu den Rhynchosauriden. Die Zähne der Dentalen sind zusätzlich konisch bis mesiodistad zusammengedrückt, ähnlich den Zähnen von Hyperodapedontinen. Zusammen mit unbeschriebenen Resten aus Brasilien, repräsentieren die hier vorgestellten Reste den ältesten Nachweis von Rhynchosauriern aus Argentinien beziehungsweise Südamerika. Die Rhynchosaurierknochen stammen aus einem Niveau, dass vor allem durch Dicynodonten dominiert ist, während Cynodonten seltener vorkommen. Die hier vorgelstellten Reste erweitern daher die bekannte Fauna der Chañares Formation um eine weitere Gruppe und belegen zusätzlich zeitliche Unterschiede in der Faunenzusammensetzung innerhalb der Formation.

Schlüsselwörter Archosauromorpha · Rhynchosauria · Rhynchosauridae · Südamerika · Los Chañares Lokale Fauna

Institutional abbreviations

CRILAR-Pv   Centro Regional de Investigaciones y Transferencia Tecnológica de La Rioja, Paleontología de Vertebrados, Anillaco, La Rioja, Argentina

Introduction

The Triassic witnessed the origin of multiple reptile clades, including several archosauromorph lineages with disparate morphologies (e.g. Erythrosuchidae, Proterochampsidae, Phytosauria, Ornithosuchidae, Aetosauria, Silesauridae; Langer et al. 2010a, 2013; Butler et al. 2011; Nesbitt 2011; Baczko and Ezcurra 2013; Ezcurra et al. 2013; Stocker and Butler 2013; Desojo et al. 2013; Trotteyn et al. 2013). One of the most successful of these Triassic archosauromorph clades were the rhynchosaurs. Rhynchosaurs were small to medium-sized, quadrupedal, herbivorous or frugivorous animals with subtriangular skulls in dorsal view, bearing characteristic multiple tooth rows in the middle and/or posterior portions of the upper and lower jaws (e.g. Benton 1983a, 1984, 1990). The oldest possible rhynchosaur is *Noteosuchus colletti* from the lowermost Triassic rocks of the *Lystrosaurus* Assemblage Zone of South Africa (Watson 1912; Carroll 1976; Dilkes 1998), but no other possible rhynchosaur remains are currently known from the Early Triassic. The Middle

Triassic rhynchosaur record is considerably richer, being composed of several basal species from North America, Europe and Africa (e.g. *Ammorhynchus navajoi*, *Bentonyx sidensis*, *Fodonyx spenceri*, *Howesia browni*, *Mesosuchus browni*, *Rhynchosaurus articeps*, *Stenaulorhynchus stockleyi*; Owen 1842; Watson 1912; Haughton 1932; Huene 1938; Benton 1990; Dilkes 1995, 1998; Nesbitt and Whatley 2004; Hone and Benton 2008; Langer et al. 2010b). In particular, the Middle Triassic rhynchosaur record is numerically quite abundant in the Manda Beds of central Africa (Benton 1983b). Nevertheless, it was not until the early Late Triassic that rhynchosaurs became truly abundant worldwide, during which time the hyperodapedontine genus *Hyperodapedon* became the numerically dominant member of several South American, African, Indian and European vertebrate assemblages (Sill 1970; Chatterjee 1974, 1980; Benton 1983a, b; Raath et al. 1992; Langer 2005). In particular, the rhynchosaur record of Argentina is currently restricted to the genus *Hyperodapedon* from the Ischigualasto Formation of late Carnian–earliest Norian age (Sill 1970). Here, we extend the Argentinean rhynchosaur record into the Middle Triassic with the description of specimens collected during recent fieldwork in the lowermost levels of the Chañares Formation.

Fieldwork in May 2011 in the lower lithological unit of the Chañares Formation (Ischigualasto–Villa Unión Basin) of the La Rioja Province in northwestern Argentina yielded multiple tetrapod remains close to the head of the Gualo River (Fig. 1a). The new locality was named Brazo del Puma and includes the entire stratigraphic sequence of the Chañares Formation (Fig. 1b). The currently sampled fossiliferous levels of the locality are stratigraphically lower than those of the "Los Chañares" locality discovered by Alfred S. Romer, which has yielded most of the tetrapod remains currently known from the Chañares Formation (Romer 1966, 1970, 1973; Rogers et al. 2001). The fossil-bearing levels of Brazo del Puma are located 5 m above the calcrete level situated at the boundary between the Tarjados and Chañares formations, whereas "Los Chañares" locality is situated approximately 20 m above this level. The tetrapod assemblage of Brazo del Puma is composed of dicynodonts, rhynchosaurs, doswelliids and indeterminate archosauriforms and tetrapods (Fiorelli et al. 2011). The rhynchosaur remains are represented by three tooth-bearing bones (CRILAR-Pv 461–463) and were collected in very fine sandstones between isolated coarse sandy palaeo-river channels in the lowermost levels of the Chañares Formation (Fig. 1b). These rhynchosaur remains are the first record of the group in the Chañares Formation and the oldest from Argentina.
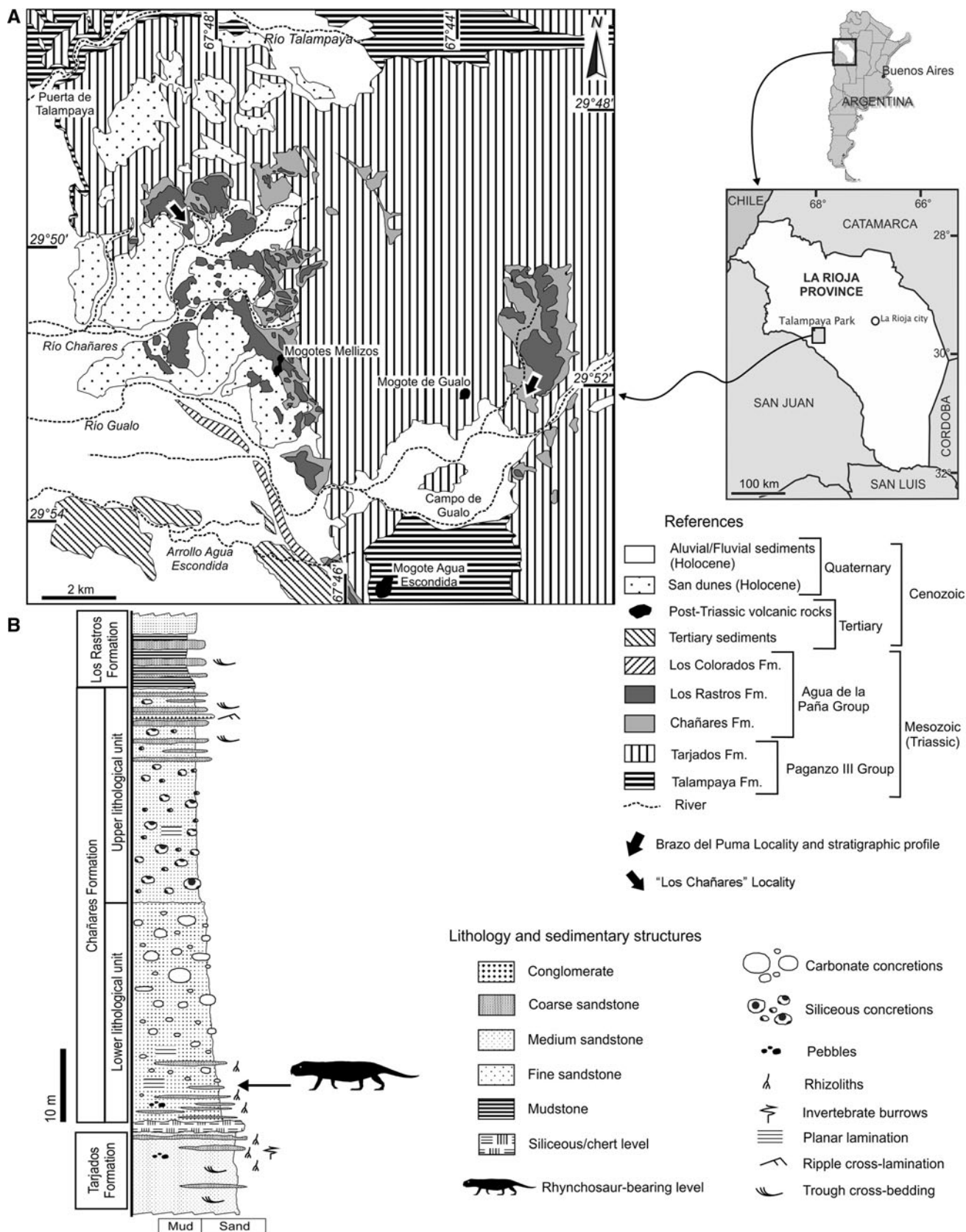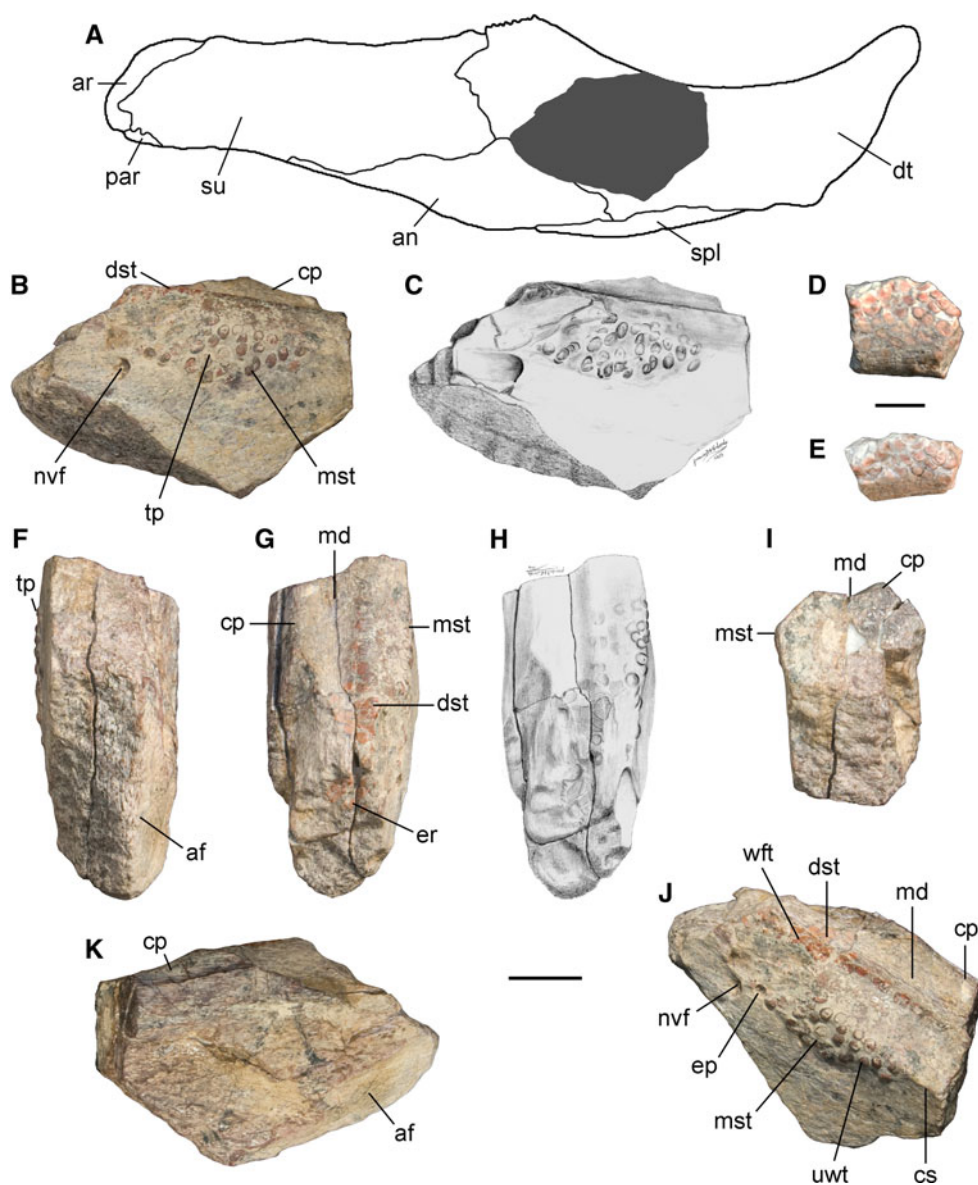
Fig. 1 **a** Geological map of the Talampaya National Park area showing the Brazo del Puma and Romer's "Los Chañares" localities (*black arrows*) of the Chañares Formation. **b** Stratigraphic profile of the Chañares Formation at the Brazo del Puma locality showing the rhynchosaur-bearing levels

Fig. 2 a Silhouette of rhynchosaur lower jaw showing the approximate position of the partial dentary CRILAR-Pv 461. **b, c, f–k** CRILAR-Pv 461. **b** Medial (=lingual); **c** line drawing of medial view; **f** ventral; **g** dorsal (=occlusal); **h** line drawing of dorsal view; **i** anterior; **j** dorsomedial views; **k** lateral. **d, e** CRILAR-Pv 462 in two different indeterminate views. *af* articular facet for angular or surangular, *an* angular, *ar* articular, *cp* coronoid process, *cs* change in slope, *dst* teeth of dorsal surface, *dt* dentary, *ep* erosion pit, *er* exposed roots, *md* median depression, *mst* teeth of medial surface, *nvf* neurovascular foramen, *par* prearticular, *spl* splenial, *su* surangular, *tp* tooth plate, *uwt* unworn tooth, *wft* teeth that have been worn flat. *Scale bars* equal 1 cm in **b, c, f–k** and 5 mm in **d, e**. Silhouette not to scale and modified from Montefeltro et al. (2010, fig. 9a), and the contact between dentary and postdentary bones is based on *Teyumbaita sulcognathus*, but the facet of CRILAR-Pv 461 would have contacted either surangular of angular. Pencil drawings **c, h** drawn by J.R.A.T.

Systematic Palaeontology

Diapsida Osborn, 1903 sensu Laurin (1991)
Archosauromorpha Huene 1946 sensu Dilkes (1998)
Rhynchosauria Osborn, 1903 sensu Dilkes (1998)

Genus and species indet.
Fig. 2d, e

Materials. CRILAR-Pv 462 and 463, fragments of tooth-bearing bones.

Horizon and locality. Brazo del Puma locality (CRILAR-Pv 462: 29°52′16.5″S 67°43′02.4″W; CRILAR-Pv 463: 29°52′16.15″S 67°43′03.2″W), close to the head of the Gualo River, 5 m above the contact between the Tarjados and Chañares formations, lower levels of the lower lithological unit [for a description of this unit see Rogers et al. (2001)] of the Chañares Formation, Ischigualasto–Villa Unión Basin, Talampaya National Park, La Rioja Province, north-western Argentina (Fig. 1).

Age. The Chañares Formation is dated as Ladinian (Rogers et al. 2001) or Ladinian–earliest Carnian (Desojo et al. 2011) based on vertebrate biostratigraphy and a minimum age constraint based on radioisotopic dating of the lower levels of the overlying Ischigualasto Formation (Rogers et al. 1993; Furin et al. 2006). The stratigraphic occurrence of the rhynchosaur specimens described here in the lowermost levels of the Chañares Formation means that it is very likely that they are of late Middle Triassic age.

Rhynchosauridae Huxley, 1859 sensu Dilkes (1998)

Genus and species indet.
Fig. 2b, c, f–k

Materials. CRILAR-Pv 461, a partial left dentary.

Horizon, locality and age. Brazo del Puma locality (29°52′15.8″S 67°43′02.1″W), from the same horizon and age as CRILAR-Pv 462 and 463.

Description

Two of the rhynchosaur specimens (CRILAR-Pv 462, 463) are small fragments of tooth-bearing bones with some in situ teeth, with CRILAR-Pv 462 having a maximum linear measurement of 12.6 mm (Fig. 2d, e). Their fragmentary condition precludes determining if they represent maxillary or dentary remains. The most complete specimen (CRILAR-Pv 461) is a partial posterior left dentary that includes the alveolar margin (Fig. 2a). The specimen has a maximum preserved length of 46.7 mm and height of 29.7 mm. The partial bone represents around 44 % of the total length of the complete dentary based on comparison with the holotype of *Teyumbaita* (*T. sulcognathus*; Montefeltro et al. 2010) (Fig. 2a). The lateral surface of CRILAR-Pv 461 is mostly damaged but possesses on its most ventrally preserved region an extensive, slightly dorsoventrally convex articular facet, with a maximum preserved length of 32.1 mm and height of 10.0 mm, for the reception of the surangular or angular (Fig. 2f, k). This articular facet is posterolaterally facing and possesses multiple, thin, longitudinal striations. The main axis of the preserved portion of the facet is posterodorsally to anteroventrally oriented, but due to the strongly damaged lateral surface of the bone it is not possible to assess the actual shape of the facet. The dorsal portion of the dentary preserves the anterior tip of the coronoid process (Fig. 2b, c, g–j), which houses the lateral cutting blade in rhynchosaurids (e.g. *Hyperodapedon huenei*: Langer and Schultz 2000: fig. 5; *Teyumbaita sulcognathus*: Montefeltro et al. 2010: fig. 9). The dorsal surface of the coronoid process is concave in lateral view (Fig. 2b, c, k), restricted to the lateral half of the bone in dorsal (=occlusal) view (Fig. 2g), and has a maximum preserved width of 10.2 mm. The base of the coronoid process has an almost planar lateral surface and a strongly transversely convex dorsal surface (Fig. 2i). CRILAR-Pv 461 possesses a tooth plate restricted to the medial half of the dorsal surface of the bone that is separated from the base of the coronoid process by a wide and slightly transversely concave longitudinal median depression (Fig. 2g–j). The alveolar surface of the bone has a

straight dorsal margin in medial view. The preserved portion of the tooth plate has a length of 21 mm, extends onto both dorsal and medial (=lingual) surfaces of the bone, and is composed of, at least, five densely packed tooth rows (Fig. 2b, c, j). It is not possible to assess the total number of rows of the tooth plate or its posterior extension due to breakage of the bone. A conspicuous change in the slope of the surface of the bone of around 50° distinguishes a dorsally and dorsomedially facing alveolar surface from a medially facing one (Fig. 2i, j). The teeth of the dorsal and dorsomedial surface are worn flat and those of the medial surface are either partially worn or are mostly unworn with enamel preserved, indicating that the younger teeth are situated posteroventrally in medial view and the older teeth are situated on the dorsal surface of the bone (Fig. 2g, h). As a result, this pattern of tooth wear indicates the presence of longitudinal *Zahnreihen* (see DeMar 1971; Chatterjee 1974; Benton 1984; Dilkes 1995), as occurs in other rhynchosaurs (Benton 1984; Dilkes 1998). At least one erosion pit without a tooth (sensu Benton 1984) can be observed in the most posteroventral preserved region of the tooth plate (Fig. 2j). The teeth are ankylosed to the bone, deeply rooted, as exposed in the most posterior portion of the bone in dorsal view, and conical to mesiodistally compressed in medial view (e.g. with a mesiodistal length of 1.6 mm and width/ height of 2.2 mm) (Fig. 2b, c). The anterior end of the tooth plate is preserved and it is situated at the level of the anterior margin of the coronoid process, resembling the condition of *Teyumbaita* (*T. sulcognathus*: Montefeltro et al. 2010: fig. 5b). A large and posteriorly opening neurovascular foramen with a dorsoventral height of 3.5 mm is present posteroventral to the preserved portion of the tooth plate (Fig. 2b, c, j). This foramen is not present in other rhynchosaurs of which we are aware (e.g. *Mesosuchus browni*: Dilkes, 1998; *Hyperodapedon huenei*: Langer and Schultz 2000: fig. 5b; *Teyumbaita sulcognathus*: Montefeltro et al. 2010: fig. 9b). The medial surface of the dentary, below the tooth plate, is almost flat and should have contributed partially to the lateral wall of the Meckelian canal. The ventral border of the bone is not preserved.

Discussion

The new specimens described here (CRILAR-Pv 461–463) can be assigned to Rhynchosauria sensu Dilkes (1998) due to the presence of multiple tooth rows with densely packed teeth (Fig. 2b–e, g, h, j) (Benton 1984; Dilkes 1998). Moreover, CRILAR-Pv 461 also possesses clear longitudinal *Zahnreihen*, bolstering its assignment to Rhynchosauria. In particular, the presence of multiple medial tooth rows in CRILAR-Pv 461 is an apomorphy shared with rhynchosaurid rhynchosaurs (e.g. *Rhynchosaurus articeps*,

Stenaulorhynchus stockleyi, *Teyumbaita sulcognathus*, some species of the genus *Hyperodapedon*; Langer et al. 2000; Montefeltro et al. 2010, 2013: characters 47) and contrasts with the absence of medial dentary teeth in the basal rhynchosaur *Mesosuchus* (*M. browni*: Dilkes 1998). CRILAR-Pv 461 shares with the rhynchosaurids *Stenaulorhynchus stockleyi*, *Mesodapedon kuttyi*, the "Mariante rhynchosaur" and *Teyumbaita sulcognathus* the presence of densely packed medial teeth (Fig. 2b, c, j) (Montefeltro et al. 2010, 2013: characters 48), indicating the assignment of the Chañares specimen to Rhynchosauridae (sensu Dilkes 1998). It should be highlighted that the latter condition is restricted to the above-mentioned rhynchosaur species and is absent in the rhynchosaurids *Rhynchosaurus*, *Fodonyx*, *Bentonyx*, *Isalorhynchus* and species of the genus *Hyperodapedon* (Montefeltro et al. 2010, 2013: characters 48). As a result, CRILAR-Pv 461 should be considered a rhynchosaurid more basal than the clade composed of *Hyperodapedon* species. CRILAR-Pv 461 differs from other rhynchosaurs in the presence of a large, posteriorly opening neurovascular foramen immediately ventral to the tooth plate on the medial surface of the dentary (Fig. 2b, c, j). Although CRILAR-Pv 462 and 463 cannot be diagnosed beyond Rhynchosauria, they possess a morphology consistent with that of CRILAR-Pv 461 and it cannot be discarded that the three specimens may have belonged to the same species. CRILAR-Pv 461 might represent a new rhynchosaur species, but we have decided not to coin a new taxon because its fragmentary nature would complicate or prevent referral of additional specimens in the future.

The rhynchosaur remains reported here from the lowermost levels of the Chañares Formation are the oldest collected in Argentina and among the oldest recorded in South America, together with the still unnamed "Mariante rhynchosaur" from coeval beds of the Santa Maria Formation (Paraná Basin) of southern Brazil (Schultz and Azevedo 1990). The new rhynchosaur specimens come from levels in the Brazo del Puma locality of the Chañares Formation (Fig. 1a) in which dicynodonts are numerically dominant and cynodonts are very scarce (Fiorelli et al. 2011). This condition clearly contrasts with that observed in the well-sampled "Los Chañares" locality (Fig. 1a), which is numerically dominated by the traversodontid cynodont *Massetognathus pascuali*, with dicynodonts being considerably scarcer (Benton 1983b; Rogers et al. 2001). In addition, no rhynchosaur specimen has been collected from the "Los Chañares" locality despite intensive sampling over many years. It is striking to note that a similar pattern is observed in the assemblage zones recognized for the roughly coeval lower Santa Maria Formation of Brazil. The possibly older *Dinodontosaurus* Assemblage Zone (AZ) is numerically dominated by the

dicynodont *Dinodontosaurus* and yielded rhynchosaur specimens, whereas the possibly younger *Santacruzodon* AZ is dominated by the traversodontid cynodont *Santacruzodon* (closely related to *Massetognathus*) (Langer 2007). The latter suggests a probable biostratigraphical correlation between the lowermost levels of the Chañares Formation with the *Dinodontosaurus* AZ and the middle levels of the lower lithological unit of the Chañares Formation with the *Santacruzodon* AZ of the lower Santa Maria Formation (detailed discussion about this issue lies beyond the scope of this contribution and will be published elsewhere). As a result, it also suggests that the faunal differences between the rhynchosaur-bearing levels of the Brazo del Puma locality (ca. 5 m above the base of the formation) and the younger "Los Chañares" locality (ca. 20 m above the base of the formation) are probably a consequence of temporal variation in the fauna (Fig. 1b). Spatial variations within the basin are less probable because the palaeo-environments of both localities are similar (Fiorelli et al. 2011) and the two localities are separated by only around 10 km. Taphonomical differences may have also played an important role in these faunal differences, because in the Brazo del Puma locality almost all the specimens were not collected from the volcanic carbonate concretions that yield the vast majority of specimens in the "Los Chañares" locality. The concretions of the latter locality produced a bias towards smaller specimens that have been hypothesized to have mostly died in a mass mortality (Rogers et al. 2001). However, there is no clear evidence that taphonomical differences can account for the differences observed between the lower and middle levels of the lower lithological unit of the Chañares Formation. Accordingly, the rhynchosaur specimens reported here bolster temporal faunal differences within the Chañares Formation and add a new faunal component to this already diverse vertebrate assemblage.

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