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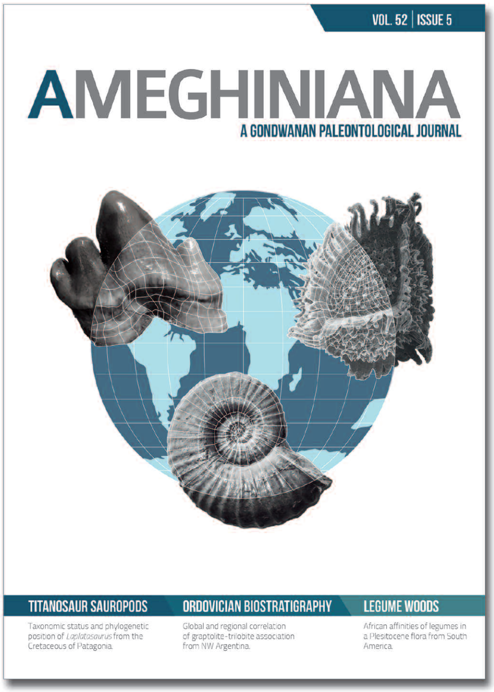

ARCHOSAUROMORPH REMAINS FROM THE TARJADOS FORMATION (EARLY–MIDDLE TRIASSIC, NW ARGENTINA)

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ARTICLES

ARCHOSAUROMORPH REMAINS FROM THE TARJADOS FORMATION (EARLY–MIDDLE TRIASSIC, NW ARGENTINA)

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Abstract. The Agua de la Peña Group of the Ischigualasto-Villa Unión Basin (northwestern Argentina) documents the evolution of archosauromorph assemblages in western Gondwana during the late Middle and Late Triassic. However, the South American archosauromorph record in the aftermath of the Permo/Triassic mass extinction (Early–early Middle Triassic) is remarkably scarce and restricted to isolated bones. Here, we describe a recently collected isolated second sacral vertebra and rib that represents one of the few fossils known from the Lower–Middle Triassic Tarjados Formation, the unit that underlies the Agua de la Peña Group. This specimen is identified as an archosauromorph because of the presence of a non-notochordal vertebra and a bifurcated distal end of the second sacral rib. A quantitative phylogenetic analysis places the new specimen as an archosauromorph more derived than protorosaurs. In particular, this specimen resembles *Pamelaria*, *Prolacerta* and early rhynchosaurs in the presence of a squared posterior projection of the bifurcated second sacral rib. The new specimen represents the first body fossil of a diapsid formally described in the Tarjados Formation and the oldest member of the group in the Ischigualasto-Villa Unión Basin. As a result, this specimen increases the high-level taxonomic richness of Archosauromorpha in South America in the aftermath of the Permo/Triassic mass extinction.

Key words. Diapsida. Archosauromorpha. Phylogeny. Mesozoic. South America.

Resumen. RESTOS DE UN ARCOSAUROMORFO DE LA FORMACIÓN TARJADOS (TRIÁSICO TEMPRANO–MEDIO, NO ARGENTINA). El Grupo Agua de la Peña de la Cuenca de Ischigualasto-Villa Unión (noroeste de Argentina) documenta la evolución de las faunas de arcosauromorfos en el oeste de Gondwana durante el Triásico Medio tardío y Triásico Tardío. Sin embargo, el registro de arcosauromorfos sudamericanos luego de la extinción masiva permo/triásica (Triásico Temprano–Medio temprano) es particularmente escaso y restringido a huesos aislados. Describimos aquí una vértebra y costilla sacra colectada recientemente, que representa uno de los pocos fósiles conocidos de la Formación Tarjados (Triásico Inferior–Medio), unidad que subyace al grupo Agua de la Peña. Este espécimen es identificado como un arcosauromorfo debido a la presencia de una vertebra no notocordal y un extremo distal birfurcado de la segunda costilla sacra. Un análisis filogenético cuantitativo ubica al nuevo espécimen como un arcosauromorfo más derivado que los protorosaurios. En particular, este ejemplar se asemeja a *Pamelaria*, *Prolacerta* y rincosaurios basales en la presencia de una proyección posterior cuadrangular del extremo distal de la segunda costilla sacra. El nuevo espécimen representa el primer registro fósil corpóreo formalmente descripto de un diápsido en la Formación Tarjados y el más antiguo para el grupo en la Cuenca de Ischigualasto-Villa Unión. Como resultado, este ejemplar incrementa la riqueza taxonómica de Archosauromorpha en América del Sur inmediatamente después de la extinción masiva Permo/Triásica.

Palabras clave. Diapsida. Archosauromorpha. Filogenia. Mesozoico. América del Sur.

The Ischigualasto-Villa Unión Basin crops out in northwestern Argentina as a sequence of approximately 6,000 metres of continental sedimentary rocks (Stipanicic and Bonaparte, 1979; Stipanicic and Marsicano, 2002; Mancuso and Caselli, 2012). Abundant and exquisitely preserved fossils have been collected from the Agua de la Peña Group of this basin (*i.e.*, Chañares, Los Rastros, Ischigualasto and Los Colorados formations) and document the evolution of vertebrate assemblages in western Gondwana during the late Middle and Late Triassic (Rogers *et al.*, 2001; Arcucci *et al.*, 2004; Fiorelli *et al.*, 2013; Martínez *et al.*, 2013). In particular, this sedimentary sequence documents the early diversification of archosauromorphs, one of the major groups of diapsid reptiles, which includes approximately 10,000 living species of birds and crocodilians (Clements, 2007) and all extinct species more closely related to these extant groups than to lepidosaurs (Gauthier, 1984; Gauthier *et al.*, 1988; Dilkes, 1998). The oldest known archosauromorphs are represented by four nominal species restricted to Upper Permian rocks of Europe and Africa (*e.g.*, *Protorosaurus speneri* Meyer, 1832; *Archosaurus rossicus* Tatarinov, 1960; *Eorasaurus olsoni* Sennikov, 1997; *Aenigmastropheus parringtoni* Ezcurra, Scheyer and Butler, 2014; Meyer, 1830; Sennikov, 1988; Gower and Sennikov, 2000; Gottmann-Quesada and Sander, 2009). In the aftermath of the Permo/Triassic mass extinction (Early–early Middle Triassic), the archosauromorph fossil record is considerably more abundant worldwide and morphologically diverse, including members of Rhynchosauria, Tanystropheidae, Prolacertidae, Proterosuchidae, Erythrosuchidae, Euparkeriidae, and Archosauria (Charig and Reig, 1970; Charig and Sues, 1976; Carroll, 1976; Dilkes, 1998; Gower and Sennikov, 2000; Butler *et al.*, 2011; Nesbitt, 2011; Sennikov, 2011; Ezcurra *et al.*, 2013; Sookias and Butler, 2013). However, the South American Early–early Middle Triassic archosauromorph record is remarkably scarce, being restricted to isolated bones from the Early Triassic Sanga do Cabral Formation of southern Brazil (Langer and Schultz, 1997; Dias-da-Silva, 1998; Langer and Lavina, 2000; Da-Rosa *et al.*, 2009; Dias-da-Silva and Da-Rosa, 2011) and the Permo–Triassic Buena Vista Formation of northeastern Uruguay (Ezcurra *et al.*, 2015). The only previous record of an Early Triassic archosauromorph from Argentina is based on a partial postcranium that represents the holotype of *Koilamasuchus gonzalezdiazi* Ezcurra, Lecuona and Martinelli, 2010 (Bonaparte, 1981), but it was recently redated as Middle–Late Triassic based on a single radioisotopic dating (Ottone *et al.*, 2014; however, correlations based on vertebrate biostratigraphy still suggest an Early Triassic age; see Bonaparte, 1981; Martinelli *et al.*, 2009; Ezcurra *et al.*, 2010). Here, we increase the South American early archosauromorph record with the description of a new specimen collected in the Early–Middle Triassic Tarjados Formation, which was found during fieldwork in the Ischigualasto-Villa Unión Basin in the southern Spring of 2014. This specimen represents the first diapsid formally described from this sedimentary unit and, at the same time, the oldest record of the group in the Ischigualasto-Villa Unión Basin.

GEOLOGICAL AND PALAEONTOLOGICAL SETTING

The specimen described here comes from the upper levels of the Tarjados Formation that are exposed at the Campo de Córdoba locality, Talampaya National Park, southwestern La Rioja Province, NW Argentina (Fig. 1). Although the specimen was found on the surface (not in-situ) and with some degree of transport, the sedimentary matrix containing the fossil corresponds to the same fine to medium reddish-grey quarzitic sandstone that is characteristic of the sandy upper levels of the Tarjados Formation. At the Campo de Córdoba locality, the middle section of the Chañares Formation unconformably overlies the upper portion of the Tarjados Formation. Romer and Jensen (1966) divided the Tarjados Formation into lower and upper members mainly because of their difference in colour, being reddish-brown and reddish-grey, respectively. Both members are interpreted as ephemeral fluvial systems interbedded with eolian sandstone and playa-lake deposits (Krapovickas *et al.*, 2013). The upper member of the Tarjados Formation is characterized by thick and massive sandstone bodies and sporadic lenses interbedded with coarse sandy and conglomeratic river channels, some of them showing cross-bedding stratification (Rogers *et al.*, 2001; Fiorelli *et al.*, 2013; Krapovickas *et al.*, 2013). The Tarjados Formation was deposited in a climate with high seasonality, alternating wet and dry conditions in a semi-arid environment (Krapovickas *et al.*, 2013). The unit is alternatively dated as Early (*e.g.*, Morel *et al.*, 2001) or Middle Triassic (*e.g.*, Rogers *et al.*, 2001; Mancuso and Caselli, 2012). As a result of the poor chronostratigraphic constraint of the unit, we consider the Tarjados Formation as Early–Middle Triassic in age because it is overlied by the late Middle–early Late Triassic Chañares Formation (Desojo *et al.*, 2011; Irmis *et al.*, 2013). The age of the Chañares Formation, and consequently the upper age of the Tarjados Formation, is based on biostratigraphical correlations (Rogers *et al.*, 2001; Desojo *et al.*, 2011) and radioisotopic datings (Irmis *et al.*, 2013).

The Tarjados Formation outcrops extensively in the Talampaya National Park, being considerably better exposed than the Chañares Formation (Rogers *et al.*, 2001; Fiorelli *et al.*, 2013). Nevertheless, only one previous body fossil

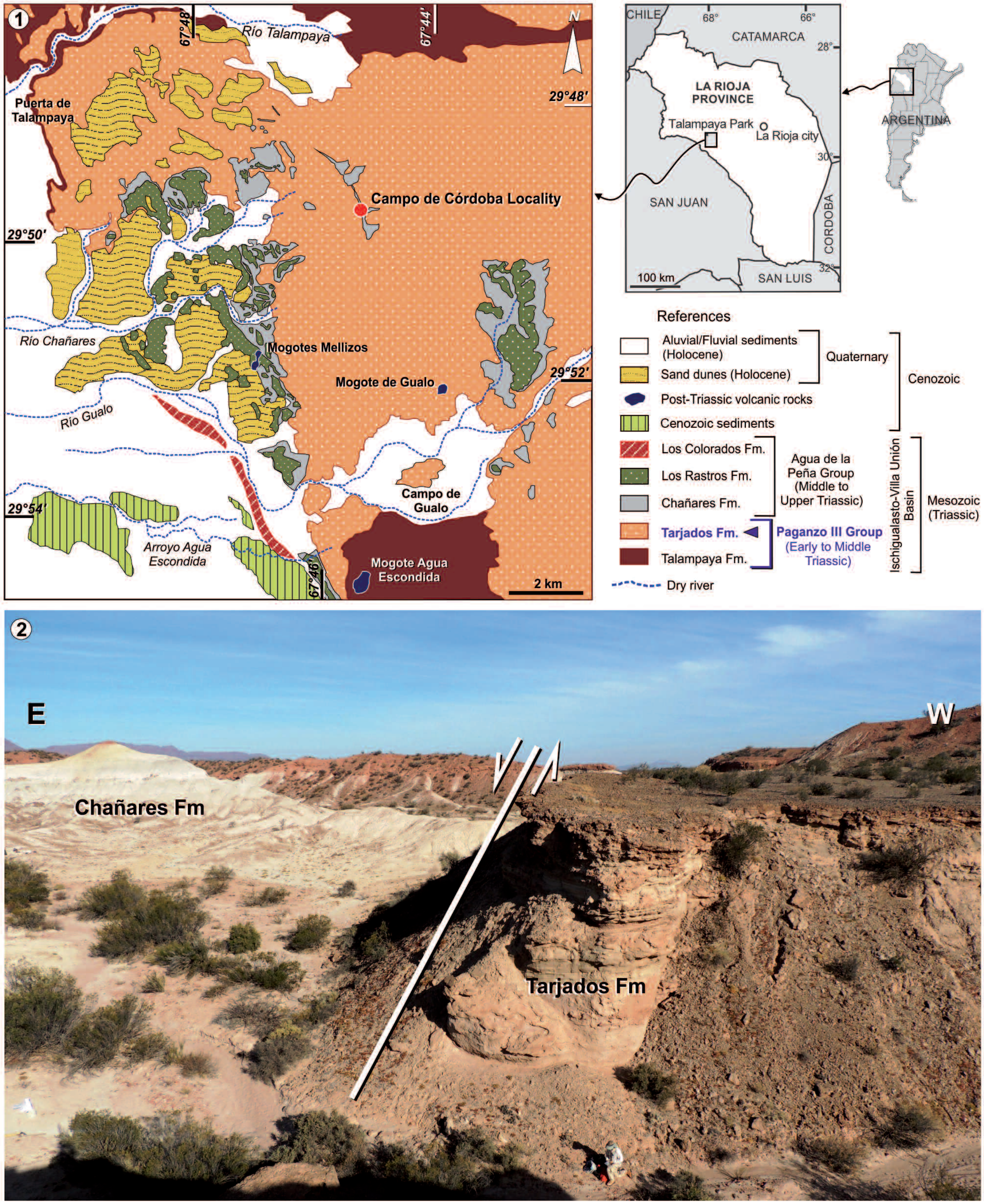

Figure 1. Geological and geographic occurrence of CRILAR-Pv 499. **1,** Geological map of the outcrops in the area of the Talampya National Park (modified from Fiorelli *et al.*, 2013); **2,** photograph of the Campo de Córdoba locality showing the area where the specimen was collected.

record has been documented from the Tarjados Formation in the Talampaya National Park area. That record corresponds to fragmentary dicynodont bones (MCZ 3468, 3469; Fig. 2) reported by Romer (1966, p. 8; pers. obs. based on Romer's original geological map) and assigned to an indeterminate kannemeyeriid by Bonaparte (1969). Outside the Talampaya National Park, unpublished medium-sized archosaur and small therapsid remains have been preliminary reported from the Patquía area (Mancuso *et al.*, 2010). The vertebrate ichnological record of the Tarjados Formation is composed of the ichnogenera *Rhynchosauroides* and *Synaptichnium* (Melchor and de Valais, 2006; Klein and Lucas, 2010) and large burrows probably made by tetrapods (Mancuso *et al.*, 2010).

Institutional abbreviations. **AM,** Albany Museum, Grahamstown, South Africa; **BP,** Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), University of the Witswatersrand, Johannesburg, South Africa; **CRILAR-Pv,** Centro de Investigaciones Científicas y Tranferencia Tecnológica, Paleontología de Vertebrados, Anillaco, La Rioja, Argentina; **ISI,** Indian Statistical Institute, Kolkata, India; **MCZ,** Museum of Comparative Zoology, Harvard University, Boston, USA; **NMQR,** National Museum, Bloemfontein, South Africa; **PIMUZ,** Paläontologisches Institut und Museum der Universität Zürich, Zurich, Switzerland; **SAM-PK,** Iziko South African Museum, South Africa; **SHYMS,** Shropshire Museums, Ludlow, UK; **SMNS,** Staatliches Museum für Naturkunde, Stuttgart, Germany.

SYSTEMATIC PALAEONTOLOGY

Diapsida Osborn, 1903 *sensu* Laurin (1991)
Sauria Gauthier, 1984 *sensu* Gauthier *et al.* (1988)
Archosauromorpha Huene, 1946 *sensu* Dilkes (1998)

Gen. et sp. indet.
Figure 3

Material. CRILAR-Pv 499, partial second sacral vertebra and right rib.

Horizon and locality. Campo de Córdoba locality (29°49′ 58.8″ S; 67°45′ 03.8″ W), upper levels of the Tarjados

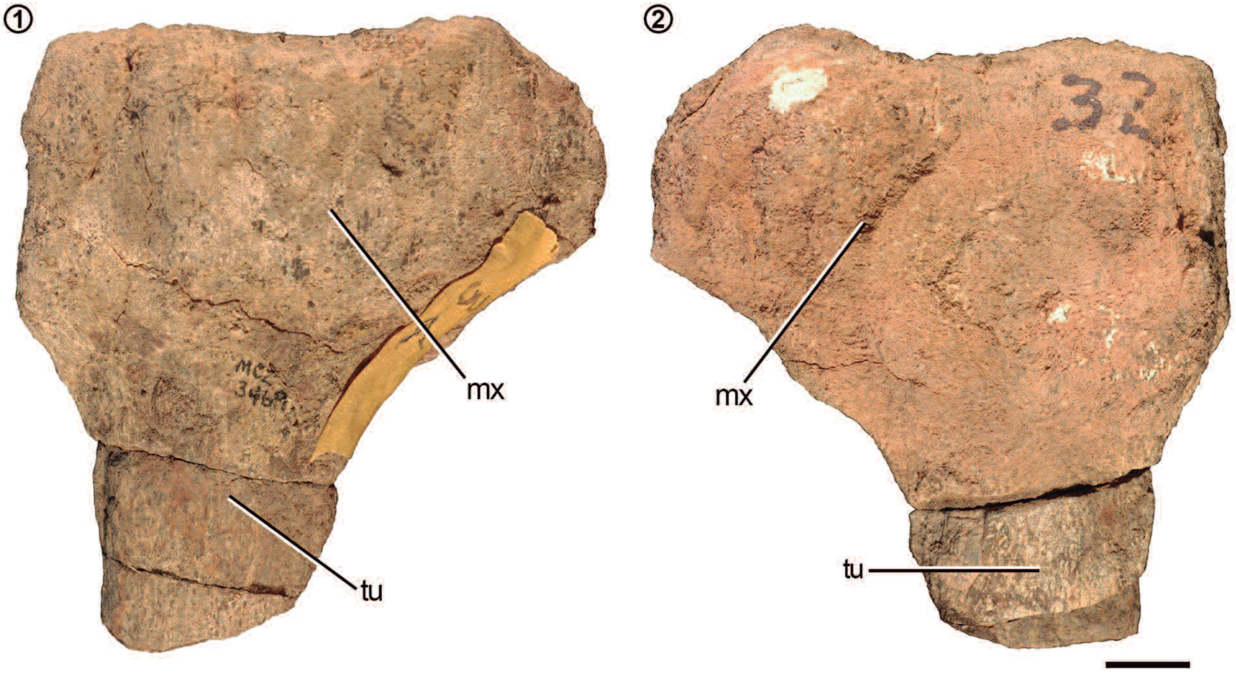

Figure 2. Indeterminate kannemeyeriid dicynodont partial left maxilla from the Tarjados Formation (MCZ 3469); **1,** lateral view; **2,** medial view. Abbreviations: **mx,** maxilla; **tu,** tusk. Scale bar= 2 cm. Photographs courtesy of Roland Sookias.

Formation (Early–Middle Triassic), Paganzo III Group, Ischigualasto-Villa Unión Basin, Talampaya National Park, La Rioja Province, northwestern Argentina (Fig. 1).

Description

The specimen (CRILAR-Pv 499) is represented by an isolated partial vertebra preserving the anterior third of the centrum, the base of the left transverse process, the right transverse process fused to the rib, and the natural mould of part of the neural canal (Fig. 3). The rib is fairly complete, though it is missing the anterior end of the distal articular surface and the dorsal surface is damaged. CRILAR-Pv 499 is interpreted as a sacral vertebra because the base of the transverse process is anteroposteriorly long and adjacent to the anterior margin of the centrum, and the rib is transversely short. The posterior end of the distal articular surface of the rib is level with the neural canal, as occurs with the second sacral ribs of other diapsids (*e.g.*, *Petrolacosaurus kansensis* Lane, 1945: Reisz, 1981; *Youngina capensis* Broom, 1914: BP/1/3679; *Mesosuchus browni* Watson, 1912: SAM-PK-6046; *Prolacerta broomi* Parrington, 1935: BP/1/2675). By contrast, the entire distal articular surface of the first sacral rib is situated more ventrally –level with the ventral half of the centrum– in diapsids (*e.g.*, *Prolacerta broomi*: BP/1/2675). As a result, CRILAR-Pv 499 is identified as a second sacral vertebra.

The vertebra is not notochordal and the anterior articular surface is moderately concave (Fig. 3: aas). This articular surface is slightly broader transversely than tall dorsoventrally (Table 1) and D-shaped in contour, with a straight to gently concave dorsal margin. The centrum is moderately compressed transversely in ventral view, acquiring its

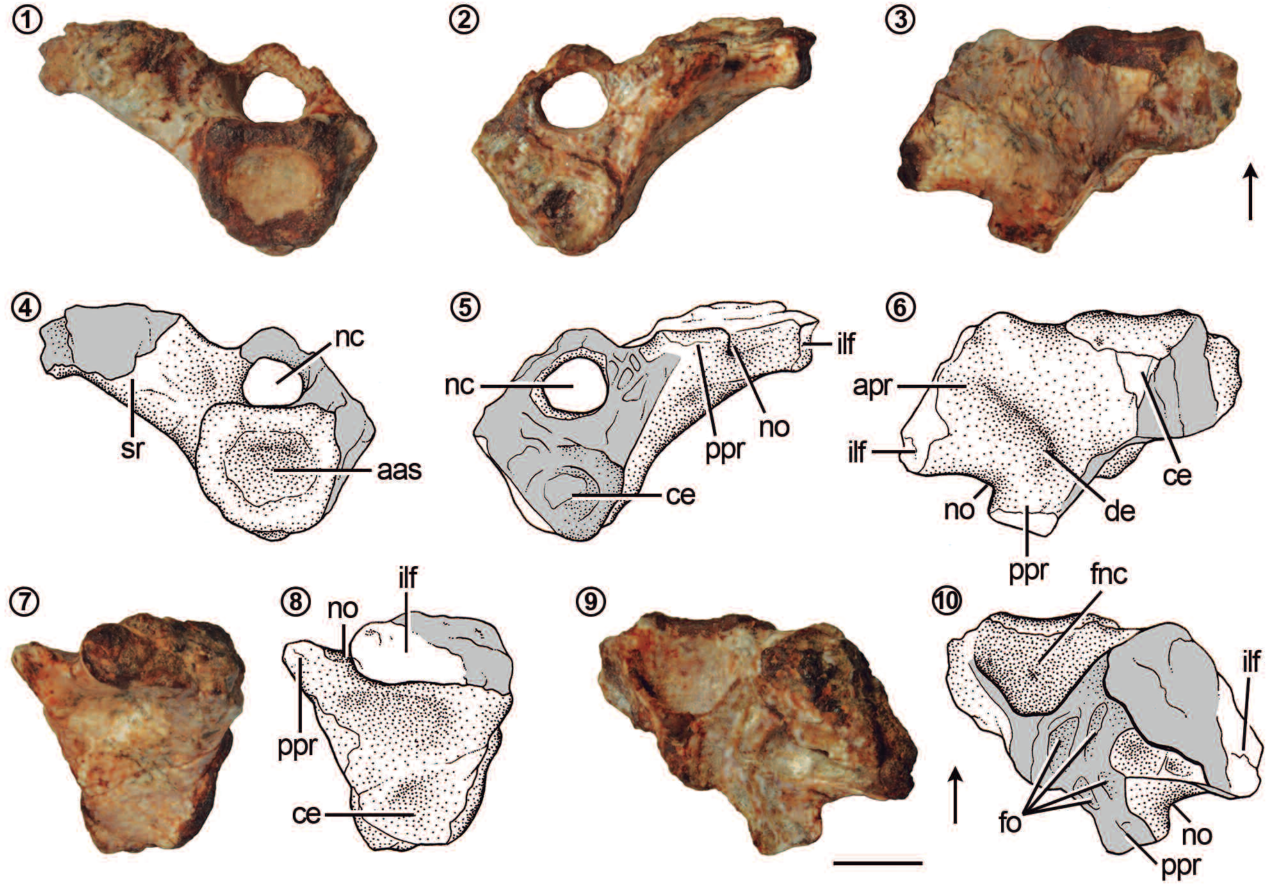

Figure 3. Archosauromorph partial second sacral vertebra and right rib (CRILAR-Pv 499); **1, 4,** anterior view; **2, 5,** posterior view; **3, 6,** ventral view; **7, 8,** right lateral view; **9, 10,** dorsal view. The arrows in Figures 3.3, 3.6, 3.9 and 3.10 indicate anterior direction. Abbreviations: **aas,** anterior articular surface; **apr,** anterior projection; **ce,** centrum; **de,** depression; **fnc,** floor of the neural canal; **fo,** fossae; **ilf,** iliac articular facet; **nc,** neural canal; **no,** notch; **ppr,** posterior projection; **sr,** sacral rib. Scale bar= 5 mm.

Table 1. List of measurements of CRILAR-Pv 499 in millimetres.

Measurement	*Length*	*Width*	*Height*
Centrum	*[8.1]*	-	-
Anterior facet of the centrum	-	*8.3*	*8.1*
Anterior exit of the neural canal	-	*8.2*	*4.9*
Right transverse process + rib	-	*14.0*	-

Values between square brackets indicate incomplete measurements (due to post-mortem damage) and the value given is the maximum measurable. Maximum deviation of the calliper is 0.02 mm but measurements were rounded to the nearest 0.1 millimetre.

maximum degree of compression where it is broken off. The ventral surface is transversely convex, without a median longitudinal groove or keel. The lateral surface of the centrum is gently concave anteroposteriorly and lacks depressions. The neurocentral suture is still visible on the right side of the element. This suture extends posteroventrally from the anterodorsal corner of the centrum. The surface for articulation with the pedicle of the neural arch is exposed on the left side and possesses the same orientation as the neurocentral suture of the right side.

The mould of the neural canal indicates that this opening was subcircular and subequal in width to the anterior surface of the centrum (Fig. 3: nc; Table 1). The base of the transverse process is placed level with the dorsal margin of the centrum and occupies the entire preserved anteroposterior length of the neural arch. The transverse process is dorsolaterally oriented, contrasting with the laterally or ventrolaterally oriented transverse processes of the second sacral vertebrae of other basal archosauromorphs (*e.g.*, *Tanystropheus longobardicus* Bassani, 1886: SMNS 54631; *Pamelaria dolichotrachela* Sen, 2003: ISI R333/1; *Mesosuchus browni*: SAM-PK-6046; *Erythrosuchus africanus* Broom, 1905a: NHMUK R3592). This condition potentially represents a unique feature of CRILAR-Pv 499. The transverse process + rib are 1.7 times transversely wider than the anterior articular surface of the centrum (Table 1). One of the most conspicuous features of the rib is its deeply birfurcated distal end (Fig. 3: no), as occurs in the second sacral rib of several basal saurians (Dilkes, 1998) (see Discussion). The anterior distal projection of the rib (Fig. 3: apr) harbours the facet for articulation with the ilium, but only the posterior portion of this projection is preserved (Fig. 3: ilf). This articular surface appears to be restricted dorsally, being placed level with the neural canal. However, the anterior half of the articular surface should have extended anteroventrally towards the level of the anterodorsal corner of the centrum to contact the posterior margin of the articular surface of the first sacral rib, as occurs in other basal diapsids (*e.g., Prolacerta broomi*: BP/1/2675). The posterior distal projection of the rib is shorter (Fig. 3: ppr), being considerably less laterally projected than the anterior projection. The posterior projection possesses a non-articular distal end that is dorsoventrally thin and squared in dorsal view, as occurs in a few basal archosauromorphs (see Discussion).

The vast majority of the dorsal surface of the transverse process + rib is not preserved and the internal structure of the bone seems to be exposed as a result of this breakage. This internal structure possesses a series of trabeculae that delimit fossae of different sizes and shapes (Fig. 3: fo). The largest fossa is placed in the posteromedial half of the anterior projection of the rib. A thick, anterolaterally-to-posteromedially oriented ridge subdivides this fossa into a very small tear-drop-shaped depression anteriorly and a larger subtriangular area posteriorly in dorsal view. The borders and the floor of this fossa are natural, indicating that this feature is not a taphonomic artefact and, as a result, the transverse process + rib possessed large internal cavities. A considerably smaller, tear-drop-shaped internal cavity is situated adjacent to the posterior margin of the base of the posterior projection of the rib. This cavity is anterolaterally-to-posteromedially oriented. The medial borders of the large and small cavities are defined by an anteroposteriorly oriented ridge. This ridge extends along the entire anteroposterior length of the base of the transverse process. The ventral surface of the transverse process + rib possesses a large and moderately deep depression placed close to the junction between the anterior and posterior projections of the distal end of the rib (Fig. 3: de). This depression is suboval with an anterolaterally-to-posteromedially oriented main axis.

Discussion

The fragmentary condition of CRILAR-Pv 499 implies that the number of phylogenetically informative characters that can be evaluated in this specimen is low. However, CRILAR-Pv 499 preserves some characters that have been recently recovered as apomorphies of Archosauromorpha or lesser inclusive clades (Ezcurra *et al.*, 2014). As a result, we included CRILAR-Pv 499 in the data matrix recently published by Ezcurra *et al.* (2014) in order to quantitatively test the phylogenetic relationships of this specimen. The presence of a non-notochordal vertebra in CRILAR-Pv 499 suggests that the specimen is included within Archosauromorpha (Ezcurra *et al.*, 2014). Therefore, the taxon sampling of the data matrix of Ezcurra *et al.* (2014), which is composed of basal synapsids, basal sauropsids and archosauromorphs, is adequate to test the phylogenetic position of CRILAR-Pv 499 among basal sauropsids. The original character 187 in that analysis (presence and shape of the bifurcation of the distal end of the second sacral rib) here was split into two different characters. The first character (number 187) describes the absence/presence of a bifurcation in the distal end of the second sacral rib and the second new character (number 188) describes the shape (tapering or squared) of the posterior projection of the distal bifurcation of this rib. The new scorings that resulted from this modification are detailed in the Supplementary Online Information. The terminal taxon, *Proterosuchus fergusi* Broom, 1903, was relabelled as *Proterosuchus* spp. following a recent taxonomic revision of the genus (Ezcurra and Butler, 2015), but the scorings of this terminal are the same as in Ezcurra *et al.* (2014). The data matrix was analysed under equally weighted parsimony using TNT 1.1 (Goloboff *et al.*, 2008). A heuristic search of 1,000 replications of Wagner trees (with random addition sequence) followed by the tree bisection and reconnection (TBR) branch-swapping algorithm (holding 10 trees per replicate) was conducted. The best tree(s) obtained at the end of the replicates were subjected to a final round of TBR branch swapping. Zero length branches among any of the recovered most parsimonious trees (MPTs) were collapsed (rule 1 of Coddington and Scharff, 1994). We used the same additive characters as in Ezcurra *et al.* (2014). As measures of tree support, decay indices (= Bremer supports) were calculated and a bootstrap resampling analysis, with 10,000 pseudoreplicates, was performed, reporting both absolute and GC (*i.e.*, difference between the frequency that the original group and the most frequent contradictory group recovered in the pseudoreplicates) frequencies.

The search recovered eleven most parsimonious trees (MPTs) of 862 steps, with a consistency index of 0.3364, a retention index of 0.6454, and the best score hit 217 times out of the 1,000 replications. The topology of the strict consensus tree is consistent with that obtained by Ezcurra *et al.* (2014), but a polytomy is recovered within Archosauromorpha, including rhynchosaurs, *Prolacerta broomi*, CRILAR-Pv 499 and archosauriforms (Fig. 4). The polytomy is a result of the alternative positions that CRILAR-Pv 499 acquires in the MPTs, namely as the sister-taxon of all archosauromorphs more derived than protorosaurs and *Trilophosaurus*, sister-taxon of *Prolacerta broomi*, a rhynchosaur or a basal archosauriform. In addition, consensus is currently poor on the position of *Trilophosaurus buettneri* among basal archosauromorphs (Ezcurra *et al.*, 2014) and the probable close relationship of the latter with *Pamelaria dolichotrachela* (Nesbitt *et al.*, 2013; which also possesses a squared posterior projection of the second sacral rib, see below) renders possible that CRILAR-Pv 499 could be also potentially related to the *Trilophosaurus* lineage.

The inclusion of CRILAR-Pv 499 within Archosauromorpha is supported by the presence of a non-notochordal vertebra (Fig. 4). This character is present in several basal reptiliomorphs (*e.g.*, *Tseajaia campi* Vaughn, 1964: Moss, 1972), parareptiles (*e.g.*, *Milleropsis pricei* (Watson, 1957); *Procolophon trigoniceps* Owen, 1876: de Braga, 2003), basal synapsids (*e.g.*, *Ophiacodon retroversus* Cope, 1878: MCZ 1426), basal sauropsids (*e.g.*, *Captorhinus aguti* (Cope, 1882): Fox and Bowman, 1966; *Coelurosauravus jaekeli* Weigelt, 1930: Evans and Haubold, 1987; *Petrolacosaurus kansensis*:

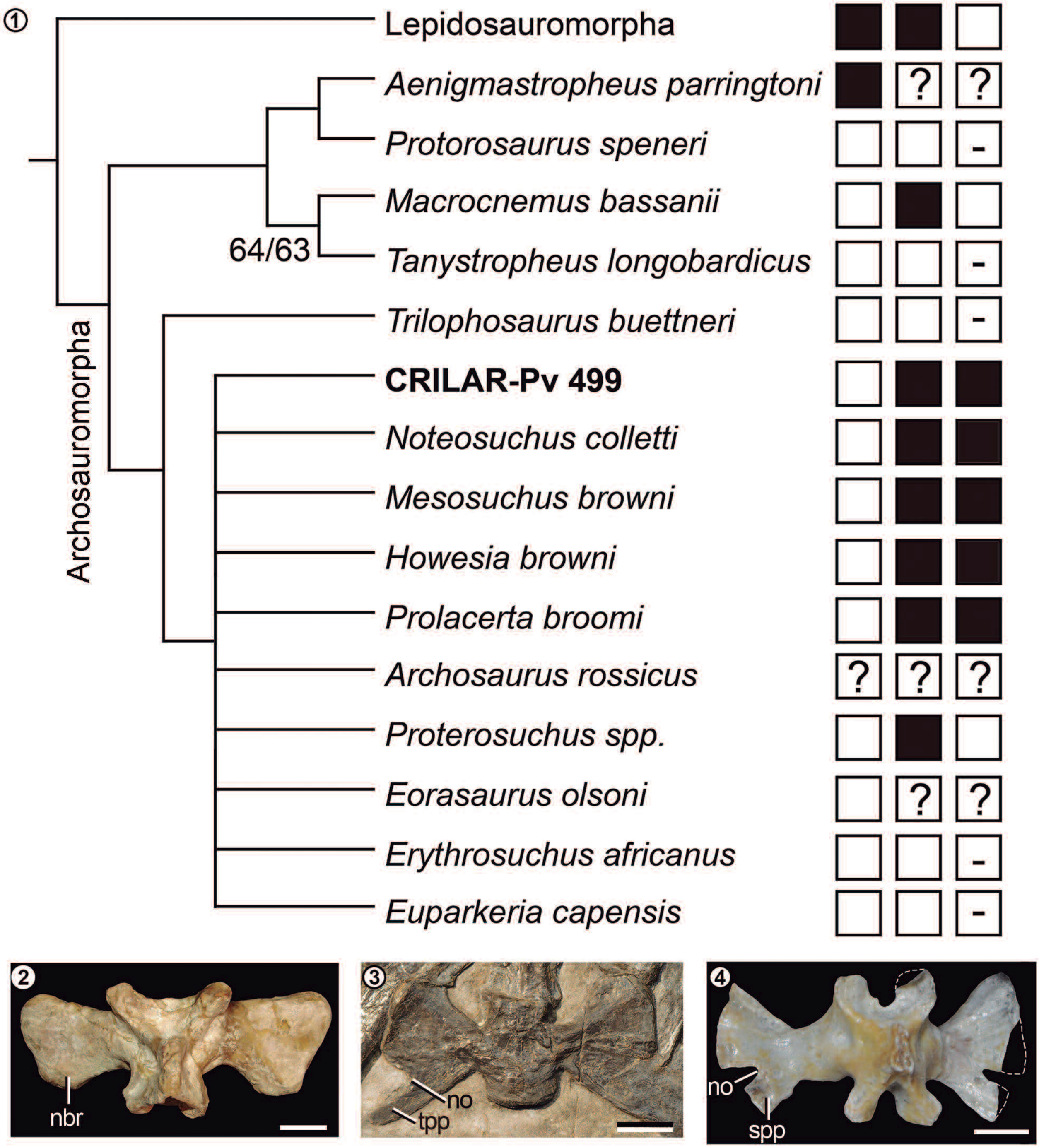

Figure 4. Phylogenetic position of CRILAR-Pv 499. **1,** Simplified strict consensus tree showing the phylogenetic position of CRILAR-Pv 499 and distribution (presence: black box; absence: white box) of notochordal vertebrae (left box), a bifurcated second sacral rib (centre box) and a squared posterior projection of the second sacral rib (right box). Dashes within the boxes represent non-applicable characters and question marks represent missing data; **2–4,** second sacral vertebrae of Triassic archosauromorphs in dorsal view showing: **2,** absence of a bifurcated sacral rib (*Tanystropheus longobardicus*: SMNS 54631); **3,** presence of a bifurcated sacral rib with a tapering posterior projection (*Macrocnemus bessanii*: PIMUZ T2472); **4,** presence of a bifurcated sacral rib with a squared posterior projection (*Mesosuchus browni*: SAM-PK-6046). Abbreviations: **nbr,** non-bifurcated rib; **no,** notch; **spp,** squared posterior projection; **tpp,** tapering posterior projection. Scale bars= 2 cm in (**2**) and 5 mm in (**3, 4**).

Reisz, 1981; *Araeoscelis gracilis* Williston, 1910: Vaughn, 1955; *Acerosodontosaurus piveteaui* Currie, 1980; *Youngina capensis*: BP/1/3859), drepanosaurs (Colbert and Olsen, 2001; Fraser and Renesto, 2005), the enigmatic neodiapsid *Helveticosaurus zollingeri* Peyer, 1955 (Rieppel, 1989), and basal lepidosauromorphs (*e.g.*, *Gephyrosaurus bridensis* Evans, 1980: Evans, 1981; *Planocephalosaurus robinsonae* Fraser, 1982: Fraser and Walkden, 1984). The only archosauromorph with notochordal vertebrae is *Aenigmastropheus parringtoni*, but the presence of this condition is interpreted as a reversal in the phylogenetic analysis of Ezcurra *et al*. (2014) or alternatively as evidence for a very basal position of the species within the clade (Ezcurra *et al*., 2014).

The presence of a distally bifurcated second sacral rib is found as a synapomorphy of a lesser inclusive clade within Archosauromorpha, including rhynchosaurs, *Prolacerta broomi*, CRILAR-Pv 499, possibly the *Trilophosaurus-Pamelaria* lineage (*sensu* Nesbitt *et al.*, 2013) and archosauriforms (Fig. 4). This bifurcation is also present in some protorosaurs (*e.g.*, *Macrocnemus bassani* Nopsca, 1930: PIMUZ T2472; *Amotosaurus rotfeldensis* Fraser and Rieppel, 2006: SMNS 90552) and lepidosauromorphs (*e.g.*, *Planocephalosaurus robinsonae*: Fraser and Walkden, 1984), but they are optimized as independent acquisitions within Sauria. The presence of a non-bifurcated distal end of the second sacral rib is apomorphically reversed in most archosauriforms more derived than proterosuchids. In particular, CRILAR-Pv 499 resembles *Prolacerta broomi* (Gow, 1975), *Pamelaria dolichotrachela* (ISI R333/1; *contra* Sen, 2003) and early rhynchosaurs (*i.e.*, *Noteosuchus colletii*: AM 3591; *Mesosuchus browni*: SAM-PK-6046; *Howesia browni* Broom, 1905b: SAM-PK-5886) among basal archosauromorphs in the presence of a squared posterior projection of the bifurcated distal end of the rib (Fig. 4). By contrast, the posterior projection of the bifurcated second sacral rib tapers distally in other saurians (*e.g.*, *Planocephalosaurus robinsonae*: Fraser and Walkden, 1984; *Clevosaurus hudsoni* Swinton, 1939: Fraser, 1988; *Macrocnemus bassani*: PIMUZ T2472; *Amotosaurus rotfeldensis*: SMNS 90552; *Howesia browni*: SAM-PK-5886; *Rhynchosaurus articeps* Owen, 1842: SHYMS 5; *Proterosuchus alexanderi* (Hoffman, 1965): NMQR 1484). Under suboptimal constrained topologies, only one additional step is necessary to force the position of CRILAR-Pv 499 as sister-taxon of *Trilophosaurus buettneri*, and two additional steps to force it as a more basal archosauromorph or to place it outside Archosauromorpha (*e.g.*, as the sister-taxon of Sauria). The low number of additional steps to move CRILAR-Pv 499 to a more basal position among diapsids is expected because of its fragmentary condition and the low number of characters scored for the specimen (four scorings, see Supplementary Online Information). In conclusion, the phylogenetic position of CRILAR-Pv 499 can be only constrained as an archosauromorph more derived than protorosaurs, but more basal than erythrosuchids and more crownward archosauriforms, which lack a distally bifurcated second sacral rib (*e.g.*, *Erythrosuchus africanus*: Gower, 2003; *Euparkeria capensis* Broom, 1913: Ewer, 1965).

The presence of a basal archosauromorph in the Tarjados Formation is expected because of the previous record of the ichnotaxon *Rhynchosauroides* in this unit, which is interpreted to be the trace of a basal archosauromorph (probably a rhynchosaur) (Melchor and de Valais, 2006). CRILAR-Pv 499 represents the first body fossil of a diapsid in the Tarjados Formation and the oldest member of the group in the Ischigualasto-Villa Unión Basin together with a preliminarily reported archosaur vertebra (Mancuso *et al.*, 2010). This new specimen increases the record of archosauromorphs in the Early–Middle Triassic of South America. Unfortunately, CRILAR-Pv 499 cannot be compared with specimens collected in other Permo–Triassic or Lower Triassic South American units (*i.e.*, the Buena Vista Formation of Uruguay and the Sanga do Cabral Formation of southern Brazil) because no sacral vertebrae are preserved among their archosauromorph samples (Langer and Schultz, 1997; Dias-da-Silva, 1998; Langer and Lavina, 2000; Da-Rosa *et al.*, 2009; Dias-da-Silva and Da-Rosa, 2011; Ezcurra *et al.*, 2015). The archosauromorphs previously described from the Permo–Triassic of South America include long-necked non-archosauriform archo-sauromorphs (Langer and Schultz, 1997; Langer and Lavina, 2000; Ezcurra *et al.*, 2015) and cf. proterosuchids (Ezcurra *et al.*, 2015). The new specimen can be phylogenetically constrained as more derived than Protorosauria/Tanystropheidae and differs from members of Proterosuchidae. Accordingly, CRILAR-Pv 499 increases the recorded taxonomic richness of archosauromorphs in South America in the aftermath of the Permo/Triassic mass extinction.

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