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Tetrapod burrows from the Middle–Upper Triassic Chañares Formation (La Rioja, Argentina) and its palaeoecological implications

Lucas E. Fiorelli[a,b,*], Sebastián Rocher[a,b], Agustín G. Martinelli[c,d], Martín D. Ezcurra[a,d], E. Martín Hechenleitner[a,b], Miguel Ezpeleta[a,e]

[a] Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Avenida Rivadavia 1917, C1033AAJ Ciudad Autónoma de Buenos Aires, Argentina
[b] Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja (CRILAR), Provincia de La Rioja, UNLAR, SEGEMAR, UNCa, CONICET, Entre Ríos y Mendoza s/n, (5301) Anillaco, La Rioja, Argentina
[c] Laboratório de Paleontologia e Bioestratigrafia, Departamento de Geociências, Universidade Federal do Rio Grande do Sul, Ave. Bento Gonçalves 9500, Agronomia, 91540-000 Porto Alegre, RS, Brazil
[d] Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Av. Ángel Gallardo 470, Buenos Aires C1405DJR, Argentina
[e] Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), Av. Vélez Sarsfield 1611, Ciudad Universitaria, X5016GCA Córdoba, Argentina

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A B S T R A C T

We describe tetrapod burrows from the uppermost Middle–lower Upper Triassic (latest Ladinian–early Carnian) Chañares Formation (Ischigualasto-Villa Unión Basin), La Rioja Province, northwestern Argentina. The burrows were found in different localities of the unit, but restricted to the lowermost 17 m of the formation. They occur at the same interval as a tetrapod assemblage composed of erpetosuchid and basal paracrocodylomorph pseudosuchians, basal traversodontid and chiniquodontid eucynodontians, and stenaulorhynchine rhynchosaurids. This assemblage differs from the typical Chañares fauna that occurs in stratigraphically higher levels. The burrows were found within the deposits of moderately developed palaeosols formed in volcanically-influenced braided fluvial facies under semi-arid climate conditions. The burrow systems are cylindrical to sub-cylindrical in cross-section, up to 25 cm in diameter, and characterized by long, multiple branching tunnels, several metres long, that meander horizontally or are slightly inclined (< 30°), forming a complex network that is a result of passive fill of a previously open burrow. In general, these structures have a similar architecture and three-dimensional organization to those previously described from the upper parts of the Ischigualasto Formation in the same basin. It is hypothesised that some of these burrows were formed by small eucynodonts (e.g., basal traversodontids, chiniquodontids), and their co-occurrence with diverse, medium to large pseudosuchian predators (e.g., *Luperosuchus*, *Tarjadia*), suggests these non-mammaliaform eucynodonts would excavate burrows to live and avoid climate-stress conditions and/or predation. The new discovery of burrows in the Chañares Formation sheds light on the evolution of the palaeoecology of mammaliaform precursors during the dawn of the archosaur domain.

1. Introduction

A tetrapod burrow is a simple hole or a more complex structure (e.g. branching tunnels in the ground) that is excavated in the substrate to create a space suitable for habitation or as a temporary haunt, usually to avoid adverse weather conditions on the surface and/or predators (Andersen, 1988; Groenewald et al., 2001; Miller et al., 2001; Hasiotis et al., 2004; Dentzien-Dias and Figueiredo, 2015). These biogenic sedimentary structures are considered as a behavioural response to extreme environmental/ecological conditions (see Hembree, 2010) and are dug to create a soil-buffered microenvironment more suitable to the animal requirements for survival (Hasiotis et al., 2007). For instance, a moist and fresh burrow with stable underground temperatures is critical for survival in hot and arid regions or to avoid droughts (Kinlaw, 1999; Jackson, 2000; Dentzien-Dias and Figueiredo, 2015; Martin, 2017). Burrowing habits are recorded in all major tetrapod clades (Voorhies, 1975; Ahlbrandt et al., 1978; Schaetzl and Anderson, 2005; Doody et al., 2014) and mostly in mammals (Voorhies, 1975; Buol et al., 2011). Burrows are built in a wide variety of substrates, such as floodplain and eolian deposits, being more common in soil profiles (Retallack, 2001; Schaetzl and Anderson, 2005; Buatois and Mángano, 2011; Martin, 2017). Vertebrate burrows range in complexity from a

* Corresponding author.
E-mail addresses: lucasfiorelli@gmail.com, lfiorelli@conicet.gov.ar (L.E. Fiorelli).

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simple tube of a few centimetres long to a complex network of interconnected tunnels with chambers of hundreds of metres (Kinlaw, 1999). Behavioural signals are not frequent in the fossil record, being mostly represented by footprints, nests, and burrows (e.g., Barnard, 2004). Burrowing activity has a tremendous impact on the landscape (Kinlaw, 1999; Retallack, 2001) but reports of fossil tetrapod burrows are not as common as we might expect on the basis of extant evidence (Voorhies, 1975; Hasiotis et al., 2007). Many factors, such as preservation, interpretation bias, and/or sedimentation and evolutionary biases, are responsible for the paucity of knowledge about the burrowing habits of fossil vertebrates (e.g., Voorhies, 1975).

Tetrapod burrows and trackways are frequently abundant and diverse in floodplain deposits (Buatois and Mángano, 2011) and only recently, however, the rich record of these fossils in palaeosols has begun to be revealed. Burrow concentrations –as well as other fossil traces such as rhizoliths or tap roots– can be used to recognize the top of palaeosol profiles because they record periods of reduced or no deposition in which sediments were bioturbated (Retallack, 2001; Kraus and Hasiotis, 2006). Tetrapod fossorial behaviour evolved early in the Carboniferous (Olson and Bolles, 1975; Hembree et al., 2005; Dentzien-Dias and Figueiredo, 2015), but the most common and best-documented fossil records of this biological activity are from the Permian to the present (e.g., Groenewald et al., 2001). During the Permian and Triassic, several tetrapod groups had fossorial habits as a strategy of protection against predators and the harsh climate in low and middle palaeolatitudes of Pangaea (e.g., Cluver, 1978; Simms and Ruffell, 1990; Parrish, 1993; Colombi et al., 2008; Benton, 2016). The adverse atmospheric conditions during these times (i.e., major greenhouse spikes of the end Guadalupian and lower Carnian) allowed extensive exploitation of fossorial behaviour in different substrates (Groenewald et al., 2001; Retallack et al., 2003; Smith and Botha, 2005; Bordy et al., 2011; Colombi et al., 2012). The development of different tetrapod burrow systems implies complex evolutionary patterns of vertebrate fossoriality through the late Permian to Late Triassic in Pangaea along different clades (e.g., Smith, 1987; Colombi et al., 2012; Krummeck and Bordy, 2017).

The Ischigualasto-Villa Unión Basin represents a late Permian to Late Triassic continental-rift basin developed along the southwestern margin of Pangaea (López-Gamundí et al., 1994; Milana and Alcober, 1994; Kokogian et al., 1999; Gulbranson et al., 2015). The units of this basin crop out extensively in La Rioja and San Juan provinces of northwestern Argentina and bear one of the most fossiliferous Triassic continental tetrapod assemblages worldwide (Romer, 1966; Bonaparte, 1971; Rogers et al., 2001; Arcucci et al., 2004; Martínez et al., 2013). In particular, the Chañares Formation is a relevant unit for knowing the evolution of terrestrial faunas during the Triassic (Romer and Jensen, 1966; Rogers et al., 2001; Fiorelli et al., 2013; Mancuso et al., 2014; Marsicano et al., 2016; Ezcurra et al., 2017). The fossil record of the Chañares Formation is key to understanding the origin and diversification of modern tetrapod clades, such as pseudosuchians, dinosauromorphs, and eucynodonts (Ezcurra et al., 2017). In the Ischigualasto-Villa Unión Basin, tetrapod burrows were previously described for the Lower–Middle Triassic Tarjados Formation (Krapovickas et al., 2013) and the Upper Triassic Ischigualasto and Los Colorados formations (Colombi et al., 2012). These burrow records are characterized by an increase in structural complexity throughout the stratigraphic sequence, from short simple diagonal tubes in the Tarjados Formation to complex and branched networks of several metres in the Upper Triassic units (Colombi et al., 2012; Krapovickas et al., 2013). However, no burrows have been reported yet in the Chañares Formation, which is stratigraphically bracketed by the latter units.

Here we report the first tetrapod burrow complexes from the uppermost Middle–lowermost Upper Triassic Chañares Formation (Talampaya National Park, La Rioja, northwestern Argentina) (Fig. 1). The burrows were found in different localities of the unit within moderately developed palaeosols within braided fluvial facies in the lowermost metres of the formation. The main aim of this paper is to describe these tetrapod burrows and to characterize the geological setting in which they were developed. These ichnological structures fill a gap in the distribution of tetrapod burrow-bearing assemblages within the Ischigualasto-Villa Unión Basin. Finally, we comment on the evolution of the fossorial habits and behaviours of their small producers prior to the appearance of the first dinosaurs.

2. Materials and methods

The tetrapod burrows described here come from the Chañares Formation, which crops out in the Talampaya National Park, western La Rioja province (Fig. 1). The burrow moulds were sampled systematically and collected in three successive field trips during the springs of 2014–2016 in three different localities: El Torcido (29°49′33″S–67°47′22″W), Campo Córdoba Norte (29°49′5″S–67°45′13″W), and Brazo del Puma (29°52′21″S–67°42′57″W) (Figs. 1, 2). The limits and stratigraphic extent of the Chañares Formation have been determined through the analysis of satellite images and field observations during several field seasons between 2011 and 2017. Grain size, sedimentary structures, and stratigraphic relationships were observed directly in the field. Classical field techniques were used for the collection of sedimentary and palaeontological information. In the field we used Brunton® compass, Garmin Oregon® GPS, Jacob Staff, tape-measure, Estwing® geological tools, acrylic glue CIANO®, Butvar® polyvinyl butyral resin (B-15, B-72, and B-76), and the classic equipment for palaeontological field works. The Chañares tetrapod burrows and the sampled sediments described here are housed in the Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja (CRILAR), Anillaco, Argentina. The specimens were labelled under the acronyms CRILAR-Ic 19 and CRILAR-Ic 24 and the sediment samples were labelled as CRILAR-S 23 and CRILAR-S 24. Thin sections of the burrows and sediments were conducted after the following protocol. The specimens were washed in distilled water and cut with a PetroThin® slicer, dried at 40 °C in an oven during 24 h, and subsequently glued with compound glue (Araldit CY 248 and hardening HY 956) on glass slides of 28 × 48 × 1.8 mm. The thin sections were carried out at the CRILAR Petrography Laboratory. Observations were performed under a petrographic microscope (Leica® DM2500 P) and photographs were captured with a digital camera attached to the microscope and connected to a computer for image processing, editing, and measuring. The images and figures were designed and edited with CorelDRAW® X8 and CorelPHOTO-PAINT®.

The fossil burrows were described following the criteria of Groenewald et al. (2001), Hasiotis et al. (2007), Bordy et al. (2011, 2017), Colombi et al. (2012), Dentzien-Dias and Figueiredo (2015), and Doody et al. (2015). We follow the nomenclature used by these authors for the architectural and superficial morphologies, complexity and tortuosity, branching architecture, and infilling sediments. We focus this research not only on ichnology, but also on behavioural biology, looking for a junction between both disciplines according to the "taphonomy of behaviour" (Plotnick, 2012).

3. Geological setting and palaeontology of the Chañares Formation

3.1. Geology

The tetrapod burrows are found in several tuffaceous sandstone levels in the lowermost 17 m of the Chañares Formation (Fiorelli et al., 2013; Ezcurra et al., 2017) (Figs. 1, 2). This unit is part of the Ischigualasto-Villa Unión Basin (López-Gamundí et al., 1994; Stipanicic and Marsicano, 2002), a rift system with a well-defined NW-SE trend associated with the pre-break-up of Pangaea (Uliana and Biddle, 1988) that records an upper Permian to Upper Triassic continental succession of around 4000 m of alluvial, fluvial, and lacustrine deposits (López-