



The Chañares Formation: a window to a Middle Triassic tetrapod community

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The Chañares Formation is known worldwide for its diverse and well-preserved Ladinian non-marine tetrapod assemblage, including a wide variety of archosauriform reptiles (proterochampsids, early offshoots of the crocodylian line and dinosaurian precursors) and synapsids represented by dicynodonts and cynodonts. This tetrapod record offers an opportunity to evaluate, within a taphonomic context, the palaeoecology of this Middle Triassic fauna. The taphonomic analysis of the Chañares assemblage, under precise stratigraphical control, indicates that it is a good representation of the original faunal composition allowing us to address the palaeoecological interactions between its components. Mass estimations and morphology-based palaeobiological inferences of Chañares tetrapods are used to reconstruct the trophic structure of the community. Chañares tetrapod fauna was numerically dominated by middle-sized herbivorous and small faunivorous cynodonts, whereas middle-sized faunivorous cynodonts and large dicynodonts were less common. In contrast to the therapsids, which show a low species-richness and high abundance, the archosauriforms are less abundant, but are the most taxonomically diverse group. The large paracrocodylomorphs (estimated body masses between 350 and 500 kg) are identified as the top predators of the community, and the traversodontid cynodonts and dicynodonts (estimated body masses reaching approximately 43 and 360 kg, respectively) are identified as the base herbivores of the trophic pyramid. We conclude that the worldwide faunal composition in the Ladinian reveals two continental assemblages: an eastern Laurasian assemblage dominated by temnospondyl amphibians; and a western Gondwanan assemblage dominated by therapsids but including a wide diversity of archosauriforms. □ *Chañares Formation, community reconstruction, Ischigualasto-Villa Union Basin, Ladinian faunas, taphonomy.*

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Terrestrial faunas from the upper Middle Triassic are poorly represented globally. In Gondwana, faunas of this age are best documented in South America, particularly through discoveries in the Santa Maria Formation in southern Brazil (*Dinodontosaurus* Assemblage Zone) and the Chañares Formation in western Argentina (Romer & Jensen 1966; Rogers *et al.* 2001; Langer *et al.* 2007). Several taxa are shared between these assemblages (Rogers *et al.* 2001; Langer *et al.* 2007), suggesting that they were approximately contemporaneous. In addition, two taxa from these South American faunas (i.e. the carnivorous cynodont *Chiniquodon* and the dicynodont *Stahleckeria*) were recently identified in the uppermost strata of the Omingonde Formation of central

Namibia, indicating a putative Ladinian age for these levels as well (Abdala & Smith 2009; Abdala *et al.* 2013).

The Chañares Formation is part of an entirely non-marine succession deposited in the Ischigualasto-Villa Unión Basin, which represents one of the most continuous continental Triassic successions in South America (Stipanovic & Marsicano 2002). The diverse and well-preserved Ladinian non-marine tetrapod assemblage from the Chañares Formation includes a high diversity of archosauriforms (e.g. proterochampsids, pseudosuchians, ornithomirans) and high abundance of synapsids (large dicynodonts and smaller cynodonts). Because of this abundance and diversity, the fossil remains recovered from this

formation constitute one of the best records of Middle Triassic tetrapods (Romer & Jensen 1966; Rogers *et al.* 2001). It also provides a key to understand the evolution of terrestrial faunas during the Triassic, including the origin and early diversification of dinosaurs and the dominance of therapsids (Serenio & Arcucci 1993, 1994; Abdala & Giannini 2000, 2002).

Romer (1966) was the first to establish background knowledge about the Chañares assemblage. He performed extensive fieldwork in La Rioja Province and collected abundant vertebrate remains during 1964 and 1965 (Romer 1966). He thereafter produced a series of publications consisting of mostly anatomical studies and a sketch of the geology of the Triassic units at the Chañares and Gualo localities (Romer 1966, 1967, 1969, 1971a,b, 1973; Romer & Jensen 1966; Cox 1968; Jenkins 1970; Romer & Lewis 1973). Beginning in 1970, Bonaparte conducted several field trips to the area, including Talampaya National Park where he worked almost continuously for a decade. He produced an important collection of fossils from the Chañares Formation, currently housed at the Instituto Miguel Lillo, Universidad Nacional de Tucumán, Argentina. Bonaparte has also published on the geology (Bonaparte 1967; Stipanovic & Bonaparte 1979) and vertebrate palaeontology of the Chañares Formation (Bonaparte 1975). Palaeontological contributions on Chañares fossils have steadily continued from the 1980s to the present (Arcucci 1986, 1987, 1990, 1996, 2011; Serenio & Arcucci 1994; Abdala 1996; Arcucci & Marsicano 1998; Abdala & Giannini 2000, 2002; Desojo & Arcucci 2008; Lecuona & Desojo 2011; Trotteyn & Desojo 2011; Leardi 2012). In addition, an exhaustive taphonomic study (Rogers *et al.* 2001) characterized the vertebrate preservation of the Chañares fauna from a particular concretion-hosted assemblage. Rogers *et al.* suggested that extensive volcanism in the area was the main cause of mass mortality and created a high potential for carcass preservation.

The main objective of this contribution is to discuss the palaeoecology of the Chañares tetrapod components within a palaeoecological and taphonomic framework. For this, we gathered anatomical and taphonomical information of nearly all the fossil material available from the unit and combined with additional evidence obtained from fieldworks conducted by the authors over the last 10 years. Considering the high preservational potential, the diverse and abundant Chañares faunal record allows us to hypothesize about the interaction between the components of the community and its role in the under-

standing of other Middle Triassic faunas from Gondwana.

Geological setting

Triassic non-marine sediments in Argentina are concentrated in half-graben rift systems located along the western Gondwana margin and associated with the pre-break-up of Pangaea (Uliana & Biddle 1988). The Ischigualasto-Villa Unión Basin is one of the most extensive of these rift basins, both in its geological record and surface extent. It is elongated in a NW–SE direction and filled with a 2000–6000 m non-marine succession of alluvial, fluvial and lacustrine sediments (Stipanovic 2002). Several Triassic localities with abundant faunal and floral remains are known from this basin (Artabe *et al.* 2001; Marsicano *et al.* 2001). The best-exposed outcrops are located along the border between San Juan and La Rioja provinces (Fig. 1A).

The Triassic deposits of the Ischigualasto-Villa Unión Basin rest unconformably upon thick continental Palaeozoic deposits (Caselli 1998). The initial infilling of the basin (Fig. 1B) is represented by the red alluvial fan, ephemeral fluvial and playa lake deposits of the Talampaya and Tarjados formations (López-Gamundí *et al.* 1989; Caselli 1998). The latter is unconformably overlain by the Agua de la Peña Group, which comprises the Chañares, Los Rastros, Ischigualasto and Los Colorados formations (Mancuso 2005a,b). The Chañares Formation (Fig. 1B) is characterized by tuffaceous sandstones and siltstones deposited in fluvial–lacustrine environments, with orthoconglomerates and paraconglomerates deposited in alluvial fans in the northwest part of the basin (Rogers *et al.* 2001; Mancuso *et al.* 2004; Mancuso 2005a,b). The unit is transitionally replaced upward by the lacustrine deltaic sandstones and black shales of the Los Rastros Formation, which in turn is overlain by the fluvial sandstones, mudstones and tuffs of the Ischigualasto Formation. Finally, the mudstone and sandstone red beds of the Los Colorados Formation, interpreted as a moderate-sinuosity fluvial system deposit (Caselli *et al.* 2001), represent the end of the Triassic succession. A regional unconformity separates the Triassic sequence from the fluvial conglomerates and sandstones of the putative Cretaceous Cerro Rajado Formation (López-Gamundí *et al.* 1989; Caselli *et al.* 2001).

The Agua de la Peña Group is considered to span the Middle–Late Triassic (Fig. 1B) (Stipanovic *et al.* 1996; Kokogian *et al.* 2001), with a Late Carnian–Early Norian age (following the Geologic

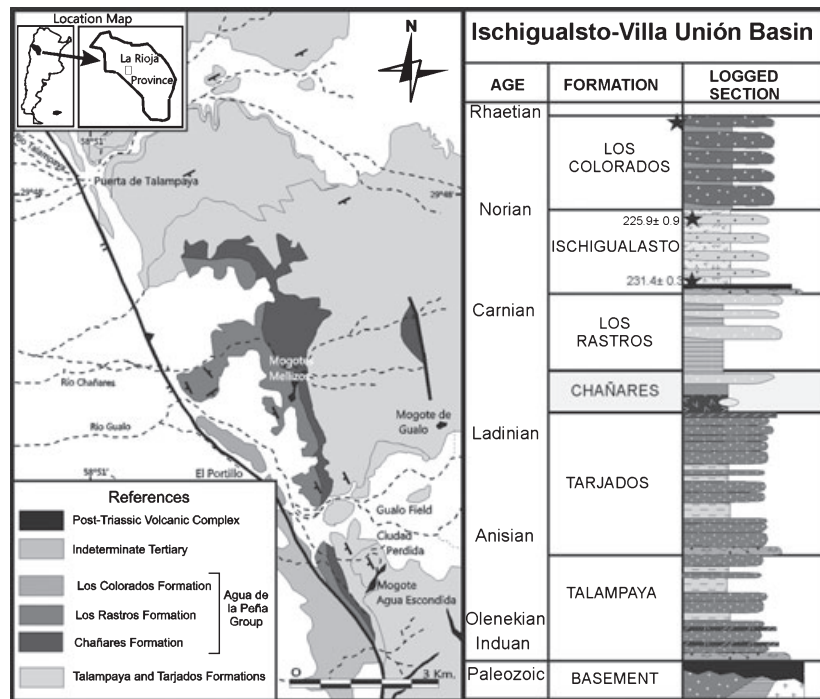


Fig. 1. Geological map of the Ischigualasto-Villa Unión Basin in La Rioja Province, Argentina. Modified from Mancuso (2005a); Triassic lithostratigraphy and chronostratigraphy in the Ischigualasto-Villa Unión Basin. Dates in millions of years are from the *Geologic Time Scale* (Ogg 2012). *231.4 ± 0.3 and 225.9 ± 0.9 Ma radioisotopic age of Ischigualasto Formation (Martinez *et al.* 2011); *the top of the Los Colorados Formation is Middle Norian in age (Santi Malnis *et al.* 2011).

Time Scale – see Ogg 2012; see also Irmis *et al.* 2011) for the lower and upper sections of the Ischigualasto Formation (231.4 ± 0.3 Ma and 225.9 ± 0.9 Ma, respectively; Martinez *et al.* 2011). A Ladinian age is inferred for the Chañares Formation based on its faunal composition and its stratigraphical relationships with the Ischigualasto Formation (Kokogian *et al.* 2001; Rogers *et al.* 2001).

Chañares Formation palaeoenvironment

The Chañares Formation in Talampaya National Park (La Rioja Province; Fig. 1) is characterized at its base by a sandstone–siltstone fluvial facies with distinct lower and upper levels (Table 1 and Fig. 2). The lower levels of this facies are composed of light olive grey fine-grained sandstones (Sh, Sp) with silicified root traces, scattered pebbles and locally abundant small brown carbonate concretions (5–25 cm in diameter). This facies covers the palaeotopography of the silicified top of the Tarjados Formation (Mancuso & Caselli 2012). The upper levels of the fluvial facies include fine-grained sandstones and siltstones that preserve vertebrate remains.

The overlying tuffaceous claystone–siltstone facies (TFm) is laterally persistent, and the beds display ‘popcorn’ weathering typical of bentonitic deposits (e.g. Terry *et al.* 1998). Abundant large

brown calcareous concretions, approximately 2 m in diameter, crop out in two discrete levels (Fig. 2). Additionally, some smaller and randomly distributed concretions are present in this facies. The concretions are composed of a blueish grey silty sandstone; in thin section, the matrix is composed of grains of quartz, plagioclase and corroded lithic fragments with cusped glass shards that have been altered to calcite and iron oxide (Rogers *et al.* 2001). Most Chañares vertebrate fossils have been recovered from the lower concretionary level in the mid section of the TFm facies, whereas the upper concretionary level lacks body fossil remains (Romer & Jensen 1966; Rogers *et al.* 2001; personal observations). This upper concretionary level is associated with a white tuff layer, and some of these concretions contain vertical burrows (1 cm diameter; Fig. 2). Some vertebrate remains showing a random areal distribution were found directly embedded in the tuffaceous clay–siltstones or in small concretions below the mid section concretionary level. Lithological and geometrical features (Table 1) suggest that the tuffaceous sandstones were deposited by river channels, whereas the tuffaceous claystones and siltstones were deposited on alluvial floodplains (Rogers *et al.* 2001; Mancuso 2005a). The dominance of bedload sedimentation in the fluvial system is probably associated with the influx of pyroclastic sediment (Rogers *et al.* 2001; Mancuso 2005a).

Table 1. Summary of the facies associations of the Chañares Formation.

Facies and interpretation	Lithology	Structures	Bedding	Fossil content	Lateral and vertical relationships
CH-A <i>Fluvial</i>	Moderate, sorted, light olive grey, fine-grained sandstone and siltstone, with scattered thin quartzite pebbles. (Sh, Sp)	Horizontal and low-angle laminated, small carbonate concretions.	Individual beds are tabular with 0.2–0.5 m of thick and extend laterally for tens of metres, and have planar non-erosional boundaries.	Root traces, horizontal burrows, occasional tetrapod remains.	Sh and Sp facies commonly overlie Tarjados Formation and is overlain by TFm facies.
	Light bluish grey tuffaceous very fine-grained sandstone, siltstone, and claystone. (TFm)	Massive to nodular, with large calcareous concretions.	Beds are tabular with 0.15–0.3 m of thick and laterally persistent for hundreds of metres, and have non-erosional boundaries.	Abundant tetrapod remains inside and outside concretions	TFm facies commonly overlies Sh and Sp facies and is overlain by Fm and Fl facies (CH-B).
CH-B <i>Shallow lake</i>	Light grey, pale olive, tuffaceous siltstone–claystone. (Fm, Fl)	Massive to nodular, and horizontally laminated.	Beds are tabular and 0.05–0.1 m in thickness and persist laterally for hundreds of metres, and have non-erosional boundaries.	Commonly burrowed with sub-vertical burrows 10–12 cm in length and 0.8 cm in width.	Fm and Fl facies overlie TFm facies (CH-A) and are overlain by Los Rastros Formation.

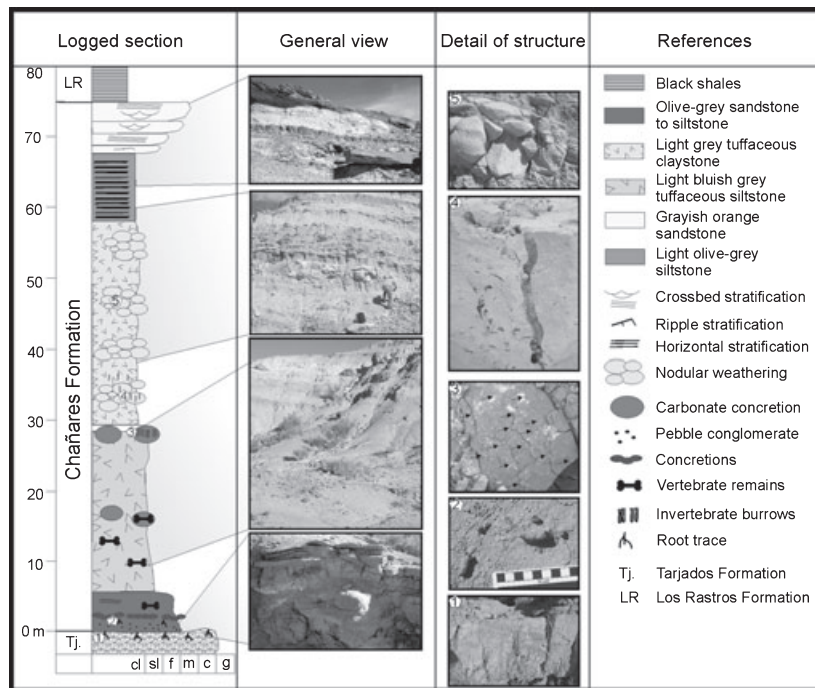


Fig. 2. Schematic section of the Chañares Formation in the Gualo area showing the fossiliferous levels. Pictures show details of the section and structures: (1) Palaeotopography of the silicified top of the Tarjados Formation; (2) Silicified root traces in the Chañares Formation; (3) Abundant invertebrate vertical burrows in the upper concretionary level of the Chañares Formation; (4) Sub-vertical invertebrate burrow exhibiting meniscate infillings; (5) Nodular weathering.

The succession ends with laterally persistent, light grey and pale olive claystones and siltstones (Fm, Fl; see Table 1 and Fig. 2) that also show ‘popcorn’ weathering. Abundant sub-vertical invertebrate burrows (10–12 cm long and 0.8 cm wide) and some exhibiting meniscate infillings (Fig. 2) are dispersed randomly throughout the succession

and are assigned to the ichnogenus *Taenidium* (Rogers *et al.* 2001). The fine-grained lithologies and sedimentary structures (along with other features summarized in Table 1) support the interpretation that these mudrocks were deposited in a shallow lake environment (Rogers *et al.* 2001; Mancuso 2005a).

Materials and methods

We have examined all the palaeontological collections housing Chañares vertebrate remains: Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa (BPI), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina (CPBA-V), Centro Regional de Investigaciones de La Rioja, Argentina (CRILAR), Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Argentina (MACN-PV), Museum of Comparative Zoology, Harvard University, Cambridge, USA (MCZ), Natural History Museum, London, United Kingdom (NHMUK), Colección Paleontología Lillo, Universidad Nacional de Tucumán, Argentina (PVL) and Museo de Paleontología, Universidad Nacional de La Rioja, Argentina (UNLR). The abundance of each taxon (at the genus level) and diversity of represented lineages were estimated by taking into account the number of specimens and taxa observed in the collections.

The ecological role of the fossil taxa was inferred through comparison of their anatomy with that of extant taxa. Identification of mainly herbivorous or carnivorous taxa was based on the morphological analysis of teeth. Taxa bearing sectorial (i.e. labiolingually compressed) teeth were interpreted as primarily carnivorous or insectivorous, whereas edentulous forms or those with labiolingually expanded and basined teeth are regarded as mainly herbivorous (Romer 1967, 1972a; Crompton 1972; Kemp 1982, 2005; Abdala & Giannini 2000). It should be noted, however, that the diet of some extant mammals with a specialized carnivorous dentition can include a large proportion of fruits (e.g. foxes, see Catlin 1988 and references there cited).

We used body mass estimations together with morphological traits to infer possible feeding habits (Table 5). Body mass estimations provide a rationale for inferring possible prey items for each faunivorous taxon. Most of the taxa analysed are known from more than one specimen (Table 3) representing individuals of different body sizes. Thus, there is overlap among the ranges of body size estimations of various taxa. Nevertheless, based on the estimated body mass of the largest specimen (assumed to have been an adult; see Table 3), we assigned each taxon to one of four body size categories.

Archosauriform and synapsid body masses were estimated using equations based on extant crocodylians (Farlow *et al.* 2005) and mammals (van Valkenburgh 1990). We are aware that the estimates calculated from these equations might

not be precisely accurate because the extant taxa used to produce the formulas (Fariña *et al.* 1998; Farlow *et al.* 2005; Pol *et al.* 2012; Taborda *et al.* 2013) could have different body proportions and thus not be very appropriate analogies. Nevertheless, we regard these formulas as the best proxies available for estimating the body mass of the Chañares animals within an order of magnitude. To normalize the implicit error in the body mass estimates among taxa, when possible, we apply a single equation for all forms included in each major taxonomic group (i.e. archosauriforms, cynodonts and dicynodonts). Hence, we expect the mass estimates species within the same taxonomic group to be similarly biased.

Because we are dealing with extinct taxa subjected to the biases and problems inherent in the fossil record, it is not possible to be certain about the maximum and minimum body sizes for any particular taxon. We adopted a conservative methodology by considering that the body mass of the largest specimen known for each taxon represents the maximum size that could be reached by the species, although this may result in an underestimation of the maximum size that a particular taxon could reach.

Farlow *et al.* (2005) base their estimations on measurements of the crocodylian femur and skull. We used the equations based on femoral and, in special cases, skull length for our proxies. Estimates based on femoral length were preferred because the femur was known for most taxa; otherwise, skull length was employed. The equations using skull (1), or femoral length (2), as proxies are given below:

$$\log(\text{body mass}) = 3.48 \log(\text{skull length in millimetres}) - 6.97 \quad (1)$$

$$\log(\text{body mass}) = 3.33 \log(\text{femoral length in millimetres}) - 5.72 \quad (2)$$

Several body mass estimators defined for cranial, dental and limb measurements, as well as for total body length (Anderson *et al.* 1985; Janis 1990; Scott 1990; van Valkenburgh 1990; Fariña *et al.* 1998), are available for modern mammals (e.g. ungulates, carnivores, felids and ursids). The body masses for dicynodonts and cynodonts were estimated using the equations for ursids (3) and carnivores (4), respectively (van Valkenburgh 1990):

$$\log(\text{body mass}) = 2.02 \log(\text{skull length in millimetres}) - 2.80 \quad (3)$$

$$\log(\text{body mass}) = 3.13 \log(\text{skull length in millimetres}) - 5.59 \quad (4)$$

The selection of these mammal groups as proxies takes into account the general body size and proportions inferred for these therapsids.

The specimens were measured by us whenever possible, and in other cases, measurements were obtained from the literature (Abdala 1996; Abdala & Giannini 2000, 2002; Domnanovich 2010). Only one specimen's measurements (UNLR 057) were obtained from a published figure (Desojo & Arcucci 2009).

Data for the taphonomic and environmental inferences were obtained from fieldwork and the review and study of specimens housed in collections (including semi-prepared fossil-bearing concretions). Taphonomic analysis of *in situ* fossils was conducted according to current methodologies (e.g. Behrensmeyer 1991; Rogers 1994; Eberth *et al.* 2007). The taphonomic attributes were documented in each accumulation, regardless of whether the fossil specimens were inside or outside concretions. However, these data were used for testing whether there are some differences between the fossil assemblages located inside or outside concretions.

The degree of articulation of skeletons was assessed as one of four different states: articulated (A) where the bones retain their anatomical positions; partially articulated (PA) where only some of the bones are in their anatomical positions; disarticulated but associated (DA) where the bones are all separated but remain in the immediate vicinity; and isolated and dispersed (ID) where the bones are widely separated. Voorhies groups (i.e. VG I, VG II and VG III) are indices of the resistance of skeletal elements to movement and dispersal (Voorhies 1969; Fiorillo *et al.* 2000). VG I includes individual skeletal elements that are most readily transported such as vertebrae or phalanges, and VG III being those that are most resistant to transport such as skulls and mandibles (Lyman 1994). The frequencies plotted in the ternary diagram were estimated from the total number of elements preserved in each accumulation. The attitude of the bones in each accumulation is recorded to understand their relationship with the entombed sediment. Thus, we were able to determine whether the skeletal elements in the accumulation show some spacial orientation and whether the skeletal elements cross cut the bedding planes. This helps to resolve any reorientation by an agent of transport and if they were deposited before or together with the entombing sediment. Finally, bone weathering stages were measured *sensu* Behrensmeyer (1978, 1991).

Palaeocological aspects, diversity and abundance of the Chañares tetrapods

Cynodonts. – Despite being represented by only three species (*Chiniquodon theotonicus*, *Massetognathus pascuali* and *Probainognathus jenseni*), cynodonts are by far the most common tetrapods found in the Chañares Formation (Fig. 3), comprising 73.7% of the tetrapod specimens recovered (Table 2). Fragmentary cynodont bones, mostly of *Massetognathus*, were rarely collected by previous field parties, resulting in an underrepresentation in the collections of cynodonts as a whole, and of *Massetognathus* specifically. Indeed, one of the hallmarks of the Chañares assemblage is the numerical dominance of traversodontid cynodonts, with *Massetognathus pascuali* representing 62.3% of the cynodont sample and 46.0% of all amniote remains recovered (Table 2). Additionally, the number of sectorial-toothed cynodonts is approximately half as abundant as *Massetognathus* in the fauna (Table 2). The dominance of traversodontid cynodonts in the Chañares Formation is not an isolated phenomenon. High percentages of these forms are also known in older and younger Triassic faunas from Gondwana, such as the Anisian assemblages from the Cerro de las Cabras Formation in western Argentina and the Lifua Member of the Manda Formation in Tanzania (Crompton 1955; Bonaparte 1969; Abdala *et al.*

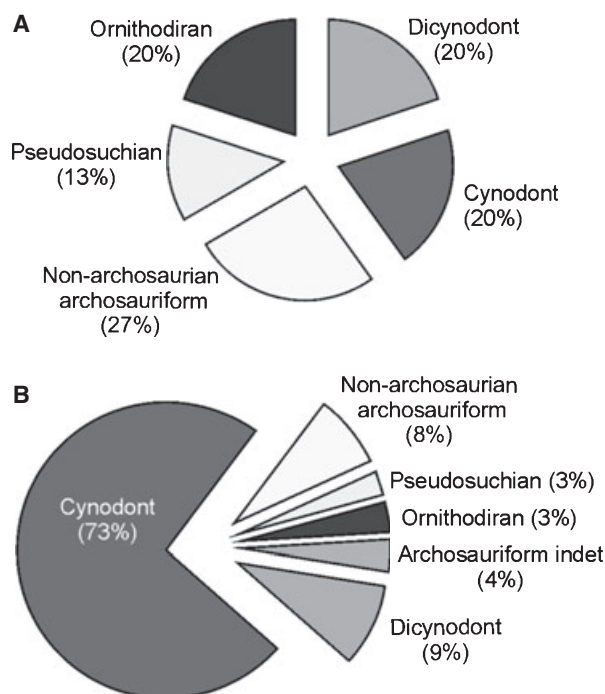


Fig. 3. A, taxonomic diversity of Chañares fauna (species level). B, taxonomic abundance of the different taxa of the Chañares tetrapod assemblage.

Table 2. Relative abundance of Chañares taxa.

				N° of specimens	% of total tetrapods		
Therapsida (82.7%)	Anomodontia (9.0%)	Dicynodontia (9.0%)	<i>Dinodontosaurus</i>	11	3.3		
			Dicynodont indet	19	5.7		
	Theriodontia (73.7%)	Cynodontia (73.7%)	<i>Massetognathus</i>	154	46		
			<i>Chiniquodon</i>	29	8.7		
			<i>Probainognathus</i>	57	17		
			Cynodont indet	7	2.1		
Archosauriforms (17.3%)	Non-archosaurian archosauriforms (7.8%)	Proterochampsida (7.2%)	<i>Chanaresuchus</i>	12	3.6		
			<i>Tropidosuchus</i>	10	3		
			<i>Gualosuchus</i>	2	0.6		
			<i>Tarjadia</i>	2	0.6		
			<i>Gracilisuchus</i>	6	1.8		
	Pseudosuchia (2.7%)	Basal Suchia (1.8%)	Paracrocodylomorpha (0.9%)	<i>Luperosuchus</i>	2	0.6	
				Paracrocodylomorphs indet.	1	0.3	
	Ornithodira (4.5%)	Non-dinosauriforms (1.5%)	Non-dinosaurian dinosauriforms (3%)	<i>Lagerpeton</i>	5	1.5	
				<i>Lewisuchus</i>	1	0.3	
				<i>Marasuchus</i>	5	1.5	
		Archosauriforms indet. (2.4%)	Archosauriforms indet. (2.4%)	Archosauriformes indet.	<i>Pseudolagosuchus</i>	4	1.2
					Archosauriformes indet.	8	2.4

Table 3. Body mass estimations for the Chañares taxa considering skull or femoral length. Skull length was measured from the anterior-most tip of the snout to the basi-occipital condyles. Asterisk depicts measurements from published figures.

Taxa		Specimen	Skull length (mm)	Femoral length (mm)	Estimated mass (kg)	
Archosauriforms	<i>Chanaresuchus</i>	MCZ 4035	–	128.7	20.18	
		MCZ 4036	–	138.3	25.64	
		MCZ 4038	–	124.88	18.25	
	<i>Gualosuchus</i>	PVL 4575	–	124.4	18.02	
		PVL 4576	–	98.07	8.16	
		<i>Tropidosuchus</i>	MCZ 9482 (1)	–	62.49	1.82
	<i>Marasuchus</i>	MCZ 9482 (2)	–	50.6	0.9	
		PVL 4601	–	68.2	2.43	
		<i>Pseudolagosuchus</i>	PVL 3871	–	62.97	1.87
		<i>Lagerpeton</i>	PVL 4629	–	115	13.87
		<i>Gracilisuchus</i>	MCZ 4121	–	62.6	1.83
		<i>Luperosuchus</i>	MCZ 4117	–	10.889	1.31
		<i>Probainognathus</i>	UNLR 04	–	55.45*	379.12
		<i>Chiniquodon</i>	PVL 4673	84	–	2.71
	Cynodonts	<i>Massetognathus</i>	PVL #?	121.4	–	8.58
PVL 44			126.7	–	9.81	
PVL 4728			182.5	–	30.74	
CRILAR-PV914			135	–	11.97	
UBA 14182			92	–	3.6	
Dicynodonts	<i>Dinodontosaurus platyceps</i>	UNLaR 14	450	–	362.65	
		<i>Dinodontosaurus brevirostris</i>	UNLaR 15	310	–	170.82

2009) and the lower Carnian faunas from the *Santa-cruzodon* Assemblage Zone, Santa María Formation in Brazil (Soares *et al.* 2011). A large number of traversodontid cynodonts are also recognized in the Late Carnian Ischigualasto Formation, although rhynchosaurs are the most abundant vertebrates in this unit (Martinez *et al.* 2011).

Massetognathus pascuali is a medium-sized cynodont represented by specimens which document different ontogenetic stages. It attains the largest size of any cynodont in the Chañares assemblage (skull length ranging from 72 to 204 mm; Abdala &

Giannini 2000) with a maximum inferred body size of approximately 43.57 kg (Table 3). *Massetognathus* is the only cynodont from the Chañares Formation with clear adaptations for herbivory, with basined, labiolingually expanded upper and lower post-canines, ensuring a rudimentary dental occlusion (Romer 1967, 1972a,b; Crompton 1972).

Chiniquodon thetonicus is a medium-sized carnivorous cynodont with sectorial post-canines that lack cingula and have a strongly recurved main cusp and smaller accessory distal cusps (von Huene 1936; Romer 1969; Abdala & Giannini 2002; Oliveira

et al. 2009). Only a few cynodonts (including extant mammals) have post-canines with strongly curved cusps, among them, pinniped carnivorans (Hillson 1990), in which the recumbent cusps prevent the escape of prey from the mouth of the animal. This suggests that *Chiniquodon* fed on animals small enough to allow the orientation of the post-canine cusps to ensure the posterior direction of food. The same interpretation is provided for the Early Triassic cynodont *Galesaurus*, which also has strongly curved main cusps lacking dental occlusion (Abdala *et al.* 2006). *Chiniquodon* probably caught, cut and swallowed whole prey items, just as most living carnivorous lizards do. The specimens of *Chiniquodon thetonicus* recovered from the Chañares Formation exhibit skull lengths ranging from approximately 67–159 mm (see also Abdala & Giannini 2002) with an inferred body mass of 19.97 kg for the largest size (Table 3). *Chiniquodon* is the least common cynodont in the Chañares assemblage (11.7% of all cynodonts and 8.7% of all tetrapods; Table 2). Representation of different ontogenetic stages is poor in comparison with *Massetognathus pascuali*, and there is an underrepresentation of very early growth stages. Considering the evidence at hand, it can be stated that there is an overlap in the size ranges of *Chiniquodon* and *Massetognathus* (Table 3).

Probainognathus jensei is the smallest cynodont from the Chañares Formation. The relative abundance of this species is about twice that of *Chiniquodon* (23.1% of cynodonts and 17.0% of tetrapods; see Table 2). Although a large sample of the ontogenetic stages of *Probainognathus* is lacking, small and relatively large representatives are known, showing a wide size range (Abdala 1996). At present, the largest specimen known (84 mm in skull length) has a body size around 2.7 kg, smaller than any of the specimens assigned to adult *Massetognathus* or *Chiniquodon* (Table 3). However, the smallest specimen of *Massetognathus* is 72 mm in skull length and that of *Chiniquodon* is only 70 mm and therefore smaller than the largest *Probainognathus* specimen. The small size and complex, cingulate sectorial post-canines of *Probainognathus* indicate a more complex faunivorous diet, probably consisting of arthropods and/or small vertebrates.

Dicynodonts. – Dicynodont remains represent 9.0% of all individual specimens from the Chañares assemblage (Fig. 3), and the only genus identified, *Dinodontosaurus* (Domnanovich 2010), represents around 3.3% of the total amniotes in the Chañares assemblage (Table 2). This genus has three recognized species: *Dinodontosaurus platyceps*, represented by two specimens, *D. brevirostris* with eight

specimens, and *D. platygnathus*, which is known only by one incomplete specimen (Domnanovich 2010).

Dinodontosaurus is a typical South American taxon and characterizes the *Dinodontosaurus* Assemblage Zone of the Santa María Formation in southern Brazil. In contrast to its poor representation in the Chañares assemblage, this dicynodont is by far the most common tetrapod from the contemporaneous Brazilian fauna (Langer *et al.* 2007), representing 61% of specimens recovered (Azevedo *et al.* 1990).

Dinodontosaurus is mid-sized by dicynodont standards, with *D. brevirostris* somewhat smaller than *D. platyceps* and *D. platygnathus*. The body sizes for *D. brevirostris* and *D. platyceps* were estimated from the skull length and ranged between approximately 170 kg and 362 kg (Table 3). Although *D. platygnathus* body mass could not be estimated due to the incompleteness of the only specimen known, Domnanovich (2010) suggested that this species was of the same size of *D. platyceps*. All Triassic dicynodonts (including *Dinodontosaurus*) lack post-canine teeth, and the anterior portion of the pre-maxilla and the dentary is interpreted to have been covered by a keratinous beak (King 1990). This morphology would have been useful in dealing with different kinds of vegetation. *Dinodontosaurus* also features a pair of well-developed maxillary tusks. An analysis of dicynodont cranial morphology suggests that these animals used the anterior part of the palate for crushing, whereas the sharp rims of the pre-maxilla and lower jaw would chop and slice food (King 1990). *Dinodontosaurus* was stocky and probably not an agile animal, comparable in size to a small extant rhinoceros (King 1990).

Surkov & Benton (2008) classified Permian and Triassic dicynodonts in three categories, reflecting their probable feeding habits. Using cranial measurements as proxies for muscular development and common head movements, those authors inferred that *Dinodontosaurus* fed on low vegetation (i.e. at or below the level of the head). *Dinodontosaurus* and *Massetognathus* have a significant difference in body size, but the evidence above suggests that both taxa made use of the same food source, feeding on ground level vegetation or on the lower branches of taller plants and shrubs. Perhaps the overall larger size in *Dinodontosaurus* allowed it to feed on additional resources not accessed by adult *Massetognathus*.

Archosauriforms. – Unlike cynodonts, which show a low species-richness and occur in great abundance, archosauriforms are represented by several clades in the Chañares fauna, all with rather low abundance,

but they are quite diverse (Fig. 3). This lineage represents 17.3% of the Chañares amniote specimens recovered (Table 2). The non-archosaurian archosauriforms, including proterochampsids and doswelliids, are the most common members of this clade (Fig. 3), representing more than half of the known specimens of archosauriforms (Table 2). Proterochampsids are the most abundant (41.4% of all archosauriforms; Table 2), and they are the most species-rich, with three different taxa (*Chanaresuchus bonapartei*, *Gualosuchus reigi* and *Tropidosuchus romeri*). *Chanaresuchus* and *Tropidosuchus* (represented by at least eleven and ten specimens respectively) are the most abundant proterochampsids and archosauriforms recorded from the Chañares Formation, whereas *Gualosuchus* is known only from two specimens. Proterochampsids show one of the largest size ranges among archosauriforms, as *Tropidosuchus* had an estimated weight of less than 3 kg, whereas the largest *Chanaresuchus* known weighed approximately 25.6 kg (Table 3).

Proterochampsids have historically been regarded as semi-aquatic and probably piscivorous (Sill 1967; Romer 1971a,b, 1972a,b) because of their low, long snout with numerous teeth and ornamented skull, combined with an inferred quadrupedal sprawling posture. However, a recent review of this group (Arcucci 2011) emphasized differences between proterochampsids and the aquatic or semi-aquatic crocodiles with which they are frequently compared. The long and low snouts of proterochampsids do not contain a complete secondary palate as in crocodiles (although there are some fully aquatic reptiles like phytosaurs that lack a bony secondary palate; Chatterjee 1978; Sereno 1991). The number of marginal teeth is approximately the same as in other archosaurs (15 in both the upper and lower jaws), and they are laterally compressed and recurved with no apparent similarity to those of confirmed piscivorous animals such as *Gavialis* and sauropterygians, in which these teeth are increased in number, conical and lack any type of carinae or keel (Massare 1987; Pierce et al. 2009). Moreover, there is no evidence that the skull ornamentation present in several patterns and degrees in many archosauromorph lineages (e.g. aetosaurids, euparkeriids, 'protosuchians' and raiisuchids) has any relationship with life in an aquatic environment. In addition, the post-cranial skeleton of proterochampsids does not show evidence of aquatic adaptations: the limbs do not show signs of digit reduction or enlargement of the distal elements, and the tail is not dorsoventrally tall, but instead is wide and thick with very low neural spines and well-developed transverse processes (Arcucci 2011). The limbs are long and slender in relation to

other archosauromorphs, such as the larger proterosuchids and erythrosuchids, suggesting that the posture was not sprawling, having some degree of adduction of the limbs, although not fully vertical. Given the absence of clear aquatic adaptations, the proterochampsids from Chañares are regarded as mainly terrestrial forms, as are most archosauriforms (Nesbitt et al. 2009).

Tarjadia ruthae was originally regarded as an archosauriform of uncertain affinities (Arcucci & Marsicano 1998), but recently has been identified as a doswelliid (Desojo et al. 2011). Doswelliids have been interpreted either as terrestrial or aquatic (Weems 1980). The latter view has been the most widely accepted, based on the animal's heavily ornamented skull, broad osteoderms, long mandible with conical teeth and dorsally directed orbits (Desojo et al. 2011). Little can be said about the body size of *T. ruthae* because the two known specimens from the Chañares Formation are very fragmentary. Even though most of the above-mentioned characters cannot be observed in *T. ruthae*, we considered this taxon to be a semi-aquatic, like other better-known doswelliids.

The Chañares archosaurian record includes representatives of both major clades in almost equal abundance (pseudosuchians 2.7% and ornithomirans 4.5% of all amniotes in the Chañares fauna) and species-richness (each group represented by three taxa: Table 2 and Fig. 3). Pseudosuchians are represented by the basal pseudosuchian *Gracilisuchus stipanicorum*, the paracrocodylomorph *Luperosuchus fractus* and isolated paracrocodylomorph remains that represent arguably the largest archosaur of the formation (CRILAR 417; see Leardi 2012). The pseudosuchians are clearly divided into two very different size categories (Table 3): *Gracilisuchus* represents one of the lightest forms (with an estimated weight of less than 1.5 kg) and, in strong contrast, the large paracrocodylomorphs have estimated masses around 350–500 kg (see Leardi 2012). The latter are very scarce in the Chañares Formation (only 5.2% of the archosauriform specimens), being represented by two *Luperosuchus* specimens (UNLR 04 and 057), only one of which is a large animal (Table 3), and by the large unnamed taxon reported by Leardi (2012). With the exception of *Revuelto-saurus*, aetosaurus and shuvosaurids, pseudosuchians are usually regarded as predatory animals (Nesbitt 2011). Additionally, paracrocodylomorphs are considered predators on the basis of their huge, labiolingually compressed teeth with serrated carinae (Gower 2000) and are usually the largest predatory forms in their community. *Gracilisuchus* does not have any particular adaptations for a specialized

diet, and it is considered faunivorous in concordance with most of the members of the Pseudosuchia, probably preying on arthropods or small vertebrates.

As mentioned previously, ornithomirans represent 25.9% of Chañares archosauriforms and comprise exclusively non-dinosaurian dinosauromorphs: the basal dinosauromorph *Lagerpeton chanarensis* and the dinosauriforms *Marasuchus lilloensis*, *Lewisuchus admixtus* and *Pseudolagosuchus major* (a potential synonym of the *Lewisuchus* -Nesbitt *et al.* 2010). This clade is homogenous in body mass, being comprised of small animals whose estimated weights do not exceed 2 kg (Table 3), except in the case of *Pseudolagosuchus*, which is interpreted as a significantly larger form. We were not able to estimate the mass of *Lewisuchus*, as the material available for this taxon (UNLR 01) does not allow for a quantitative estimate of body size. Even though few tooth-bearing jaws of basal dinosauromorphs have been found, they are usually regarded as generalized predators probably feeding on small arthropods or small vertebrates, as they lack any particular adaptations to omnivorous or herbivorous diets (Nesbitt *et al.* 2010; Barret *et al.* 2011). *Lewisuchus* has been assigned to the Silesauridae (Nesbitt *et al.* 2010; Nesbitt 2011), a group showing adaptations to omnivory or herbivory (Nesbitt *et al.* 2010), but a recent phylogeny recovered the taxon outside silesaurids (Bittencourt *et al.* 2011). Given its contested phylogenetic position and putative lack of omnivorous/herbivorous adaptations (ABA, personal observation; Bittencourt *et al.* 2011), *Lewisuchus* is here considered as a generalist faunivore.

For diversity and abundance estimates, specimens assigned to *Lagosuchus talampayensis* are considered as indeterminate archosauriforms (2.4% of all amniotes in the Chañares fauna). The assignment of *Lagosuchus* to Dinosauriformes is controversial (see Sereno & Arcucci 1993) as the affinities of these taxa are problematic. In many cases, individuals assigned to this genus include specimens that do not even belong to Archosauria but represent proterochampsids (ABA and JML, personal observation *Lagosuchus*: UNLR 09, PVL 3871, MCZ 4137, MCZ 9483R, *Pseudolagosuchus*: MACN 18954). To solve this problem, a thorough revision of the material assigned to these taxa is needed, but that remains is beyond the scope of this present study.

Taphonomy

In Talampaya National Park, the Chañares Formation outcrops cover approximately 22 km². This unit also crops out in Ischigualasto Provincial Park

and the Cerro Bola area, but to date, without any fossil vertebrates having been found. While the Chañares area has long been considered the richest fossil locality of the unit (Romer & Jensen 1966; Rogers *et al.* 2001), the highest abundance and diversity of fossils actually come from the Río Chañares-Río Gualo outcrops in Talampaya National Park (Fig. 1). In this area, approximately 330 vertebrate specimens were found in the last 50 years resulting in an average fossil density of 15 specimens/km². The fossils have a random areal distribution (Romer & Jensen 1966; Rogers *et al.* 2001; Mancuso 2005a) and are confined to levels in the lowest 15 m of the formation where they occur in light olive grey and light bluish grey tuffaceous siltstones (TFm) without any perimineralization, and within brown calcareous concretions (Fig. 2). The fossil-bearing large concretions are restricted to a single, lower concretionary level (Fig. 2) 15 m up from the base of the unit, *sensu* data of Romer & Jensen (1966), Rogers *et al.* (2001) and personal observations. Below this lower concretionary level, the fossils are found outside the concretions or in small concretions with random stratigraphical distribution.

Taphonomic attributes of fossils located both outside and inside concretions (O-CF and I-CF, respectively) are documented here. These data include both field- and collection-based observations and are summarized in Figures 4–6.

Some 63.2% of the O-CF and I-CF fossil assemblages preserve remains of a single individual, 23.4% two or more individuals of a single taxon and 13.2% remains of two or more taxa (Fig. 4A). Thus, the assemblages include different combinations of archosauriforms, cynodonts and dicynodonts. The assemblages with two or more individuals of a single taxon consist in general of cynodonts. Mixed fossil accumulations are composed of associations of archosauriforms and therapsids, different therapsid clades (cynodont and dicynodont) or different groups of archosauriforms. It is worth noting that large archosaurian and dicynodont remains are never perimineralized and are only found in the lowermost levels.

Different states of articulation are present in the remains recovered from the Chañares fauna (Fig. 4B). There is dominance of articulated and partially articulated remains inside the concretions and of isolated and dispersed remains outside them (Fig. 4C). The archosauriforms are mostly articulated, partially articulated or disarticulated but associated. The articulated and partially articulated archosauriform remains are principally preserved in concretions, whereas the remains found outside the

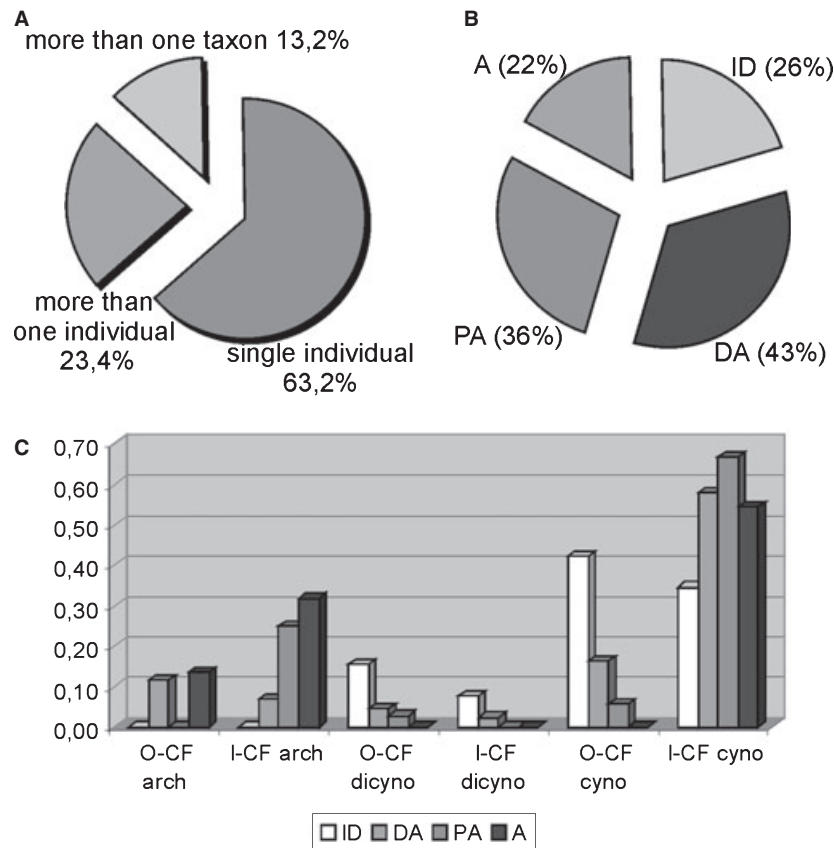


Fig. 4. Taphonomic attributes. A, percentage of the assemblage with single individuals (63.2%), two or more individuals of a taxon (23.4%) and two or more taxa (13.2%). B, abundance of different stages of fossil inside concretion articulation. C, fossil outside concretion proportion of the stages of articulation in the different taxa. archo, archosauriform; cyno, cynodont; dicyno, dicynodont; A, articulated; PA, partially articulated; DA, disarticulated but associated; ID, isolated and dispersed; I-CF, inside concretion fossil; O-CF, outside concretion fossil.

concretions are mainly disarticulated but associated. The majority of dicynodonts are found as isolated and dispersed bones. The cynodonts are preserved in all four categories; however, there is a dominance of partially articulated remains within the concretions and isolated and dispersed bones outside concretions.

The skeletal representation observed for different taxa between O-CF and I-CF (Fig. 5) suggests that the taphonomic processes acted differently. The I-CF cynodont remains show a higher representation of skeletal elements that are more abundant in the skeleton. On the other hand, there is an anomalous abundance of mandibles and skulls among the O-CF cynodont remains. In general, dicynodont post-crania are underrepresented in both O-CF and I-CF. The archosauriforms show a similar distribution of skeletal elements between O-CF and I-CF assemblages, with a dominance of post-cranial elements.

For the taphonomic analysis, the Voorhies groups of the Chañares fossils were divided between O-CF and I-CF and grouped according

to the relative abundance of skeletal elements assignable to each Voorhies group. The frequencies for each assemblage were plotted in a ternary diagram (Fig. 6A). The frequency distribution of O-CF and I-CF fossil assemblages do not show significant differences, suggesting that both were subjected to similar hydrodynamic conditions during burial. The results (Fig. 6A) show a concentration of assemblages in VG III representing assemblages that suffered the removal of low-mass skeletal elements such as vertebrae, ribs and phalanges. Another relatively large concentration close to VG I includes nearly complete skeletons that represent fossils accumulating without transport. The assemblages concentrated near VG I, excluding elements of VG II or VG III, represent the accumulations where the most readily transported elements were carried by low-energy currents.

A significant number of fossils studied here were discovered in concretions not collected by us, and many lack contextual information, including the provenance and original position. In these cases,

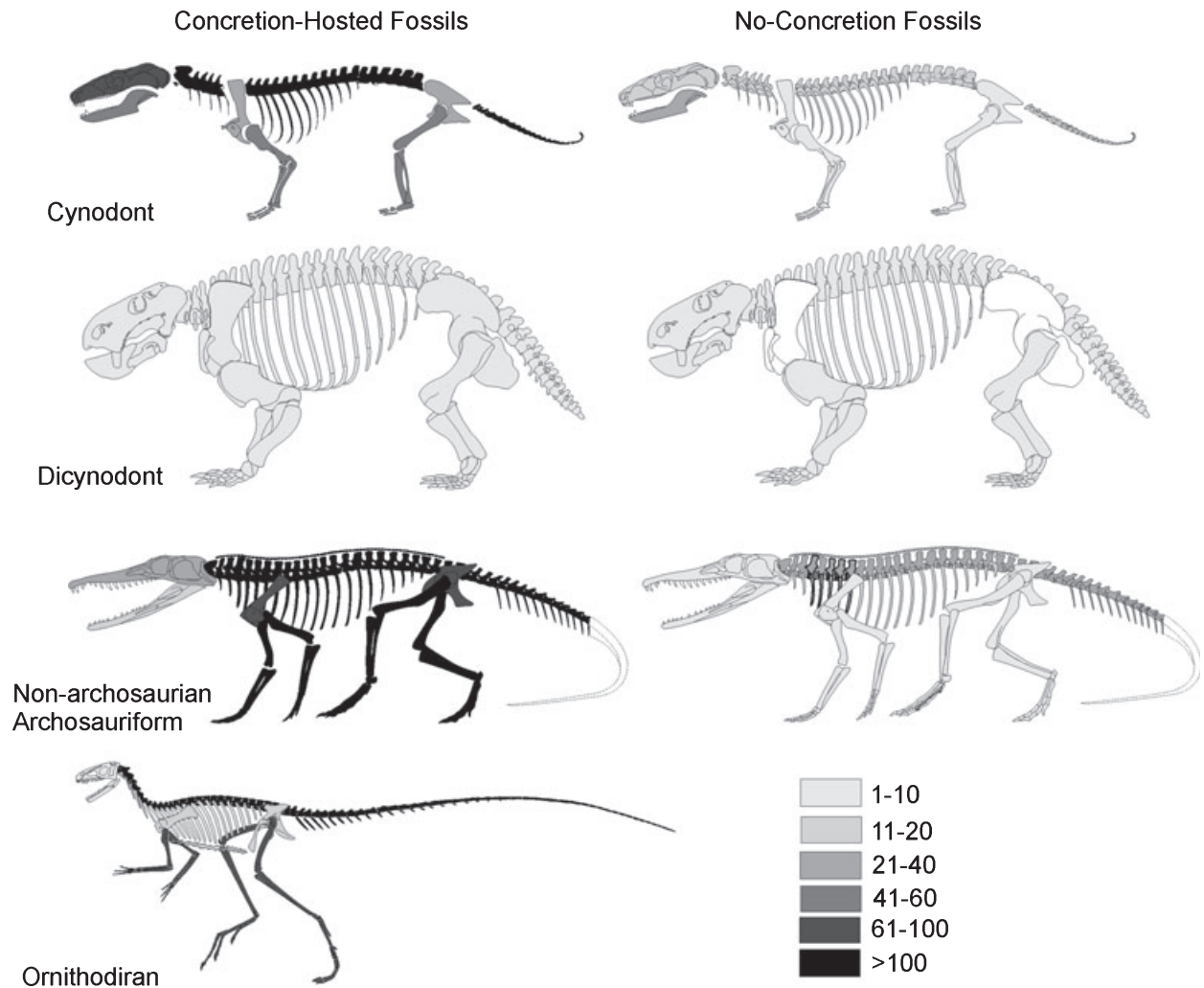


Fig. 5. Taphonomic attributes. Skeletal representation for different taxa. The greyscale in the skeletons represents the relative abundance of skeletal elements collected.

only the orientation of the bones can be used to analyse the influence of taphonomic agents, and inferences regarding global trends for the concretion-bearing level are not possible. Figure 6B shows the percentage of long bone long axis orientations for the O-CF and I-CF assemblages. I-CF assemblages have a higher proportion of skeletal elements oriented and cross cutting the bedding plane than O-CF assemblages (Fig. 6B). Aligned bones in I-CF assemblages are less common, although the cross-cutting bones in I-CF suggests more interaction between the remains and the entombing sediment.

Most skeletal elements lack surface modification (e.g. abrasion, rounding or tooth marks). The breakage patterns are transverse fractures attributed to post-mineralization damage. In general, there is no evidence of macroscopic weathering on the bone surfaces (weathering stages between 0 and 1; Fig. 6C). The I-CF bones show equal number of weathering stages 0 and 1, whereas the

O-CF assemblages present weathering stage 0 twice as often as stage 1. Rogers *et al.* (2001) observed a degree of superficial oxidation and corrosion in backscatter electron images of selected bones inside concretions.

Discussion

Taphonomy

The fossil accumulations of the Chañares assemblage are considered to be the product of two different taphonomic pathways (Rogers *et al.* 2001; Mancuso 2005a): (1) attritional accumulation associated with natural deaths of individuals by predation, disease and old age; and (2) mass mortality of animals associated volcanic events. Here, we discuss whether all the evidence gathered so far supports this interpretation and test these findings with our new data.

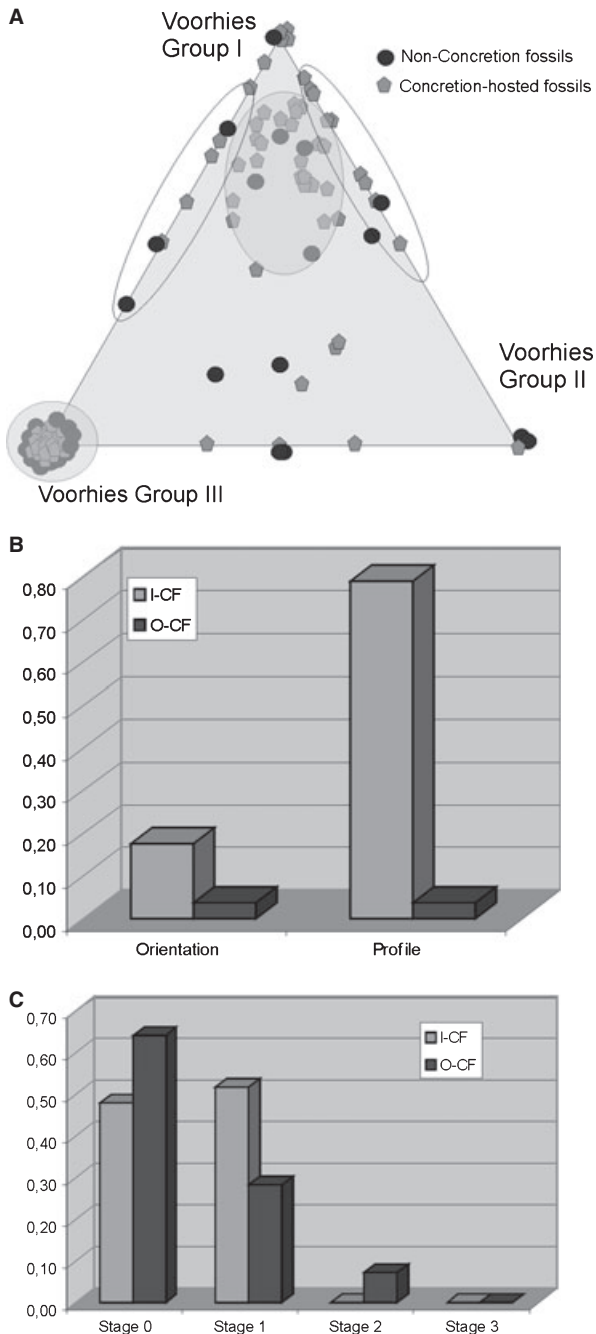


Fig. 6. Taphonomic attributes. A, ternary diagram of frequencies of the skeletal elements showing the clustering of the assemblages with regard to Voorhies groups. The main concentration of assemblages is indicated by grey circles. B, percentage of assemblages with orientation on the surface and in depth. C, weathering stages *sensu* Behrensmeier (1978). I-CF, inside concretion fossil; O-CF, outside concretion fossil.

The remains found in lowest levels (below the lower concretion level), outside concretions and in some small concretions, are considered by us as products of attritional mortality. They have random stratigraphical and areal distributions and are usually found directly embedded in the olive grey

and light blueish grey tuffaceous siltstones or in small concretions. Most of these accumulations include a single individual represented by isolated and dispersed, and disarticulated but associated bones and, to a lesser extent, partially articulated bones. Regarding cynodont specimens, the dentary, skull and limbs are overrepresented, whereas dicynodonts are mainly represented by skulls. Taphonomic sorting removed most of the readily transported skeletal elements, especially from disarticulated cynodont and dicynodont carcasses. In addition, the remains of large taxa, including some archosauriforms and dicynodonts, were found outside concretions. The Chañares fossil record from the lowest level represents mainly VG III accumulations (Fig. 6A), suggesting that low- and medium-mass skeletal elements (e.g. vertebrae, ribs, girdle, limb bones) were removed by low-energy currents and entombed basinward. The 3D orientation shows an interaction between the remains and the entombing sediment. Post-mortem modifications of the bones, including the weathering stage, suggest that the remains represent accumulation by attritional mortality and did not suffer trampling or surface exposure for very long periods of time. Thus, after the death of the animals, the skeletons remained exposed on the floodplain for some time, during which they were disarticulated and dispersed by scavengers and/or low-energy hydraulic flows that caused the sorting recorded in these assemblages.

In the lower concretion level, anomalous concentrations of articulated tetrapod remains are interpreted as evidence of a mass mortality event. The stratigraphical distribution is restricted (Fig. 2), whereas the areal distribution is extensive, at least in Talampaya National Park. The assemblages range from a single individual to several individuals of one or more taxa, which are usually articulated or partially articulated, with some occurrences of disarticulated but associated bones. Small- to medium-sized cynodonts and archosauriforms are best represented in the concretions, and, in general, these groups show similar frequencies of skeletal parts. The mass mortality individuals recovered in concretions show less evidence of sorting agents, with the assemblages concentrated near VG I (predominance of complete skeletons, Fig. 5). The accumulation plotted near VG I represents untransported remains, whereas the accumulation near VG I, lacking elements of VG III or II, includes remains that were transported by low-energy currents. Bones in concretions show no preferred orientation in plan and profile views, suggesting a combined depositional event for the remains and the entombing sediment. The mass mortality event seems to have preferentially affected

Table 4. Features of the two taphonomic modes.

	Attritional mode	Mass mortality mode
Killing mechanism	Natural death by predation, disease or old age	Catastrophic volcanic event
Stratigraphic distribution	Random in lowest 15 m of the unit	Restricted to lower large concretion level
Areal distribution	Random	Extensive
Host-rock	Olive grey and light bluish grey tuffaceous siltstones or sometimes in small concretions	Large concretions
Accumulation	Single individual	Multi-individual, multi-taxa
Taxon size	Complete spectrum	Small and medium
Completeness	Low completeness	High completeness
Articulation	Isolated and dispersed/disarticulated but associated	Articulated/partially articulated
Weathering	0–1	0, and few 1
Scavenging	Evidenced by dispersion	Not evidence
Voorhies Groups	VIII	VI, and few VII and VIII
Orientation	3D orientation, entombed with sediment	No preferred orientation
Burial	Rapid	Very rapid
Breakage	Transverse fracture	Transverse fracture

small- to medium-sized cynodont and archosauriform taxa. The carcasses remained on the floodplain for a very short time (much less than the carcasses produced by attritional mortality) and were rapidly buried by a low-energy flow that reoriented some elements. The mass mortality event not only caused the death of the animals, but also supplied the sediment that facilitated their rapid entombment, preventing scavenging, trampling or exposure to weathering agents.

In summary, two clearly different patterns – attritional and mass mortality – are supported by the current taphonomic analysis (Table 4). Bone accumulations in the lowest levels (outside concretions or in small concretions) are explained as having accumulated through attritional mortality, and these preserve the remains of the largest animals of the fauna. The tetrapod record of the attritional accumulation is nearly 3:1:1 (cynodont:dicynodont:archosauriforms). A signature of this pattern is the disarticulation and dispersion of skeletons produced by scavengers and/or low-energy hydraulic flows. Accumulations of carcasses in concretions are mostly a by-product of mass mortality and resulted in the preservation of a large quantity of completely or partially articulated skeletons and, on rare occasions, some sorting followed by rapid burial. In this case, the accumulation is nearly 20:1:7 (cynodont:

dicynodont:archosauriforms). In the mass mortality event, there is a clear bias towards preservation of individuals representing smaller-sized to mid-sized taxa (e.g. *Massetognathus*). The underrepresented large taxa (dicynodonts and paracrocodylomorphs) in the concretion level is not only the result of the lower abundance in the fauna, but also that the mass mortality agent affected differentially the small- to medium-sized taxa and large taxa. The differences between attritional and mass mortality assemblages from the Chañares Formation include not only a different mode of death, but also the intensities in the occurrence of the taphonomic processes such as weathering exposure, disarticulation and sorting. Thus, the taphonomic characteristics and the concentrated stratigraphical interval, in which the Chañares fauna is recorded, permit the accurate palaeoecological examination of this tetrapod record as a community and allow for the inference of trophic interactions between the different taxa.

The Chañares tetrapod community

The largest forms of the Chañares fauna, having body masses estimated in hundreds of kilograms, are represented by three species of the dicynodont *Dinodontosaurus* (*D. platyceps*, *D. platygnathus* and *D. brevisrostris*) and paracrocodylomorphs (*Luperosuchus* and CRILAR 417; Table 3). The medium-sized forms, with body masses estimated in tens of kilograms, include *Chanaresuchus*, *Chiniquodon*, *Gualosuchus*, *Massetognathus* and *Pseudolagosuchus*. Finally, the most diverse group includes the smallest taxa, which probably did not exceed 3 kg, represented by *Gracilisuchus*, *Marasuchus*, *Lagerpeton*, *Lewisuchus*, *Probainognathus* and *Tropidosuchus* (Table 3).

The Chañares assemblage is clearly dominated by forms in the range of tens of kilograms, mainly therapsids, representing ~60% of the specimens (Fig. 7). The next most common body size is of forms weighing no more than 3 kg, representing

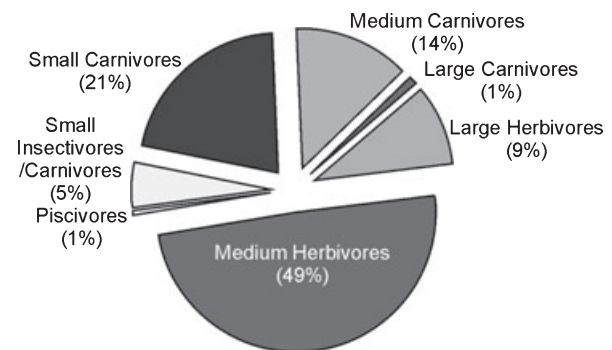


Fig. 7. Relative distribution of the interpreted ecological guilds recognized for vertebrate fossils from the Chañares fauna.

approximately 26% of the individuals, and clearly dominated by archosauriforms. The largest forms (over 100 kg) are the least common (~10% of the tetrapods) and are represented mainly by dicynodonts.

In a trophic reconstruction of the environment (Table 5), 55% of the specimens are herbivorous and 45% are faunivorous. All the herbivores are therapsids, and the most abundant by far is *Massetognathus*, representing 83.7% of all herbivorous specimens. *Probainognathus* and *Chiniquodon* are the most abundant faunivorous forms. *Tarjadia* represents the only inferred piscivorous taxon (0.6% of the fauna).

Studies on extant non-scavenging carnivores have shown that these animals usually prefer prey smaller than their own body size, except when organized in hunting groups or in amphibious forms such as crocodylians (Troost *et al.* 2008). Considering information on predator behaviour in modern ecosys-

tems (Troost *et al.* 2008), three inferences can be made for the terrestrial carnivore feeding behaviour: (1) larger animals would have fed on smaller ones; (2) similar-sized predators would have preferred the same sized prey; and (3) predatory animals would have fed on herbivores (predation on carnivores by carnivores is uncommon).

These modern analogues are helpful when reconstructing the food chains of past ecosystems. The first one supports the use of body size to establish the predator ranking and the preferred prey of each faunivorous form. The second inference highlights the problem of comparing body mass estimates obtained through different equations and corresponding to animals with dissimilar anatomical proportions. When extinct archosauriforms are compared to therapsids of similar body mass, the skull size of the archosauriforms is relatively smaller (see reconstructions by Cox 1965; Jenkins 1970; Romer 1972a,b; Parrish *et al.* 1986; Kemp 2005). Thus, the body size of the proposed prey of a terrestrial archosauriform should be smaller than that of a synapsid with similar body mass. Finally, the third inference favours a predator–prey relationship between to faunivorous–herbivorous forms.

Due to the difficult task of assigning a scavenging habit based solely on fossil data and to enable us to reconstruct the trophic network (see below), we consider all faunivorous taxa to be active hunters. *Tarjadia* is excluded from this discussion as it is considered here as a piscivorous form, based on the anatomy of the mandible of other known doswelliids (*Doswellia*: Dilkes & Sues 2009).

Small faunivores ate invertebrates and tiny vertebrates, whereas medium-sized faunivores likely fed preferably on juvenile *Massetognathus* and dicynodonts. Additionally, the slightly larger *Chanaresuchus* and *Pseudolagosuchus* also preyed on sub-adult individuals of *Massetognathus*. *Luperosuchus* and the unnamed paracrocodylomorph represent the top predators in the reconstructed community. They certainly preyed on all the other members of the assemblage, including fully grown dicynodonts and *Massetognathus* (Table 3). However, predation of relatively large herbivores by medium-sized carnivorous forms (e.g. *Chiniquodon*) hunting in groups cannot be ruled out. Considering the abundance of the herbivorous cynodont *Massetognathus*, it is clear that this taxon represents the main food resource in the Chañares assemblage. Considering its overwhelming role as main prey, there is no evidence of predatory bone modification on any of the many *Massetognathus* bones recovered. This finding is in contrast to what is expected of most carnivore–carcass interactions.

Table 5. Abundance and ecological guilds of Chañares tetrapod fauna.

Taxa	N° of specimens	Side	Ecological role
Therapsida	277		
Anomodontia			
Dicynodontia	30		Herbivores
Dicynodont indet	19	>100 kg	
<i>Dinodontosaurus</i>	11	>100 kg	
Theriodontia			
Cynodontia	247		
Cynodont indet	7		
<i>Massetognathus</i>	154	>10 kg	Herbivores
<i>Chiniquodon</i>	29	~10 kg	Carnivores
<i>Probainognathus</i>	57	<3 kg	Carnivores/ Insectivores
Archosauriforms	58		
Archosauriforms indet.	12		
Non-archosaurian archosauriforms	26		
Proterochampsida	24		
<i>Chanaresuchus</i>	12	>10 kg	Carnivores
<i>Tropidosuchus</i>	10	<3 kg	Carnivores/ Insectivores
<i>Gualosuchus</i>	2	~10 kg	Carnivores
Doswelida	2		Piscivores
<i>Tarjadia</i>	2	>100 kg	
Pseudosuchia	9		
Basal suchians	6		Carnivores
<i>Gracilisuchus</i>	6	<3 kg	
Paracrocodylomorpha	3		Carnivores
Paracrocodylomorpha indet.	1	>100 kg	
<i>Luperosuchus</i>	2	>100 kg	
Ornithodira	15		Carnivores/ Insectivores
Non-dinosauriformes dinosauriforms	5		
<i>Lagerpeton</i>	5	<3 kg	
Non-dinosaurian dinosauriforms	10		
<i>Lewisuchus</i>	1	<3 kg	
<i>Marasuchus</i>	5	<3 kg	
<i>Pseudolagosuchus</i>	4	~10 kg	

Only a few forms were capable of preying on fully grown *Massetognathus*; therefore, a high predation pressure on infant, juvenile and sub-adults is expected, and this, together with a high reproductive rate, may explain the overwhelming abundance of *Massetognathus* bones preserved. Predation pressure is also expected to have affected fully grown dicynodonts, but the predicted predator–prey relationship does not explain the low observed proportion of dicynodont fossils in the Chañares area.

Traversodontid cynodonts and dicynodonts are the only specialized herbivores from the Chañares Formation. The interpretation of the dicynodont *Dinodontosaurus* as feeding on low vegetation, below or level with their heads (Surkov & Benton 2008), indicates that they likely fed on the same foliage as *Massetognathus*.

Extant specialized medium- and large-sized herbivorous mammals usually form herds and are numerically abundant in their habitats (McNaughton 1986; Estes 1991). There is evidence of gregarious behaviour in Permian dicynodonts such as *Diictodon* (King 1990; Ray & Chinsamy 2003). More compelling is the evidence of dicynodont herds in the Los Rastros Formation (Marsicano *et al.* 2010) and of gregarious behaviour recently proposed for *Dinodontosaurus* from the Brazilian Santa Maria Formation (de Oliveira Bueno *et al.* 2011; de Oliveira Bueno 2012). Considering this subsidiary evidence, we propose that the *Dinodontosaurus* from Chañares were also gregarious. However, it is difficult to reconcile this kind of behaviour in Chañares taking into account the scarce representation of the taxon in the fauna (3.3% of the total tetrapods). On the contrary, *Massetognathus* record suggests a gregarious habit, in particular concretions including several articulated specimens. This behaviour has been reported for some cynodonts that are known to have lived in burrows (Groenewald *et al.* 2001; Damiani *et al.* 2003; Talanda *et al.* 2011).

The attritional record shows the relative abundance of dicynodonts and *Massetognathus* to be similar, with slight dominance of the latter, whereas in the mass mortality event, dicynodonts have much poorer representation than *Massetognathus*. No large taxa (i.e. dicynodonts and paracrocodylomorphs) have as yet been registered in the mass mortality record, but they are represented in the attritional levels. In addition, an ichnological record of large taxa was reported from the immediately overlying levels of the Los Rastros Formation (Marsicano *et al.* 2010). The low abundance of dicynodonts in the mass mortality assemblage, when compared to the almost even ratio of *Dinodontosaurus*/*Massetognathus* remains in the attritional levels, is remarkable. We leave the final

cause of this open, just highlighting two possibilities: (1) the mass mortality affected these taxa in a different way, with increased severity on small young and/or medium-sized forms; or (2) dicynodonts were not regular inhabitants in this area of the basin.

Trophic chain in the Chañares-Los Rastros assemblage

The reconstructed Chañares tetrapod community can be enhanced by the inclusion of fossils from the Los Rastros Formation (Fig. 8). This is justified because the two formations have a transitional relationship with each other within the same depositional system, the difference between them being lithostratigraphical (Mancuso & Marsicano 2008; Mancuso & Caselli 2012). Fossils from the Los Rastros Formation include plants, insects, fishes and temnospondyl amphibians as well as fossil tracks representing two sizes of dinosauromorphs and herds of dicynodonts (Marsicano *et al.* 2007, 2010).

The base of the tetrapod trophic chain is represented by traversodontid cynodonts and dicynodonts. Small predators, including basal suchias, ornithodirans, proterochampsids and cynodonts, preyed on invertebrate or small tetrapods. The piscivorous role is occupied by doswelliids, which preyed on fish from the lake and deltas of the Los Rastros Formation. The next carnivorous level is dominated by medium-sized forms which include some proterochampsids, chiniquodontids and dinosauromorphs. This guild preyed on relative small cynodonts and dicynodonts individuals. The major predators in the Chañares-Los Rastros trophic structure are paracrocodylomorphs and large dinosauromorphs. They may represent the only direct predators of fully grown herbivorous cynodonts and dicynodonts.

Comparative analysis of Ladinian tetrapod communities

As mentioned before, there are few Ladinian terrestrial fossil assemblages that can be compared with the Chañares fauna. The closest comparison geographically and taxonomically is the *Dinodontosaurus* Assemblage Zone from southern Brazil. Three therapsid taxa, *Chiniquodon*, *Dinodontosaurus* and *Massetognathus*, are common to both faunas (Langer *et al.* 2007). Regarding archosauriforms, these faunas have records of proterochampsids (Dilkes & Arcucci 2012), but the Brazilian fauna shows low diversity of these forms. But even there are taxonomic coincidences among members of these faunas, there are major differences in the abundance of

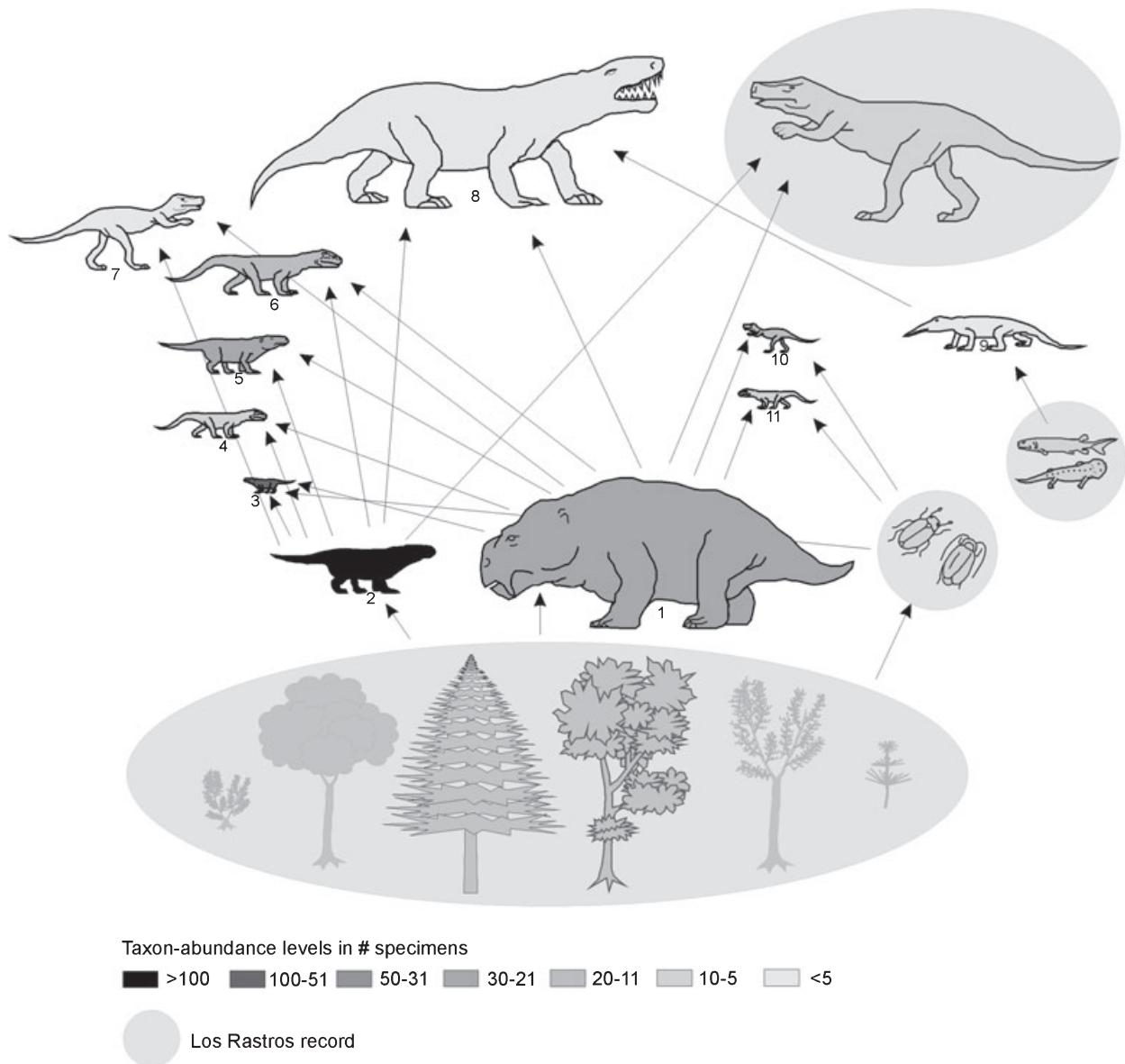


Fig. 8. Trophic structure inferred from the recovered Middle Triassic Chañares community. The greyscale represents taxon abundance levels in number of specimens. The fossil record from the Los Rastos Formation (plants, insects, fishes, temnospondils and therapsids, dinosauriforms and archosauriform tracks), added to complement the data from Chañares, is not sensu greyscale. Number code: (1) *Dinodontosaurus*; Dicynodont indet.; (2) *Massetognathus*; (3) *Probainognathus*; (4) *Tropidosuchus*; (5) *Chiniquodon*; (6) *Chanaresuchus*, *Gualosuchus*; (7) *Pseudolagosuchus* and Los Rastos footprints; (8) *Luperosuchus*, paracrocodylomorphs indet.; (9) *Tarjadia*; (10) *Lagerpeton*, *Marasuchus*; (11) *Gracilisuchus*.

specimens in different taxa and in their distribution stratigraphical and areally. The massive abundance of *Massetognathus* in Chañares can be compared with a similar predominance of the dicynodont *Dinodontosaurus* in the Brazilian fauna, representing 61% of occurrences (Azevedo *et al.* 1990; Schultz *et al.* 2000). Among archosauriforms, the abundance of proterochampsids in Chañares contrasts with that of large 'rauisuchians' in the Brazilian fauna, where a monotoxic accumulation including nine individuals was recently discovered (França *et al.* 2011). In summary, even though taxonomic similarities are

present between the Chañares and Brazilian *Dinodontosaurus* Assemblage Zone faunas, a major difference between them is the predominance of large animals in the Brazilian fauna.

Another proposed Ladinian Gondwanan assemblage is represented by the fossils from the top of the Upper Omingonde Formation of Namibia (Smith & Swart 2002; Abdala & Smith 2009; Abdala *et al.* 2013). This assemblage is similar to Chañares in the clear dominance of traversodontid cynodonts, whereas dicynodont, large archosauriforms and carnivorous cynodonts are underrepresented.

Continental Ladinian faunas are also known from western Europe, where the Erfurt Formation has a particularly important record of temnospondyl amphibians, as well as osteoderms of plagiosaurids, small archosaurs, ganoid scales, plant material (Schoch 2006, 2011a,b) and an isolated tooth of a traversodontid cynodont (Hopson & Sues 2006). In Russia, the Bukobay Formation, in the southern Cis-Urals and in the Cis-Caspian Depression, is dominated by temnospondyl amphibians and also includes plagiosaurid amphibians, erythrosuchid, rauisuchid archosaurs and dicynodonts (Lucas 1998; Shishkin *et al.* 2000; Benton *et al.* 2004). On the basis of faunal composition, two kinds of Ladinian continental faunas can be recognized: (1) eastern Laurasian faunas, in which temnospondyls are the clearly dominant tetrapods; and (2) western Gondwanan faunas, in which therapsids are dominant associated with fairly diverse archosauriforms.

Conclusion

Taphonomic analysis of the Chañares tetrapod fossil assemblage highlights two different modes of accumulation, namely attritional and mass mortal-

ity (Table 4). The attritional mortality assemblage preserves the remains of the largest animals of the fauna and is characterized by a disarticulation and skeleton dispersion pattern produced by low-energy flowing water. The mass mortality assemblage, with a large quantity of complete or partially articulated skeletons, shows some post-mortem sorting followed by rapid burial. The differences between attritional and mass mortality assemblages are the killing mechanisms and the duration and intensity of the taphonomic processes that affected the carcasses. The attritional accumulation preserves the remains of the largest animals of the fauna and is associated with the natural death of individuals by predation, disease and/or old age. After death, the carcasses were exposed on the floodplain for a short period of time, during which they were disarticulated and dispersed by scavenging and low-energy flowing water that sorted the remains. In contrast, the fossil associations recorded in the lower concretionary level show evidence of a catastrophic event. The mass mortality assemblage, with a large quantity of complete or partially articulated skeletons, shows some post-mortem sorting, followed by rapid burial that prevent the carcasses from being scavenged, trampled or exposed to weathering. The

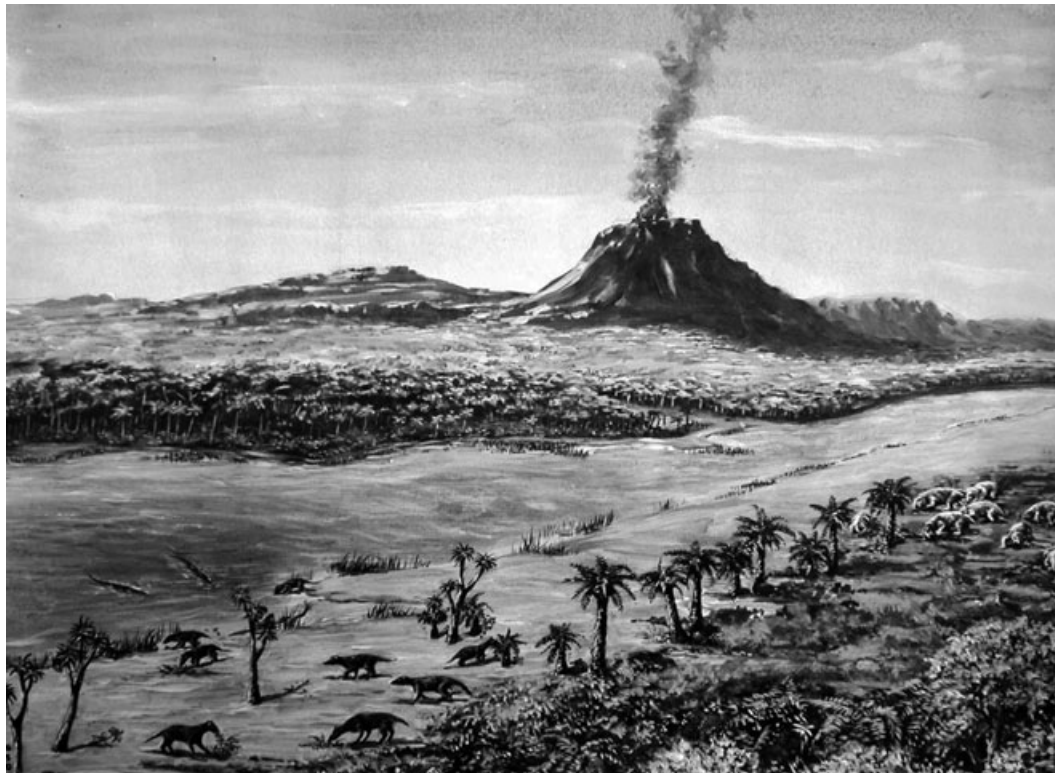


Fig. 9. Artist's reconstruction of the Chañares environment during the Middle Triassic. Note the herds of *Massetognathus* and *Dinodontosaurus* in the front and back of the scene, respectively, feeding from the same vegetative resources; archosauriform piscivores in the water stream; and the volcanic activity with the sky darkened by abundant falling ash. Art by Jorge Fernando Herrman.

volcanic activity in the area is identified as the cause of mass mortality and the origin of the sediment that facilitated the rapid entombment of part of the fauna in that level.

The gregarious herbivorous taxa at the base of the trophic chain of the Chañares-Los Rastros assemblage are the traversodontid cynodont *Massetognathus* and the dicynodont *Dinodontosaurus*. Lower predation levels are characterized by basal suchians, ornithomirans, proterochampsids and cynodonts that preyed on invertebrates or small and/or young tetrapods. Medium-sized carnivores are represented by chiniquodontid cynodonts, proterochampsids and dinosauromorphs, which preyed on sub-adult herbivores. As the major predators in the community, paracrocodylomorphs and large dinosauromorphs were the major predator in the community, representing the only direct predators of fully grown herbivorous taxa. *Tarjadia* is the only proposed piscivorous form (Fig. 9).

In Gondwana, faunas of Ladinian age are best documented in South America, particularly in the Santa Maria Formation in southern Brazil (*Dinodontosaurus* Assemblage Zone) and the Chañares Formation in western Argentina (Romer & Jensen 1966; Rogers *et al.* 2001; Langer *et al.* 2007). Although there are shared genera between the Triassic faunas in Argentina and Brazil, notable differences in the abundance of therapsids and diversity of archosauriforms are recognized. The Chañares assemblage is dominated by cynodonts and also shows a high diversity of archosauriforms, whereas the Brazilian *Dinodontosaurus* Assemblage Zone is dominated by dicynodonts with a low diversity of archosauriforms. Another important contrast is that larger forms seem to be better represented in the Brazilian fauna. The proposed Ladinian Upper Omingonde Formation assemblage of Namibia shows clear dominance of traversodontid cynodonts and a low representation of other forms, as occurs in the Chañares assemblage. Finally, we can now recognize two kinds of Ladinian terrestrial faunas: an eastern Laurasian fauna with amphibians as the dominant tetrapods; and a western Gondwanan fauna, where therapsids are dominant along with a fair diversity of archosauriforms.

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