



# Large tetrapod burrows from the Middle Triassic of Argentina: a behavioural adaptation to seasonal semi-arid climate?

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We report the discovery of large burrow casts in the early Middle Triassic Tarjados Formation, at Talampaya National Park, north-western Argentina. Facies analysis indicates the burrows are preserved in sandbars deposited by an ephemeral river under semi-arid and seasonal climatic conditions. The structures are mostly preserved in longitudinal cross-section and consist of an opening, an inclined tunnel (ramp), and a terminal chamber. The ramp is 8–14 cm in height, up to 130 cm in length and penetrates 49–63 cm below the palaeosurface with an inclination of 22°–30°. We studied burrow cast dimensions, overall architectural morphology, surficial marks, and compared them with other large burrows of both invertebrate and vertebrate origin. A tetrapod origin of the burrow casts was established based on: distinctive architecture, and size, which is more than twice the most common size range for large terrestrial invertebrate burrows. Comparison with other Upper Permian and Triassic tetrapod burrows allows us to identify three general morphological groups: (1) simple inclined burrows; (2) helical burrows; and (3) burrow network complexes, representing different behaviours. A study of tetrapod body fossils preserved within other Upper Permian and Triassic burrows shows that the Tarjados structures were most likely produced by non-mammalian cynodonts. The environmental and climatic context suggests that aridity and seasonality played a fundamental role selecting burrowing behaviour in therapsids and that by the Early–Middle Triassic their burrowing behaviour attained a complexity comparable to modern mammals. □ *Argentina, behaviour, palaeoclimate, Permo-Triassic, Tarjados Formation, Tetrapod burrows.*

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Recent fieldwork in the Talampaya National Park (La Rioja Province) provides information about the fossil tetrapods preserved at the initial stages of the Ischigualasto-Villa Unión Basin infill. These new discoveries include several relatively large burrow casts found in fluvial facies of the Tarjados Formation, and constitute the first time that such burrows have been described in Early–Middle Triassic strata in South America.

In general, reports of large burrows in continental deposits have greatly increased during the last two decades. Recent examples of invertebrate ichnogenera recorded in Mesozoic–Cenozoic fluvial sequences include *Camborygma*, *Loloichnus*, *Lunulichnus*, and *Capayanichnus*. Their tracemakers were attributed to freshwater crustaceans, such as crayfishes and crabs (Hasiotis & Mitchell 1993; Zonneveld *et al.* 2006;

Bedatou *et al.* 2008; Melchor *et al.* 2010). Among vertebrates, lungfish aestivation burrows are perhaps the most numerous (e.g. Vaughn 1964). However, most large burrow casts described from continental successions are interpreted as having been dug by tetrapods, particularly synapsids.

Terrestrial tetrapod burrows have been described from a number of fluvial and aeolian successions dating from the present day back to the Devonian (e.g. Barbour 1895; Olson & Bolles 1975; Voorhies 1975; Martin & Bennett 1977; Smith 1987; Hasiotis *et al.* 1993, 2004; Groenewald *et al.* 2001; Miller *et al.* 2001; Damiani *et al.* 2003; Hembree *et al.* 2004; Loope 2006, 2008; Colombi *et al.* 2008; Hembree & Hasiotis 2008; Sidor *et al.* 2008; Martin 2009; Schmeisser *et al.* 2009; Modesto & Botha-Brink 2010; Storm *et al.* 2010; Bordy *et al.* 2011; Tañanda *et al.* 2011). Upper

Permian and Lower-Middle Triassic burrows were, until now, only known from south-western Gondwana. They were described from the Teekloof, Balfour, Katberg and Driekoppen formations in the Karoo Basin of South Africa, corresponding to the *Pristeronathus*, *Tropidostoma*, *Dicynodon*, *Lystrosaurus*, and *Cynognathus* assemblage zones respectively, (Smith 1987; Groenewald 1991; Groenewald *et al.* 2001; Damiani *et al.* 2003; Modesto & Botha-Brink 2010; Bordy *et al.* 2011) and the Omingonde Formation of Namibia (Smith & Swart 2002) and the Fremouw and Lashly formations of Antarctica (Babcock *et al.* 1998; Hasiotis *et al.* 1999; Miller *et al.* 2001; Sidor *et al.* 2008). The South American record is scanty. Tetrapod burrows were recently described from the Permian of the Paraná Basin, Brazil (Dentzien-Dias 2010) and one record is only known from the Upper Triassic of Argentina (Ischigualasto Formation) (Colombi *et al.* 2008). This later occurrence and an example described from the Holy Cross Mountains of Poland (Tałanda *et al.* 2011) are the only Late Triassic tetrapod burrows described from Pangea.

In this study we analyse the dimensions, overall architectural and surface morphology of the burrow casts and discuss the possible identity of the producer of the Tarjados burrows by comparing them with extant burrows known from modern environments. We also compare the Tarjados burrows with other Upper Permian and Triassic burrows and show how their general morphology relates to the tracemaker and its behaviour. Finally, we review the palaeoenvironmental and palaeoclimatic context in which known Upper Permian and Triassic tetrapod burrows occur worldwide.

## Geological setting

In Argentina, the non-marine Triassic sedimentary record is preserved in a series of extensional basins located along the western margin of southern South America (e.g. Stipanovic 2002). Among them, the Ischigualasto-Villa Unión Basin infill is a nearly continuous continental Triassic succession that includes up to 6000 m of alluvial, fluvial and lacustrine deposits (e.g. Stipanovic & Bonaparte 1979; Stipanovic 2002). Its outcrops are widely distributed in the provinces of San Juan and La Rioja in northwestern Argentina (Fig. 1). The sequence is lithostratigraphically divided into several units: at the base, the Talampaya and Tarjados formations (Romer & Jensen 1966) unconformably rest on Palaeozoic deposits and they are unconformably covered by the Agua de la Peña Group (e.g. Stipanovic 2002; Mancuso 2005). The Ischigualasto-Villa Unión Basin is widely known for its rich

tetrapod content (e.g. Bonaparte 1997; Marsicano *et al.* 2001; Langer *et al.* 2010), nearly all described from the upper part of the succession (Agua de la Peña Group). The lower part (Talampaya and Tarjados formations) is nearly devoid of fossil remains that, until the present study consisted of a manus-pes print of a non-mammalian therapsid (Talampaya Formation) and fragmentary skeletal remains of dicynodonts from the Tarjados Formation (Cox 1968; Bonaparte 1997; Mancuso *et al.* 2010).

The basal contact of the Tarjados Formation was interpreted as an erosional unconformity over the thick red ephemeral fluvial deposits of the Talampaya Formation (Caselli *et al.* 2004). A regional unconformity constitutes the upper contact of the Tarjados Formation with the overlying tuffaceous sandstone and siltstone at the base of the Agua de la Peña Group (the Chañares Formation) (Rogers *et al.* 2001). The Tarjados Formation is divided in two members (Romer & Jensen 1966), which consist of thinning and fining-upward successions of sandstone and mudstone (Table 1, Fig. 2). Both members are interpreted as deposited by ephemeral fluvial systems interbedded with eolian sandstone and playa lake deposits (Caselli 2000; Nucci & Caselli 2000; Caselli *et al.* 2004), the most distinctive difference between them being their contrasting colour. Thus, reddish colours characterize the Lower Member and white/grey hues characterize the Upper Member where the burrows are preserved (Fig. 2).

## Palaeoenvironment

In the Río Gualo area (Fig. 1), we recorded the sedimentological section (Fig. 2). The sequence is characterized by interbedded tabular sandstones and mudstones with lenses of conglomerate (Table 1, Fig. 3). These intraformational conglomerate (Gm) lenses generally form lag deposits at the base of the channels (Fig. 3A, B). They are characterized by irregular to sub-rounded moderate red (5R4/6) mudstone clasts, ranging from 2 to 30 cm in diameter however towards the top of the Upper Member conglomerate is dominated by rounded quartz pebbles. The S facies (Table 1) is dominated by 1–2 m-thick lenticular and tabular beds of normally graded light greenish grey (5GY8/1) fine- to medium-grained sandstone with planar (Sp) and trough cross-stratification (St) and horizontal lamination (Sh) and, occasionally, massive structure (Sm) (Fig. 3A, C). The large burrow casts, fossil footprints, and root casts occur in this facies. Facies F (Table 1) is characterized by tabular beds of horizontal laminated moderate red (5R4/6) mudstone (Fl), subordinate fine-grained sandstone, locally with mottled colour. The mudstone intervals vary between 0.5 and 1 m in thickness and commonly show light

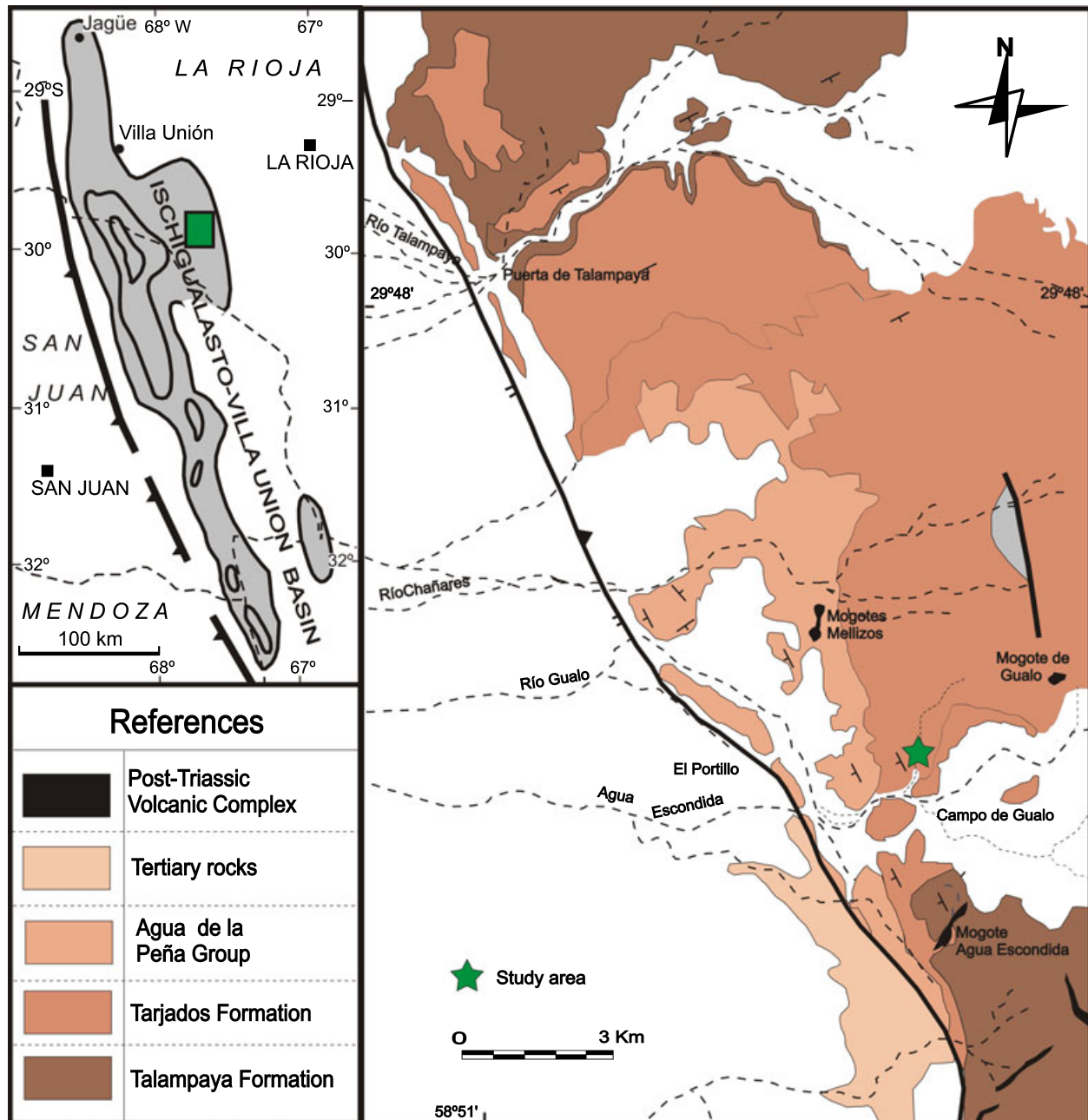


Fig. 1. Geological map of the Ischigualasto-Villa Unión Basin, in the Talampaya National Park area (modified from Caselli 1998).

greenish grey (5GY8/1) banded beds and different hierarchies of desiccation cracks (Fig. 3A, D). Invertebrate dwelling structures, such as *Palaeophycus* sp. and *Arenicolites* sp., are commonly present in this facies as well as isolated large burrow casts.

The fining-upward succession that comprises the Tarjados Upper Member is interpreted as having been deposited by an ephemeral river and it is characterized by the repeated facies sequences of 1.5–4 m thickness (Fig. 3A). Each facies sequence starts with an intraformational conglomerate (Gm), followed by

planar/trough cross-stratified medium-grained sandstone (Sp/St) that passes upward to planar cross-stratified (Sp) and horizontal laminated (Sh) fine-grained sandstone, and occasionally massive sandstone with mottled colour. The S facies are interpreted as emergent downstream prograding sand bars of ephemeral channels. The sequence terminates with horizontal laminated mudstones (Fl), commonly showing light greenish grey banding, desiccation cracks, and root marks, interpreted as deposited in a floodplain alluvium (e.g. Fisher *et al.* 2007; Pace *et al.* 2009).

Table 1. Summary of the facies of the Tarjados Formation.

Interpretation of facies	Lithology	Structures	Bedding
Lower member Fluvial system (~25 m)	Moderate red medium to fine-grained sandstone ( <b>St, Sp</b> )	Trough and planar cross-stratification	Lenticular to tabular beds with 0.5–1 m thick
	Moderate red mudstone ( <b>Fm</b> )	Massive, horizontal lamination, mudcracks	Tabular beds with 0.1–0.4 m thick and laterally persistent for hundreds of metres
Playa lake (~8 m)	Moderate reddish brown fine-grained sandstone and mudstone ( <b>Fl, Fm</b> )	Massive, horizontal lamination, mudcracks, carbonate concretions	Tabular bed with up to 8 m thick and laterally persistent for hundreds of metres
Unconfined ephemeral flows associated with floodplain and eolian deposits (~120 m)	Moderate red fine- to medium-grained sandstone ( <b>Sh, Sp</b> )	Horizontal lamination, planar cross-stratification	Lenticular to tabular beds with 0.5–3 m thick
	Moderate red mudstone ( <b>Fl, Fm</b> )	Massive, horizontal lamination, mudcracks	Tabular beds with 0.05–0.2 m thick and laterally persistent for tens of metres
	Moderate red well-sorted fine sandstone ( <b>Sap</b> )	Asymptotic planar cross-stratification	Tabular to lenticular beds with 0.2–0.5 m thick
Upper member Ephemeral fluvial system (~100 m)	Moderate red intraformational conglomerate ( <b>Gm</b> )	Irregular to sub-rounded mudstone clasts	Lenticular beds with 0.2–0.6 m thick, with erosional basal boundaries
	Light greenish grey fine- to medium-grained sandstone ( <b>St, Sp, Sh, Sm</b> )	Planar and trough cross-stratification, horizontal lamination and, massive structure occasionally mottled coloured	Tabular to lenticular beds with 0.05–0.6 m thick, with erosional and/or non-erosional basal boundaries
	Moderate red mudstone, subordinate fine-grained sandstone light greenish grey banding mudstone ( <b>Fl, Fm</b> )	Horizontal lamination, desiccation cracks, occasionally mottled coloured	Tabular beds with 0.5–1 m thick, and extent laterally for tens of metres, and have non-erosional boundaries

The stacking pattern of Tarjados Upper Member strata displays lateral and vertical variations. Laterally, the intraformational conglomerates can be absent, thus the succession starts with lenticular, erosively-based, channel bodies without lag, or lenticular to laterally extensive non-erosively-based channels. Both erosive and non-erosive channels are overlain by downstream prograding bar deposits. This lateral variation is related to the dynamics of the fluvial system, recording differences between primary (with erosive base) and secondary channels, channel migration behaviour, and waning discharge with emergence during periods when the stream system avulsed or dried up (e.g. Fisher *et al.* 2007). The vertical variation of facies sequences is commonly an upward reduction in the F facies and the amount of the mudstone clasts within the channel lags. A gradual decrease in the intraformational clasts within channel lags strongly suggests a decrease of accommodation space in the basin during the deposition of the Tarjados Upper Member (e.g. Wright & Marriott 1993).

As previously mentioned, the Tarjados Formation has been interpreted as deposited by ephemeral fluvial systems based on its repetitive fining-upward vertically stacked beds of sandstone and mudrock. The presence of hiatus surfaces in the sandstone bar deposits, evidenced by the tetrapod footprints and burrows, root casts, and colour mottling, strongly suggest periodic

fluvial activity, with alternating periods of flooding and subaerial exposure. Moreover, the light colour mottling and banding in some mudstone beds, and different hierarchies of desiccation cracks, carbonate concretions, and root marks also suggest that the water table was subject to seasonal vertical fluctuations. The small-scale sand dunes that migrated on the floodplains and the extensive mudcracks indicate prolonged dry conditions. Taken together, this evidence suggests that water supply in the Tarjados Basin was strongly seasonal, characterized by the alternation of short wet and long dry seasons, most probably under an overall semi-arid climatic regime.

## Tarjados burrow morphology

Six large burrow casts are analysed in this study. Four of them are preserved in longitudinal and transverse cross-sectional views (Figs 4–6), and two as 3-D internal casts (Fig. 7); all of them remain in the field (detail measurements of each burrow are presented on Table 2).

### *Inclined large burrow casts*

The burrow casts are inclined structures (Fig. 4) and consist of an upper proximal portion (opening), a



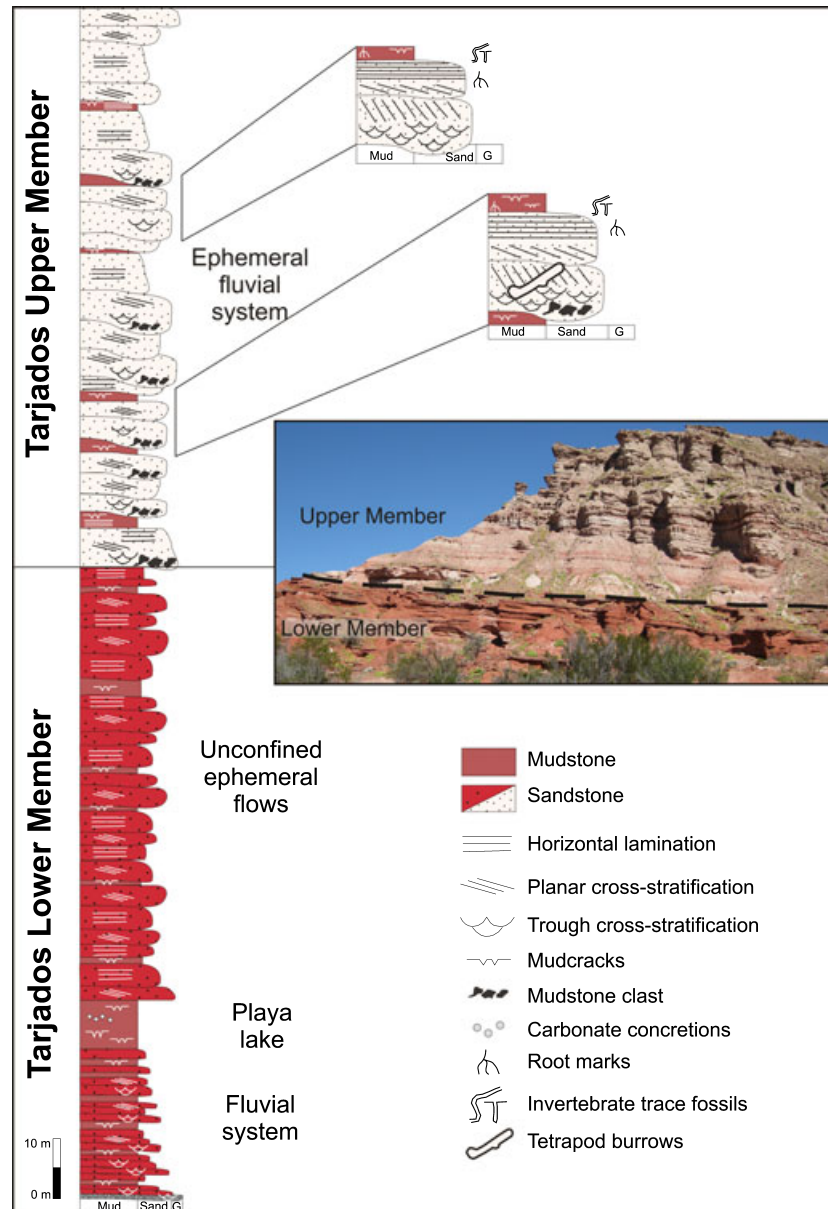


Fig. 2. Sedimentological section of Talampaya Formation in Río Gualo area (modified from Nucci, 1999) (G = pebble conglomerate). Outcrop picture of the Tarjados Formation in Río Gualo area displays the boundary (dash line) between the red Lower Member and white/grey Upper Member.

descending tunnel (ramp), and a lowermost terminal chamber. The preserved length of the burrows ranges from 122 to 136 cm, including the terminal chamber when present (burrows 2 and 4). The penetration depth ranges from 49 to 63 cm and the inclination varies from 22° to 30° (Table 2).

Branching is absent and although the outer contact is sharp and well-defined, with no impressions of a burrow lining were observed. The outer contacts of burrows 1–3 are coated by a thin gypsum deposit interpreted as a secondary, more recent precipitation, which is common in the study area (Fig. 4). The

gypsum deposit makes it difficult to see the surface markings on the burrow casts in the field.

In burrows 2 and 4 the proximal entrance of the burrow is preserved. It is funnel-shaped and tapers towards the ramp (Fig. 4C, D) and ranges from 16 to 20 cm in height. The inclined ramp has roughly parallel walls and has a height range of 8–14 cm, with an average height of 13 cm. In burrow 1, an expansion in height of the middle portion of the ramp (22 cm in height) is recorded and this is interpreted as a medial chamber (Fig. 4A, B). The height of the ramp decreases slightly from the opening down to the

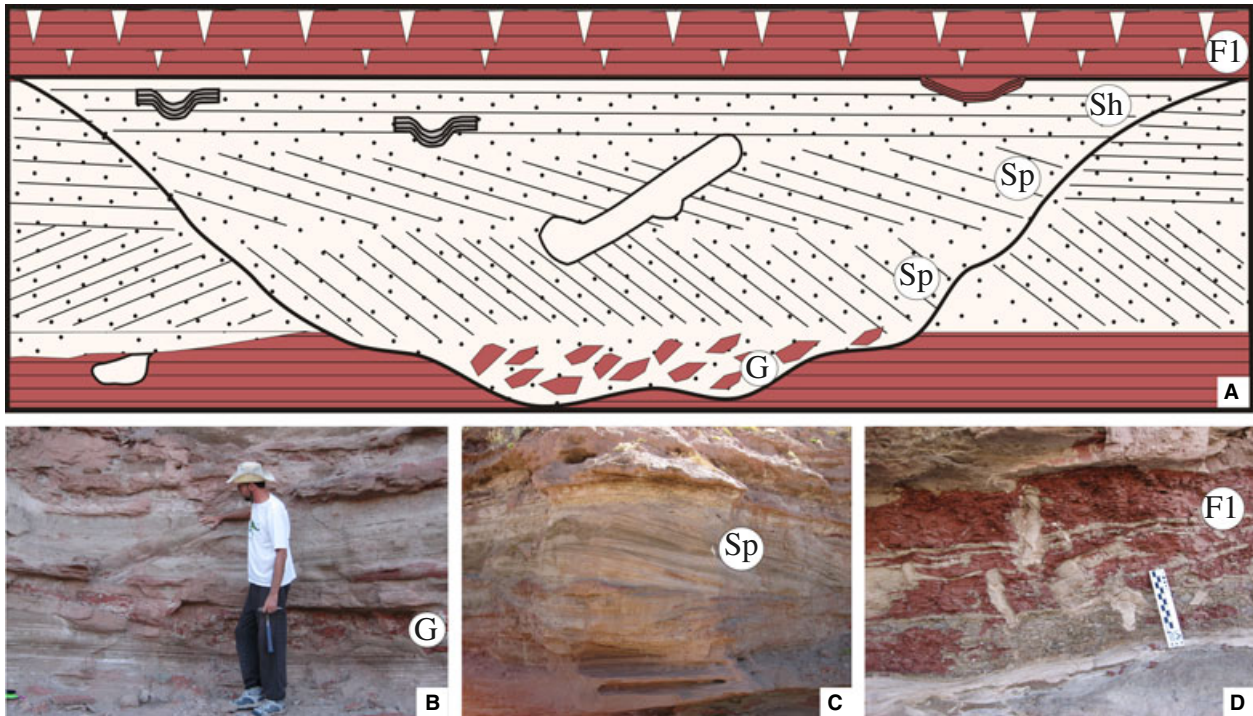


Fig. 3. A, general scheme of the Tarjados Upper Member facies sequence showing the relationship among different facies and organic structures. B, G facies with a basal lag of intraformational conglomerate. C, light greenish-grey cross-stratified sandstones of the S facies. D, medium red mudstone with light greenish grey horizontal discolouration and different hierarchies of desiccation crack from F facies.

domed terminal chamber (Fig. 4C, D) where the height again increases (Table 2). Due to the orientation of the burrow casts to the plane of the cliff exposure the transverse cross-section of the terminal chamber is only observed in burrow # 3, where it is elliptical with a bilobate ventral surface (Fig. 6).

The burrows are preserved in medium-grained massive sandstones (burrows 2–4, Figs 4C, D, 6) and medium-grained planar cross-stratified sandstones, both interpreted as facies of exposed portions of mid-channel bars (Fig. 4; burrow 1). Two types of burrow infill are recognized; massive sandstone throughout the burrow (burrows 2–4, Figs 4C, D, 6) and massive sandstone with internal erosional surfaces (burrow 1, Fig. 4A, B). With the latter angular mudstone clasts occur within the terminal portion. The internal discontinuity within the burrow fill represents a break in sediment supply and suggests two stages of burrow infilling (Fig. 4A, B). The surface also involves an expansion in height of the ramp (medial chamber) and is here interpreted as evidences for re-occupation of an abandoned, half filled burrow (Fig. 4A, B).

All studied burrows dip with an inclination of 22°–30° and with burrows 1 and 2 the entrance is orientated to the NE, while the entrance to burrow 4 is orientated to the SW (Table 2). All of them are aligned perpendicular to the palaeo-downstream direction.

### *Isolated terminal chamber internal casts*

Burrow casts 5 and 6 are short tunnels with parallel walls (ramp) that expand into a dome-shaped terminal chamber (Fig. 5). The height of the terminal chambers range from 10 to 14 cm, while its width varies between 24 and 27 cm (Table 2). The structures are preserved as three-dimensional internal casts filled with highly bioturbated, fine-grained sandstone. These casts occur at the horizon with the floodplain mudstones and are infilled with bioturbated sandstone from the overlying bed (Fig. 5). The invertebrate bioturbation is of simple dwelling structures, mostly *Palaeophycus* isp., although identification of individual trace fossils is difficult.

Similar to the inclined large burrows these are also oriented to the E-NE and perpendicularly to the palaeo-downstream direction (Table 2).

## Discussion

### *Distinguishing invertebrate and tetrapod burrows*

There is no single morphological feature that uniquely links large burrow structures to tetrapods. When body-fossils are not preserved inside the burrow, there



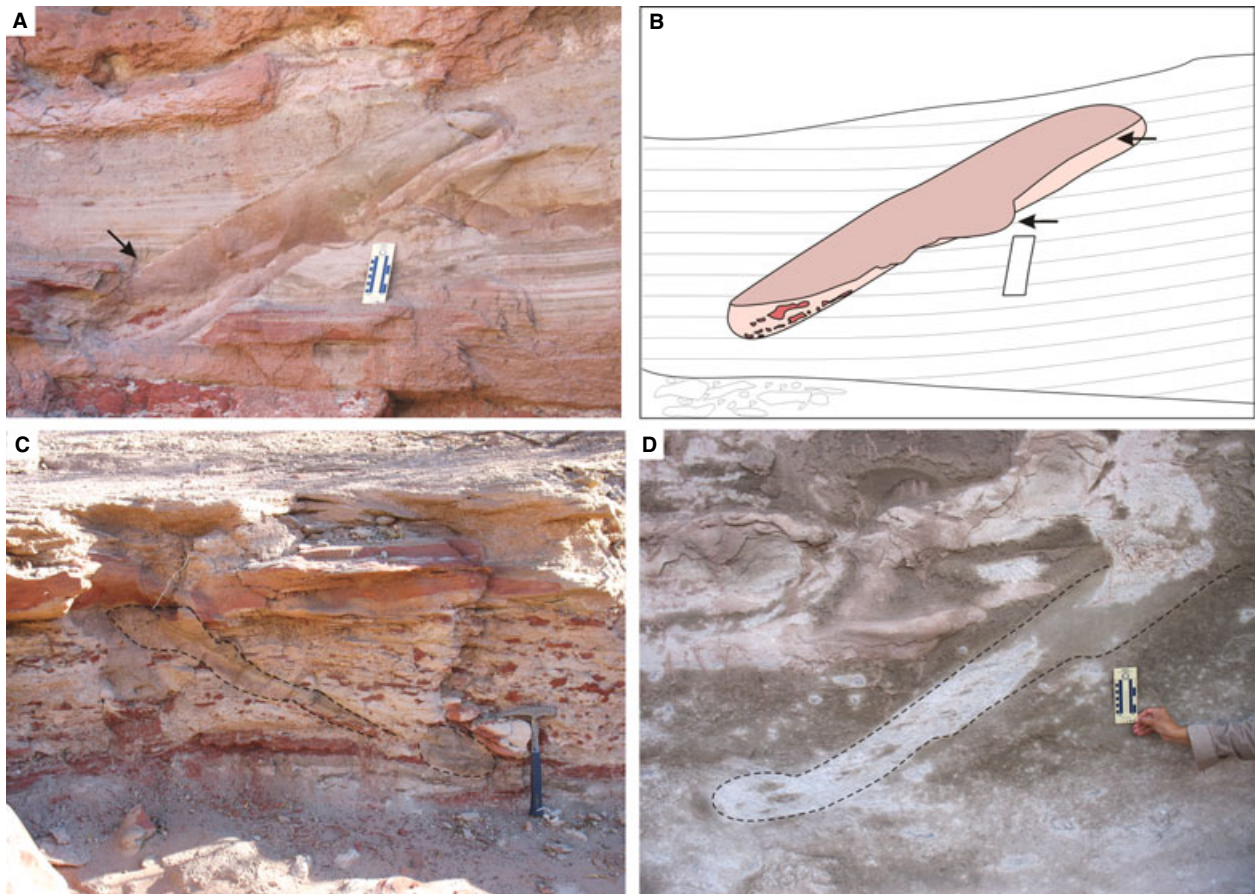


Fig. 4. Large burrows of the Tarjados Formation in longitudinal cross-section. A, burrow 1, note the upper limit marked by a gypsum deposit (arrow). B, schematic interpretation of burrow 1. Note the internal discontinuity within the burrow (upper arrow) and a medial chamber (lower arrow), denoting its reuse. C, burrow 4. D, burrow 2.

are a number of characteristics that should be studied in order to resolve the question of the original digger (Table 3). The distinction between invertebrate and tetrapod makers of large burrows is based mostly on the comparisons with modern fossorial animals, the burrow dimensions, the overall architecture, and the presence of marks on the burrow walls (e.g. Groenewald *et al.* 2001; Miller *et al.* 2001; Hasiotis *et al.* 2004; Loope 2006; Sidor *et al.* 2008).

To interpret the putative producer of a trace fossil, the size of the burrow is the first useful parameter. In solitary species the burrow dimensions closely match with the size of the tracemaker. In general, the diameter of their burrows are as small as possible to reducing the energy used in excavation (Anderson 1982; White 2005). In the Tarjados large burrows the height of the ramp and the terminal chamber ranges from 10 to 15 cm (Table 2), thus providing an approximate idea of the dimension of the tracemaker, and if a tetrapod produced the burrow, that measure would be the approximate hip height (or slightly less if the animal kept a crouching position inside the tunnel).

In non-marine environments, burrowing invertebrates have a size range that slightly overlaps that of tetrapods (Table 3). To date all the burrows containing tetrapod skeletal remains are more than 5 cm in diameter, and commonly more than 10 cm, whereas invertebrate burrows are typically 2–5 cm wide. The most common diameter of burrows attributed to crayfish, such as *Camborygma* from the Upper Triassic Chinle Formation, have a diameter range of 0.5–12.5 cm but most commonly vary between 2 and 5 cm (Hasiotis & Mitchell 1993). Other burrows attributed to crayfish, such as *Loloichnus* from the Late Jurassic–Late Cretaceous of Patagonia, ranges from 1 to 2.5 cm (Bedatou *et al.* 2008). Although the dimensions of burrows are not completely diagnostic for distinguishing those produced by invertebrates and tetrapods, the architectural morphology of the burrows is more enlightening.

Several architectural morphologies can be recognized in burrows attributed to tetrapods (Fig. 8). Many Permian and Triassic burrows that have tetrapod occupants are elliptic to circular in cross-section

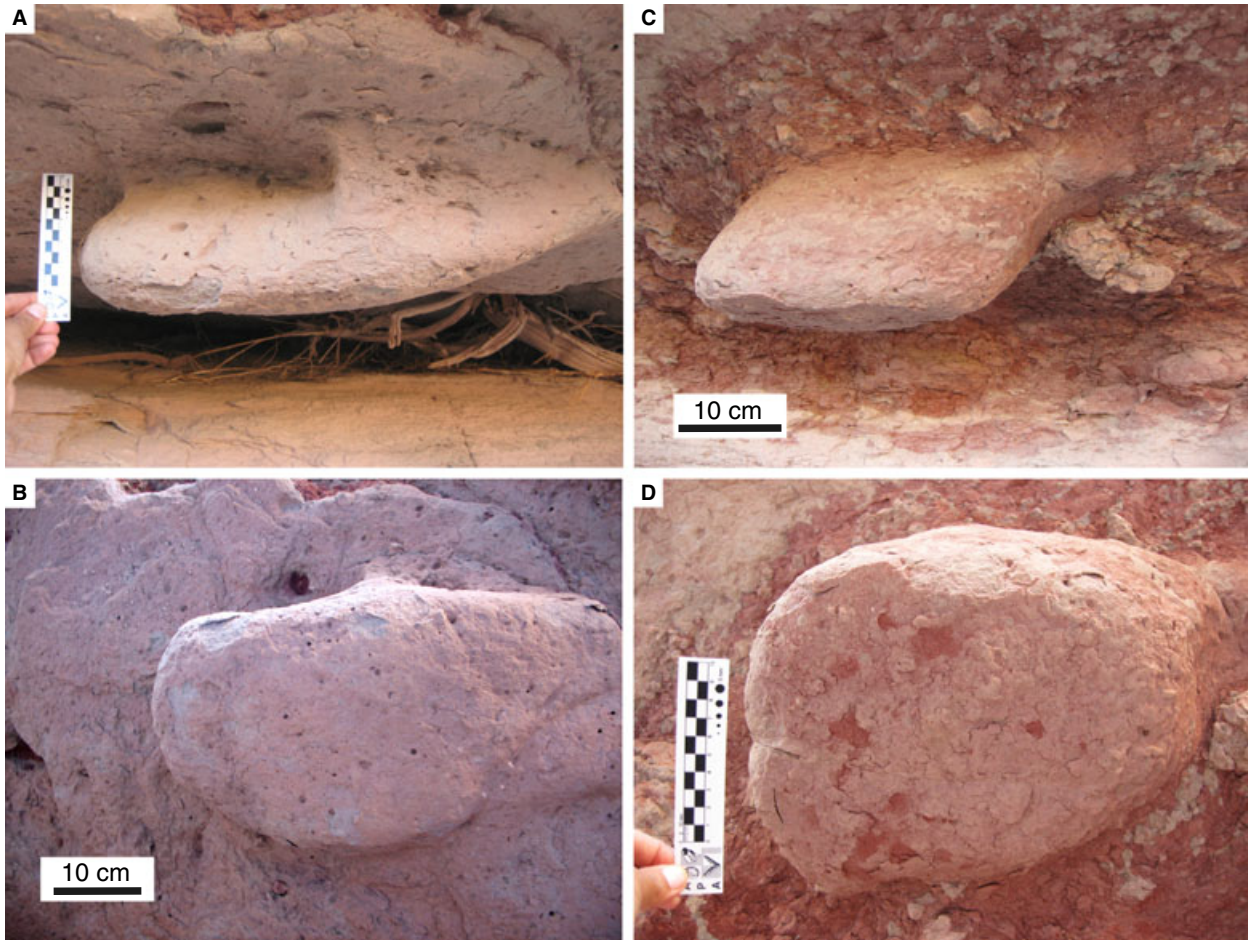


Fig. 5. Terminal chambers preserved as sandstone cast. Note bioturbation inside the burrows. Burrow 6 in lateral (A) and ventral view (B). Burrow 5 in lateral (C) and ventral view (D).



Fig. 6. Large burrow cast of the Tarjados Formation in transverse cross-section (burrow 3). Note the bilobate ventral surface profile (arrow).

and in many cases the ventral surface is bilobate, as in the Tarjados burrows (Table 3, Fig. 6). However, the cross-sectional profile varies along the burrow systems (Hasiotis *et al.* 2004), thus the presence of a bilobate

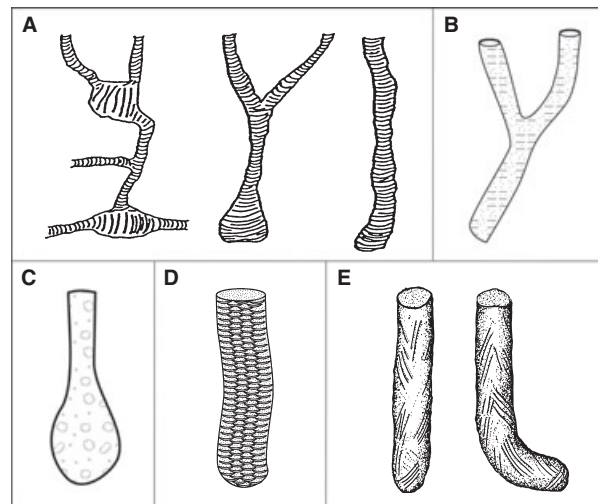


Fig. 7. Comparable invertebrate and vertebrate burrows of continental environments. A, *Camborygma*, modified from Hasiotis & Mitchell (1993). B, *Loloichnus*. C, lungfish aestivation burrow, modified from Hasiotis & Mitchell (1993). D, *Lunulichnus*, modified from Zonneveld *et al.* (2006). E, *Capayanichnus*, modified from Melchor *et al.* (2010).



Table 2. Measurements of the large burrow morphological variables.

Burrow #	Opening diameter	Ramp		Terminal chamber					
		Height	Width	Height	Width	Length	Deep	Incl	Orient.
1		13	–	–	–	129	55	22°	NE
2	20	14	–	16	–	136	63	30°	NE
3	–	–	–	11	26	–	–	–	–
4	16	8–13	–	15.5	25	122	49	24°	SW
5	–	–	–	14	24	–	–	–	E-NE
6	–	–	–	10	27	–	–	–	E-NE

floor depends on the portion of the burrow that is preserved. The significance of the bilobate floor is uncertain. Based on the large size of their burrows (diameter approximately 30 cm), and the small size of the individuals preserved inside the burrows (skull width approx. 10 cm), Groenewald *et al.* (2001) proposed that the bilobate bottom was related to a two-way traffic. In contrast, Damiani *et al.* (2003) proposed that it might represent paths worn down by the tracemaker's feet. Accordingly, documentation of burrow casts of extant skinks, which have a longitudinal median groove, are produced by the sprawling stance of one individual (Hasiotis *et al.* 2004).

The surface markings on tetrapod burrow casts appear to be most likely preserved at the base and lateral walls of the excavations, and they are aligned with the long axis of the burrow (Table 3). However, many burrow casts lack surface marks and it has been proposed that the absence of these interpreted scratch marks could be related to the age of the burrows, as the continuous use could erase the original marks (Modesto & Botha-Brink 2010). Unfortunately, the way that the Tarjados burrows are exposed (longitudinal cross-sectional view) and the presence of intense bioturbation in the terminal chamber casts precludes the observation of any surficial marks.

Burrows attributed to freshwater decapod crustaceans are potentially comparable to those of tetrapods, although most of them are predominantly vertically orientated. *Loloichnus* includes thick-walled Y-shaped burrows (Bedatou *et al.* 2008) and *Camborygma* are vertical straight shafts with a single terminal chamber, or complex structures with multiple entrances and chambers that commonly lack of a major horizontal component (Hasiotis & Mitchell 1993; Hasiotis *et al.* 1993) (Fig. 7A, B). Burrows that display a simple vertical architectural morphology with a bulbous terminus are generally identified as lungfish aestivation burrows but are often confused with those attributed to crayfish (Fig. 7C) (Hasiotis *et al.* 1993). In fact, is this type of morphology that clearly separate lungfish burrows from those produced by tetrapods (see Hasiotis *et al.* 1993). Other burrows attributed to decapod crustaceans are included in the ichnogenera

*Lunulichnus* and *Capayanichnus*, the latter interpreted as produced by freshwater crabs (Fig. 7D, E). They are predominantly simple, vertically orientated, and lack terminal enlargements. In some cases, *Capayanichnus* have an overall 'L' shape (Zonneveld *et al.* 2006; Melchor *et al.* 2010).

Based on the characters discussed above, it is possible to attribute the large burrows recorded from the Tarjados Formation to the digging behaviour of tetrapods based on: 1, their distinctive architectural morphology, as a simple inclined tunnel with a bilobate floor and a domed terminal chamber; and 2, their size, which is more than twice the most common size range described for large terrestrial invertebrate burrows.

#### Comparison with other permian and triassic burrows attributed to tetrapods

May it help in the identification of the burrow producer to consider the Tarjados burrows and other terrestrial burrows of the same age? Is the morphology of Permian and Triassic burrows characteristic of any particular tetrapod group? As a first attempt to answer these questions we analysed the reported examples of Permian and Triassic burrows from Gondwana interpreted to be produced by tetrapods (Table 3). The observed variability is resolved into three general morphological groups (Fig. 8) occurring throughout the fossil record: (1) simple inclined burrows; (2) helical burrows; and, (3) burrow network complexes. Also, isolated terminal chambers are recorded (see Table 3), although they cannot be positively assigned to any of the aforementioned morphological groups.

The results indicate that there is no strong correspondence, but a subtle coincidence, between the burrow morphology and the taxonomic group of tetrapods preserved inside. For example, dicynodonts are recorded within simple inclined and helical burrows, and cynodonts are preserved within network complexes and isolated terminal chambers. Because of the scarcity of body fossils preserved within burrows, any conclusions based on these associations are still highly speculative. The morphology of burrow system reflects how it was used and ultimately the biology of

Table 3. Permian and Triassic burrows of Gondwana.

Morph. Group	Age	Unit	Location	Name	Architecture	Orientation	Cross-Section	Branching	Surface features	Dimensions cm			Reference
										Diam.	Depth/length	Animal in burrow	
Simple inclined burrows	Middle/Late Permian	Paraná Basin	Brazil	Small Burrows	Simple straight to slightly curved with enlarged entrance	Inclined 30°	–	No	–	4–7	–/30–60	No	Dentzien-Dias (2010)
	Middle/Late Permian	Paraná Basin	Brazil	Medium Burrows	Simple straight to slightly curved with terminal chamber	Inclined 40°	Elliptical, Few ventrally bilobate	No	–	9–15	–/33–98	No	Dentzien-Dias (2010)
	Early Permian	Balfour and Katberg Formations	South Africa	Large scale <i>Scyenia</i>	Simple straight with terminal chamber	Inclined 0°–10°	–	No	Scratch marks on lateral walls	20–45	–/30	Dicynodont ( <i>Lystrosaurus</i> , <i>Dicynodon</i> )	Greenewald (1991)
	Early Permian	Balfour and Katberg Formations	South Africa	<i>Histioderma</i>	Simple straight with terminal chamber	Inclined 40°	–	No	Scratch marks on lateral walls	20–50	–/100	?Dicynodont ( <i>Lystrosaurus</i> )	Greenewald (1991)
	Early Permian	Balfour and Katberg Formations	South Africa	Small-scale <i>Scyenia</i>	Simple, strat	Inclined 20°–30°	–	No	–	3	–/30	Unidentified bone fragments	Greenewald (1991)
	Early Permian	Balfour Formations	South Africa	NMQR 3606	Relatively straight. Entry, ramp and terminal chamber	Inclined 12°	Elliptical	No	No	12 × 34	–	Dicynodont ( <i>Lystrosaurus</i> )	Modesto & Botha-Brink (2010)
	Early Permian	Fremouw Formation	Antarctica	Type L burrow	Simple, Rarely J shaped	Inclined to subhorizontal	Circular – elliptical. Few ventrally bilobate	Rare, horizontal and vertical	Scratch marks tangential to long axis	2–6.5	15/–	No	Miller et al. (2001)
	Early Permian	Fremouw Formation	Antarctica	Type G Burrow	Simple, strat to slightly curved. One possibly helically coiled	Subhorizontal to gently inclined	Elliptical	Rare	Scratch marks tangential to long axis	8–19	8–25/–	No	Miller et al. (2001)
	Early Permian	Katberg Formation	South Africa	Very large burrow	Single, relatively straight. Entry, ramp and rounded terminus	Sub-horizontal. Inclined 30°	Circular to slightly elliptical	no	Vertical and horizontal scratch marks on lateral walls	25–40	150/300	No	Bordy et al. (2011)
	Middle Permian	Lashly Formation	Antarctica	Tetrapod ichnogenus B	Simple with terminal chamber	Horizontal to gently inclined	Elliptical to ventrally bilobate	No	Scratch marks on lateral walls and floor	5	–	No	Sidor et al. (2008)
Late Permian	Keuper Formation	Poland	Large burrow casts	Straight to slightly curve, terminate in chambers	Inclined 18–36°	Elliptical	Rare	No	7–9	60–120/100–375	No	Talanda et al. (2011)	
Helical burrows	Late Permian	Teekloof Formation	South Africa	Helical burrow (daimonelles)	Helically spiraled with horizontal terminal chamber	Vertical. Ramp angle 10°–32°	Plano-convex to ventrally bilobated	No	Scratch marks on lateral walls and floor	6–16	–/50–75	Dicynodont ( <i>Diictodon</i> )	Smith (1987)
	Early Permian	Balfour and Katberg Formations	South Africa	?Helical, loosely coiled	Helical, loosely coiled	Ramp angle 10°–15°	–	No	Scratch marks on lateral walls	20–45	–	Unidentified bone fragments	Greenewald (1991)

Table 3. (Continued)

Morph. Group	Age	Unit	Location	Name	Overall architectural morphology				Dimensions cm			Reference	
					Architecture	Orientation	Cross-Section	Branching	Surface features	Diam.	Depth/length		Animal in burrow
Burrow networks complexes	Early Triassic	Balfour and Katberg Formations	South Africa	<i>Thalassinoides</i>	Complex net-like pattern of interconnected tunnels	Horizontal	–	Numerous	No	3–15	–	No	Groenewald (1991)
					Enlarged entrance, tunnels as network complex with terminal chambers.	Inclined 1°–23°	Ventrally bilobate–oval	Numerous, curved	Scratch marks along the bases	5–12	–	Cynodont ( <i>Trirachodon</i> )	Groenewald <i>et al.</i> (2001)
Terminal chambers	Late Triassic	Ischigualasto Formation	Argentina	Large diameter burrow	Vertical shaft, tunnels as network complex with intermediate and terminal chamber	Horizontal to subhorizontal	Elliptical	Numerous, winding	Scratch marks on lateral and dorsal walls.	10	–	No	Colombi <i>et al.</i> (2008)
					Terminal chamber	–	Ventrally bilobate	–	Poorly defined Scratch marks on lateral and dorsal walls	–	–	Cynodont ( <i>Thrinaxodon</i> )	Damiani <i>et al.</i> (2003)
					Terminal chamber	Subhorizontal	Ventrally bilobate	No	Scratch marks on lateral walls	15.7	–	No	Sidor <i>et al.</i> (2008)

its tracemaker (Eisenberg & Kinlaw 1999). Most of the reported Permian and Triassic burrows consist of simple inclined tunnels (Fig. 8C, Table 3). The inclined burrows of the Tarjados Formation fall in this morphological group.

Today, similar tunnels are dug by semi-fossorial animals that use burrows as climatic shelters (Kinlaw 1999), such as those constructed by the gopher tortoise (*Gopherus polyphemus*) (Hansen 1963; Doonan & Stout 1994), the American alligator (*Alligator mississippiensis*) (Voorhies 1975) and many carnivorous mammals (Voorhies 1975). The curved shaft of the helical burrows (Fig. 8B) may save horizontal space and avoid neighbouring burrows (Martin & Bennett 1977), provide more effective protection from predators, and complicate the flow of air thereby limiting circulation and increasing heat interchange (Meyer 1999). Modern mammals that dig helical burrows include gophers, golden moles, and kangaroo rats (Butler 1995). Recent examples of burrow network complexes (Fig. 8A) are typically permanent residences for their producers and are used for several purposes, including storage, latrines, breeding, and foraging (Kinlaw 1999). Modern producers of such burrows include the plains vizcacha (*Lagostomus maximus*) and the tucu-tucu (*Ctenomys mendocinus*) of Argentina (Mares *et al.* 1989; Albanese *et al.* 2010), and the prairie dog (*Cynomys leucurus*) of North America (Sheets *et al.* 1971).

### *The triassic tetrapod burrowers and possible tarjados tracemakers*

Among the Triassic burrows that contain skeletal remains, only a few can be confidently considered to preserve the remains of the original tracemaker (i.e. a skeleton or skeletons that are articulated in life position and with body sizes consistent with the diameter of the burrow) (Smith 1987; Groenewald 1991; Groenewald *et al.* 2001; Smith & Swart 2002; Damiani *et al.* 2003; Retallack *et al.* 2003; Modesto & Botha-Brink 2010). At present, the identified tracemakers are members of the therapsid clade, cynodonts and dicynodonts (see Table 3). The best-known examples are the cynodonts *Trirachodon* (Groenewald *et al.* 2001; Smith & Swart 2002) and *Thrinaxodon* (Damiani *et al.* 2003). Among dicynodonts, disarticulated remains of *Lystrosaurus* and *Dicynodon* sp. were found in simple inclined burrows (Groenewald 1991; Modesto & Botha-Brink 2010), although the evidence used to identify these taxa as the original diggers not strong.

Based on the study of their anatomy, several Early to early Middle Triassic tetrapods were proposed to have evolved burrowing adaptations such as the



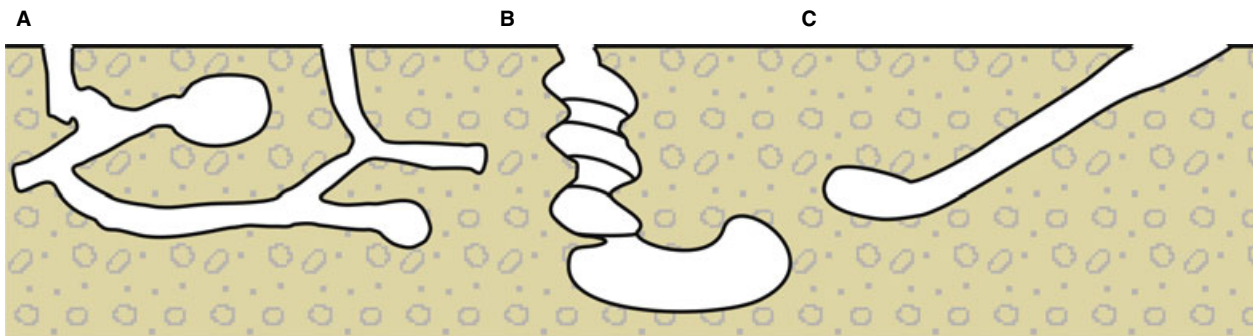


Fig. 8. Generalized morphological groups of tetrapod burrows. A, burrow network complexes. B, helical burrows. C, simple inclined burrows.

procolophonid *Procolophon*, as well as several dicynodont and cynodont taxa. The presence of large unguals (for scratch digging) and the pronounced overbite in procolophonids (i.e. to reduce the ingestion of dirt) were interpreted tentatively as burrowing adaptations (De Braga 2003). Moreover, Abdala *et al.* (2006) reported a multitaxon aggregation of the procolophonid *Owenetta kitchingorum* and the cynodont *Galesaurus planiceps*, and suggested shelter-sharing based on the high degree of articulation of the skeletal remains and the preservation of delicate bones *in situ*. Nevertheless, procolophonids have not yet been found in an unequivocal burrow structure, and a shelter-sharing behaviour does not confirm that these amniotes were diggers. Most dicynodonts exhibit postcranial features suitable for digging and a fossorial way of life, such as robust humerus relative to the femur, short antebrachium, and large broad manus with sharp broad claws (Yalden 1996; Ray & Chinsamy 2003).

However, the best-preserved dicynodont found in a burrow, the Late Permian *Diictodon* (Smith 1987), challenges this generalization. This taxon possesses a slender humerus and poorly developed olecranon process, as occur in other similarly sized Permian dicynodonts (Angielczyk *pers comm.* 2011). Nevertheless, *Diictodon* shows other features suitable for digging such as cylindrical body, short limbs with smaller distal segment compared to the proximal, stout metacarpals, and long and wide manus, among others (Ray & Chinsamy 2003). The skeletons of non-mammaliaform cynodonts have no anatomical features that particularly suggest a burrowing lifestyle, nevertheless some taxa have been found articulated within burrows (Groenewald *et al.* 2001; Damiani *et al.* 2003). Botha & Chinsamy (2004) studied the bone histology of *Trirachodon*, and some relatives, in order to explore a correlation with lifestyle habits. Comparisons of relative bone wall thickness (RBT) to extant burrowing tetrapods reinforced the inference of a burrowing lifestyle for *Trirachodon*. The same was

suggested for the South American non-mammalian cynodont *Andescynodon* due to its thick bone walls (Chinsamy & Abdala 2008). According to the discussion above, both therapsids (non-mammalian cynodonts and dicynodonts) and parareptiles (procolophonids) are potential tracemakers of Permian-Triassic burrows based on overall morphology and/or bone histology. Nevertheless, dicynodonts were the only confidently identified tracemakers of Permian burrows, and non-mammalian cynodonts to Triassic burrows.

The Tarjados Formation has yielded only fragmentary skeletal remains of relatively large dicynodonts and vertebrae of a medium size archosaur (Cox 1968; Mancuso *et al.* 2010). Both of these taxa are too large to be the producers of the burrows described herein. Stratigraphically equivalent faunas are known in Argentina from the Lower-Middle Triassic Puesto Viejo Group (southern Mendoza) and the Middle Triassic Cerro de las Cabras Formation (Cuyana Basin). From these faunas, several dicynodonts were described (e.g. Bonaparte 1978; Domnanovich 2010). However, all taxa and unidentified remains correspond to medium-to-large sized animals, too big to be the putative tracemakers of the Tarjados burrows. Several non-mammalian cynodonts also are known from the same levels (the traversodontid *Pascualmathus polanskii*, *Rusconiiodon mignoney* and *Andescynodon mendozensis*, *Cynognathus crateronotus*, the gomphodontids *Diademodon tetragonus*, and *Cromptodon mamiferoides*; see Abdala & Ribeiro 2010). Some of them display sizes that fit the range of the Tarjados burrows, such as *Pascualmathus*, *Rusconiiodon*, *Andescynodon* and *Cromptodon*. Moreover and as discussed above, *Andescynodon* has been suggested to have fossorial behaviour based on bone histology (Chinsamy & Abdala 2008).

In the Paraná Basin of southern Brazil equivalent Lower-Middle Triassic levels have yielded tetrapods that also could represent potential tracemakers. The

record of non-mammalian therapsids consist of an isolated stapes assigned to a dicynodont (Schwanke & Kellner 1999; Langer & Lavina 2000), and the non-mammalian cynodont *Luangwa sudamericana* (Abdala & Ribeiro 2010); only the latter has a size that matches the Tarjados burrows. The Brazilian beds have also yielded the parareptile *Procolophon* (see Cisneros 2008), already mentioned as a probable digger (De Braga 2003), and it also displays sizes that fit the Tarjados excavations.

Based on these observations, non-mammalian cynodonts can be suggested as likely tracemakers of the Tarjados burrows due to their size and the interpreted burrowing behaviour of some taxa (Fig. 9). Although non-mammalian cynodonts are unknown from the Tarjados Formation they are fairly diverse in the overlying succession, the Middle-Late Triassic Agua de la Peña Group. The possibility that the burrows were produced by a parareptile (*Procolophon*, or a close relative with equivalent behaviour and size) is not completely ruled out; although parareptiles are at present unknown from Argentina and their burrowing behaviour is weakly supported.

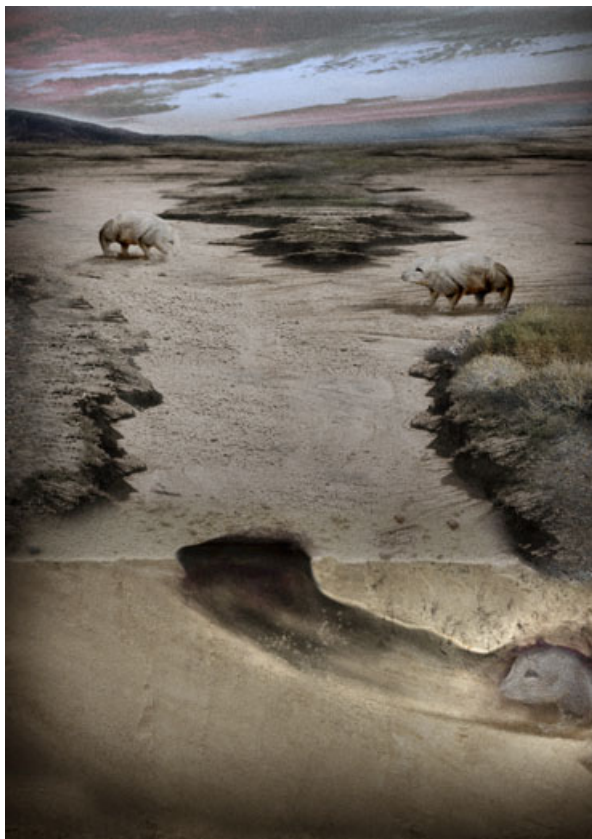


Fig. 9. Reconstruction of the Triassic Talampaya landscape, with ephemeral river sandbars and large burrows dug by non-mammalian cynodonts. Illustration by Boris Budiša.

### *Terrestrial burrowing: a response to climate?*

Most vertebrate burrows recorded in Devonian to Permian strata are interpreted as aestivation burrows of animals that lived in water bodies that seasonally dried out (e.g. Olson & Bolles 1975; Hasiotis *et al.* 1993; Hembree *et al.* 2004; Storm *et al.* 2010). Truly terrestrial burrows excavated subaerially, and attributed to tetrapods, are recorded since the Permian and have been interpreted as seasonal or permanent refuges for protection from predation, rearing of young, hibernation, and/or food storage, among others (Boucot 1990; Kinlaw 1999). Today, burrowing behaviour is common amongst tetrapods on arid or semiarid environments, in a large number of mammals, reptiles, amphibians, and a few birds (e.g. Voorhies 1975; Kinlaw 1999).

Tarjados burrows are preserved on the top of sandbars in ephemeral river channels deposited under seasonally dry conditions. The orientation of the burrows perpendicular to the channel flow direction might minimize their flooding when fluvial discharge occurred. This type of behaviour is observed in extant rodents as tuco-tucos (*Ctenomys*) in northwestern Argentina (e.g. Talampaya National Park) (V.K. pers. obs. 2011) that orientate their burrows perpendicularly to the stream direction in ephemeral rivers beds. Also, it is well known that not randomly distributed burrows can be related to environmental factors such as shading from sunlight and shielding from cold winds (Kay & Whitford 1978; Best 1988; Baumgardner 1991). For example, the cavy *Microcavia australis* orients active holes to the E thus, avoiding cold SE and S winds as is observed at the Reserve of Ñacuñán in centralwestern Argentina (Taraborelli *et al.* 2009). Also, a southern orientation is notably rare among savanna burrows of nine-banded armadillos (*Dasypos novemcinctus*) from northern Belize (Platt *et al.* 2004), and in other species of armadillos, as *Dasypos hybridus*, from Uruguay (González *et al.* 2001).

Today, burrow and soil temperatures are affected by fluctuation in ambient temperature. The soil temperatures in depths greater than 50 cm below ground are almost constant both diurnally and seasonally (Burda *et al.* 2007). The ground depth of the Tarjados burrows is on that range (49–63 cm) thus suggesting that they might be emplaced at that depth to maintain a more or less constant temperature. This is also consistent with the general idea that the more vertical burrows might be constructed for safety, thermoregulation, and canalization in the case of flooding. In contrast, the horizontal arrangement is more determined by the abundance and distribution of food resources and foraging strategies (e.g. Heth 1989; Spinks *et al.* 2000; Sumner *et al.* 2003; Burda *et al.* 2005).

The environmental context of most of studied Permian and Triassic burrows is semiarid-arid and/or marked seasonality (Smith 1987; Miller *et al.* 2001; Smith & Swart 2002; Damiani *et al.* 2003; Smith & Botha 2005; Colombi *et al.* 2008; Dentzien-Dias 2010). This is congruent with the monsoonal circulation and strong seasonality postulated for the supercontinent of Pangea during Late Permian and Triassic times (e.g. Robinson 1973; Kutzbach & Gallimore 1989; Parrish 1993; Scotese *et al.* 1999; Sellwood & Valdes 2006). Such climatic regime would have resulted in increasing aridity in the low- and mid-latitude continental interiors, and polewards expansion of relative aridity and strong seasonality of rainfall (Parrish 1993). In that context, it has been suggested that burrowing played a significant role in allowing tetrapods to tolerate the increasing aridity in southern Gondwana and also with the high carbon dioxide and low oxygen levels associated to the end-Permian extinction event (Retalack *et al.* 2003; Smith & Botha 2005; Smith & Botha-Brink 2009). This hypothesis agrees with modern studies which postulate that the possession of a cool, moist burrow with stable temperatures underground is especially critical for survival in arid and semi-arid zones that are hot and dry with greatly fluctuating temperatures on the surface (Kinlaw 1999).

It is evident that aridity and seasonality played a fundamental role in selecting for burrowing behaviour, at least, among Permian and Triassic tetrapods. Moreover, the evidence suggests that the burrowing behaviour was present in therapsids as early as the middle/late Permian. By this time burrowing was already present with two types of structures, simple inclined and helical burrows (see Table 3). During the Early–Middle Triassic burrow architecture became more elaborate including not only 3D burrow complexes but also orientated simple burrows which are specialized shelters (avoiding excessive sunlight, cold wind, and/or flooding events). This would imply that during the early Mesozoic burrowing behaviour in basal therapsids already attained a complexity comparable to modern mammal examples.

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