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## REVIEWED EXTENDED ABSTRACTS

### South American Middle Triassic continental faunas with amniotes: biostratigraphy and correlation

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South America has an extensive record of continental Triassic, in which several groups of vertebrates are represented (Bonaparte 1982; Langer *et al.* 2007). This record encompasses a diversified fauna of archosauriforms, including basal dinosauriforms, and the oldest dinosaurs, along with abundant rhynchosaurs and mammal-like therapsids (dicynodonts and cynodonts). The Middle Triassic constitutes an important transitional period, when significant changes in amniote faunas occurred. South American deposits of this age yielded a diversified fauna of dinosauriforms, as well as the first records of traversodontids, one of the most successful groups of non-mammaliaform cynodonts. In addition, the diversity of dicynodonts recovered from the Permo/Triassic extinction event, and the group is recorded globally in Laurasia and Gondwana (Surkov 2000).

Five Middle Triassic faunal assemblages, including amniote body fossils, have been recognized in South America, three in Argentina and two (or possibly three) in Brazil (Table 1). The Puesto Viejo Local Fauna represented by the upper levels of the Puesto Viejo Group, San Rafael

Basin, south of Mendoza Province (= Puesto Viejo Formation, see Stipanovic *et al.* 2007) includes the dicynodonts *Kannemeyeria argentinensis* and *Vinceria* sp. (but see Renaut & Hancox 2001 for a different interpretation of *K. argentinensis*) and the cynodonts *Pascualgnathus polanskii*, *Cynognathus crateronotus*, and the recently discovered *Diademodon tetragonus* (Bonaparte 1982; Martinelli *et al.*, in press).

The Puesto Viejo Local Fauna was correlated with the *Cynognathus* Assemblage Zone (AZ) of South Africa (Bonaparte 1982) suggesting an Olenekian (e.g. Bonaparte 1982; Lucas 1998) or Anisian age (Bonaparte 1967). The Puesto Viejo Local Fauna is strongly reminiscent of African paleofaunas, such as those of the Burgersdorp Formation of the Karoo Basin and the Omingonde Formation of Namibia (Kitching 1995; Smith & Swart 2002). These similarities include the occurrence of *Cynognathus* and *Diademodon*, the two most common cynodonts in the *Cynognathus* AZ of South Africa (Kitching 1995). In the last decade, the *Cynognathus* AZ has been informally divided into three subzones, based mainly on its temnospondyl amphibian taxa (Hancox *et al.* 1995), but also supported by other tetrapods (Abdala *et al.* 2005). Faunal comparison suggests the temporal correlation of the upper assemblage of the Puesto Viejo Group with subzones B and C of the *Cynognathus* AZ, where both *Cynognathus* and *Diademodon* are known. The record of the traversodontid *Pascualgnathus* in the Puesto Viejo Local Fauna represents an important difference between the South American and South African assemblages.

Taking into account all these points it seems possible to consider the upper fauna of the Puesto Viejo Group as Anisian in age, although the record of traversodontid cynodonts in this unit may suggest a Late Anisian age (Fig. 1). Radiometric dates are problematic. Valencio *et al.* (1975) reported variations between  $230 \pm 10$  Ma and  $236 \pm 10$  Ma for ignimbrites and  $232 \pm 10$  Ma for basalts from the lower levels of the Puesto Viejo Group (i.e. Quebrada de

Ma	SAN RAFAEL	CUYO	ISCHIGUALASTO VILLA UNIÓN	PARANÁ
228	Carnian		Ischigualasto	Hyperod.AZ
			Los Rastros	Santa Cruz do Sul
			Ischichuca	Dinod.AZ
237			Chañares	
	Anisian	Cerro de Las Cabras		?Mariante
245				
249.7	Olenekian			

Figure 1. Stratigraphic chart, showing correlations between terrestrial Middle Triassic faunas from South America. Timeframe after the Geological Time Scale 2004 (Gradstein & Ogg 2004). Abbreviations: *Dinod.*, *Dinodontosaurus*; *Hyperod.*, *Hyperodapedon*.

**Table 1.** Tetrapods from South American Middle Triassic faunas. 'A' indicates taxon more abundant in the fauna. Uncertainty as to the identity of *Kannemeyeria*/Kannemeyeriidae follows Renaut & Hancox (2001). Chañares fauna modified from Rogers *et al.* (2001); *Dinodontosaurus* Assemblage Zone fauna modified from Langer *et al.* (2007).

<b>1) ANISIAN FAUNAS</b>	Ornithodira
<b>Puesto Viejo Local Fauna, Argentina</b>	<i>Lagerpeton chanarensis</i>
Therapsids	<i>Lewisuchus admixtus</i>
Dicynodontia	<i>Marasuchus lilloensis</i>
<i>?Kannemeyeria argentinensis</i>	<i>Pseudolagosuchus major</i>
<i>Vinceria</i> sp.	<b><i>Dinodontosaurus</i> Assemblage Zone fauna, Brazil</b>
Cynodontia	Therapsida
<i>Cynognathus craternotus</i>	Dicynodontia
<i>Pascualgnathus polanskii</i> A	<i>Dinodontosaurus pedroanum</i> A
<i>Diademodon tetragonus</i>	<i>Stahleckeria potens</i>
<b>Cerro de Las Cabras Fauna, Argentina</b>	<i>cf. Ischigualastia</i>
Therapsida	Cynodontia
Dicynodontia	<i>Chiniquodon theotonicus</i>
<i>Vinceria andina</i>	<i>Massetognathus ochagaviae</i>
<i>?Kannemeyeriidae</i>	<i>Traversodon stahleckeri</i>
Cynodontia	<i>Protheriodon estudianti</i>
<i>Andescynodon mendozensis</i> A	<i>Protuberum cabralensis</i>
<i>Rusconiiodon mignonei</i>	Parareptilia
<i>Cromptodon mamiferoides</i>	Owenettidae
<b>2) ANISIAN TAXA IN BRAZILIAN TRIASSIC</b>	<i>Candelaria barbouri</i>
Cynodontia	Archosauriformes
<i>Luangwa sudamericana</i>	Proterochampsidae
Rhynchosauria	<i>?Chanaresuchus/?Gualosuchus</i>
'Mariane' rhynchosaur	Archosauria
<b>3) LADINIAN FAUNAS</b>	Crurotarsi
<b>Chañares fauna, Argentina</b>	Rauisuchidae
Therapsida	<i>Prestosuchus chiniquensis</i>
Dicynodontia	'Karamuru vorax'
<i>Dinodontosaurus platiceps</i>	<i>Barberenasuchus brasiliensis</i>
<i>Dinodontosaurus platygnathus</i>	<i>?Rauisuchidae/?Dinosauria</i>
<i>Dinodontosaurus brevirostris</i>	<i>Spondylosoma absconditum</i>
Cynodontia	<b>Santa Cruz do Sul fauna, Brazil</b>
<i>Chiniquodon theotonicus</i>	Therapsida
<i>Massetognathus pascuali</i> A	Cynodontia
<i>Probainognathus jenseni</i>	<i>Santacruzodon hopsoni</i> A
Archosauriformes	<i>Massetognathus</i> sp.
Proterochampsidae	<i>Menadon</i> -like traversodontid
<i>Chanaresuchus bonapartei</i>	<i>cf. Probainognathus</i>
<i>Gualosuchus reigi</i>	<i>Chiniquodon</i> sp.
<i>Tropidosuchus romeri</i>	Archosauriformes
Archosauria	Proterochampsidae
Crurotarsi	Unnamed proterochampsid
<i>Tarjadia ruthae</i>	
Rauisuchidae	
<i>Luperosuchus fractus</i>	
Crocodylomorpha	
<i>Gracilisuchus stipanicicorum</i>	

los Fósiles Formation; Stipanovic *et al.* 2007), which are generally considered as Lower Triassic. Considering the Geologic Time Scale 2004 (Gradstein & Ogg 2004), these dates would imply a Late Anisian-Ladinian age for the lower levels of the Puesto Viejo Group.

Another South American faunal association often interpreted as contemporaneous with the Puesto Viejo Local Fauna (e.g. Bonaparte 1982, 2002) is the Cerro de Las Cabras fauna (= Río Mendoza Local Fauna). There is some disagreement concerning its age: plant fossils indicate Early Triassic to early Middle Triassic (Morel *et al.* 2003) while palynology suggests late Middle Triassic to early Upper Triassic (Zavattieri & Arcucci 2007). In the Cerro de Las Cabras Formation, Cuyo Basin, north of Mendoza Province, body fossils are represented only by therapsids (Tables 1 & 2), among them the dicynodont *Vinceria andina* and the cynodonts *Andescynodon mendozensis*, *Rusconiiodon*

*mignonei* and *Cromptodon mamiferoides* (Bonaparte 1982). Zavattieri and Arcucci (2007) also reported a dicynodont maxillary fragment assigned to Kannemeyeriidae. Archosauriforms in the Cerro de Las Cabras Formation are represented by footprints and trackways of crurotarsan archosaurs (Marsicano *et al.* 2004; Table 2).

*Vinceria* is the only genus shared between the Puesto Viejo and the Cerro de Las Cabras faunas (e.g. Bonaparte 1982; Marsicano *et al.* 2001). The cynodont *Cromptodon* is represented by a tiny lower jaw with postcanines very similar to those of *Aleodon* from the Manda Formation in Tanzania, which is generally considered as Anisian in age (Abdala & Ribeiro 2003). Both the Puesto Viejo and Cerro de Las Cabras faunas present traversodontid cynodonts, but recent cladistic analyses of this group showed different placements for *Andescynodon* and *Pascualgnathus*. In Abdala & Ribeiro (2003) they formed a monophyletic

**Table 2.** Diversity and abundance of amniotes represented in Middle Triassic faunas from South America. Abbreviations: ARC, archosauriforms; CYN, cynodonts; DIA, diapsids; DIC, dicynodonts; PRT, parareptiles; TH, therapsids; TRC, traversodontid cynodonts. Archosauriforms in the Cerro de Las Cabras fauna are represented by footprints and trackways of crurotarsan archosaurs (Marsicano *et al.* 2004). Numbers in brackets indicate the quantity of taxa of the group represented in the fauna.

	Puesto Viejo	Cerro de Las Cabras	Chañares	<i>Dinodontosaurus</i> Assemblage Zone	Santa Cruz do Sul	Mariante
Taxa	TH	TH ARC	TH ARC	TH ARC PRT	TH ARC	TH  DIA
Diversity	CYN (3)	CYN (3)	ARC (10)	CYN (5) ARC (5)	CYN (5)	
Abundance	TRC DIC	TRC	TRC	DIC	TRC	

group in a basal polytomy of traversodontids. A more comprehensive study by Abdala *et al.* (2006) produced hypotheses in which *Pascualgnathus* is basal to *Andescynodon*. In both studies the traversodontids from the discussed faunas are basal to those from the Middle Triassic deposits of the Ischigualasto-Villa Unión Basin (i.e. *Massetognathus* from the Chañares Formation). Judging by the phylogenetic relationships of the traversodontids in Abdala *et al.* (2006), the cynodont assemblage from the Cerro Bayo of Potrerillos can prove to be somewhat younger than that of the upper fauna of the Puesto Viejo Group, possibly latest Anisian, but indeed older than the Ladinian Chañares fauna (Fig. 1). Recent radiometric dating near the top of the Río Mendoza Formation, below the Cerro de Las Cabras Formation, indicate an age of  $243 \pm 5$  Ma (Avila *et al.* 2006), corresponding to the Anisian (*sensu* Gradstein & Ogg 2004). In addition, recent dating of the lower and middle levels of the Potrerillos Formation, which overlies the Cerro de las Cabras Formation, indicates  $239.2 \pm 4.5$  Ma,  $239.7 \pm 2.2$  Ma and  $230.3 \pm 2.3$  Ma (Spalleti *et al.* 2008). All the radiometric dates are therefore consistent with an Anisian age for the Cerro de las Cabras fauna.

The South American faunas of Ladinian age are remarkably diverse if compared with older ones. Not only therapsids are represented but also procolophonoids and a large number of archosauriforms (Tables 1 & 2).

In the fauna from the Chañares Formation, Ischigualasto-Villa Unión Basin, San Juan and La Rioja provinces, central western Argentina, archosauriforms includes proterochampsids, rauisuchians, crocodylomorphs and ornithomirans (Marsicano *et al.* 2001). Archosauriforms are represented by at least ten taxa (Table 2), showing greater species diversity than cynodonts and dicynodonts combined (Rogers *et al.* 2001). Three species of dicynodonts (all included in the genus *Dinodontosaurus*) and three cynodonts are members of the fauna (Table 1). The traversodontid *Massetognathus pascuali* is, by far, the most abundant taxon (Table 2), representing approximately 58% of the identified specimens of this faunal assemblage (Rogers *et al.* 2001).

In the lacustrine levels of the Los Rastros Formation that overlie the Chañares and Ischichuca formations, amniotes are known only by indeterminate archosaur remains (Forster *et al.* 1995) and footprints and trackways of therapsids and archosauriforms (putative dinosaurs

and crurotarsal archosaurs; Marsicano *et al.* 2004). The Los Rastros Formation is well known for its rich record of pollen and fossil plants, whereas recent contributions have described invertebrate fossils (insects and conchostacans), actinopterygian fishes, and temnospondyl amphibians (Martins-Neto *et al.* 2005, 2006; López-Arbarello *et al.* 2006; Mancuso & Marsicano 2008). Radiometric dates from tuffs at the base of the Ischigualasto Formation (Rogers *et al.* 1993) indicate an age of  $227.8 \pm 0.3$  Ma, corresponding to the limit between Middle and Upper Triassic (*sensu* Ogg & Gradstein 2004; but see Muttoni *et al.* 2004, for a different opinion about the Middle/Late Triassic boundary). Consequently, the underlying Los Rastros and Chañares formations are usually interpreted as Ladinian in age (e.g. Rogers *et al.* 2001; Mancuso & Marsicano 2008; see Fig. 1). Palaeofloristic studies, however, suggested a lower Middle Triassic age (probably Anisian) for the Chañares, Ischichuca and Los Rastros formations (Spalleti *et al.* 1999). In contrast, pollen associations from the Ischichuca Formation, comparable to the Ipswich microflora from Australia, suggested a Late Ladinian to Carnian age for this unit, implying a younger, minimally Carnian, age for the Los Rastros Formation (Zavattieri & Melchior 1999).

The *Dinodontosaurus* AZ of the Santa Maria Formation, Paraná Basin, Rio Grande do Sul State in southern Brazil is commonly considered contemporaneous with the Chañares assemblage, sharing several taxa at genus level with the Argentinean fauna. The *Dinodontosaurus* AZ has procolophonoids in addition to the groups above mentioned for the Chañares fauna (Tables 1 & 2). In the Brazilian fauna the diversity of cynodonts and archosauriforms (five taxa each) is higher than that of dicynodonts (three taxa), while procolophonoids are only represented by the owenettid *Candelaria barbouri* (Cisneros *et al.* 2004). Dicynodonts are the most abundant tetrapods in the *Dinodontosaurus* AZ (Table 2), representing 61% of occurrences in the fauna (Schultz *et al.* 2000).

In an outcrop of the Santa Maria Formation usually considered within the *Dinodontosaurus* AZ (e.g. Schultz *et al.* 2000) a rhynchosaur, known as the 'Mariante rhynchosaur', was found associated with dicynodonts (Tables 1 & 2). This is the only South American record of rhynchosaurs in levels considered as Ladinian in age, and the only joint occurrence of those two groups in the



Brazilian Triassic. A recent phylogenetic analysis of rhynchosaurs by Montefeltro (2008) indicates a close relationship between the 'Mariante rhynchosaur' and Anisian taxa from India and Tanzania (see also Langer *et al.* 2007). In addition, the traversodontid cynodont *Luangwa sudamericana*, collected from an unknown locality in the Brazilian Triassic (Abdala & Sa-Teixeira 2004), is closely related to the congeneric taxa known from the Anisian of Zambia and Namibia (Kemp 1980; Abdala & Smith 2007). Based on the presence of the 'Mariante rhynchosaur' and *Luangwa sudamericana* in Brazilian beds, Abdala and Sa-Teixeira (2004) suggested an Anisian age for some of the faunas of the Santa Maria Formation, which would thus be older than the *Dinodontosaurus* AZ (Fig. 1).

The recently discovered fauna from Santa Cruz do Sul, also known as 'Santuário Schoenstatt', in outcrops of the Santa Maria Formation, has a remarkable abundance of cynodonts. Apart from one specimen assigned to Proterochampsidae, the rest of the rich deposit yielded only cynodonts (Tables 1 & 2). Among these, there are three different traversodontids: a) *Santacruzodon hopsoni* (Abdala & Ribeiro 2003); b) a taxon with affinities to *Menadon* from Madagascar and to Carnian forms (i.e. *Exaeretodon*); and c) *Massetognathus* (Schultz & Langer 2007). A fourth traversodontid, represented by a tiny portion of the maxilla with four postcanines, whose pattern was initially considered as resembling those of *Boreogomphodon* from the U.S.A., is now considered a juvenile of *Santacruzodon*, with remarkably worn teeth (Abdala, pers. obs.). Carnivorous cynodonts are documented by a couple of chiniquodontid specimens and by a tiny mandibular fragment, bearing a single tooth, assigned to *cf. Probainognathus* (Soares & Abdala 2008). Faunal resemblances of Santa Cruz do Sul to other Triassic faunas include chiniquodontids which are known in Ladinian and Carnian faunas of South America and were most recently recorded in a putative Anisian fauna from Namibia (Abdala & Smith 2007). *Massetognathus* and *Probainognathus* are also represented in the Ladinian Chañares fauna from Argentina. Yet, the more significant similarities are with the late Ladinian/early Carnian 'Isalo II' fauna from Madagascar, which yielded chiniquodontids and two traversodontids that resemble forms from the Santa Cruz do Sul fauna (Flynn & Wyss 2002; Abdala & Ribeiro 2003; Langer *et al.* 2007). The presence of Ladinian traversodontids along with taxa resembling Carnian forms was interpreted as supporting a transitional position for the Santa Cruz do Sul fauna, between the Ladinian *Dinodontosaurus* AZ and the Carnian *Hyperodapedon* AZ dominated by rhynchosaurs (Fig. 1), an thus coincident with the age proposed for the Malagasy assemblage.

An overview of the global distribution of tetrapods of Anisian age shows the first record of traversodontid cynodonts in Africa and South America, where they are diverse and, in some cases, abundant (Table 2). This group, however, is curiously absent from the extensive and highly fossiliferous Karoo Basin of South Africa, lying in a paleolatitude of approximately 55°S, and from the

upper Fremouw fauna in Antarctica which is further south. The only record of Mid Triassic traversodontids from Laurasia is based on two isolated postcanines discovered in ?Upper Anisian/Ladinian beds from Russia (Battail & Surkov 2000). The large carnivorous *Cynognathus* and the large gomphodont *Diademodon*, abundant in the Anisian beds of the Karoo, are common in Gondwana and absent from Laurasian faunas. Dicynodonts are represented by four families (*sensu* Maisch 2001) in the Anisian of Gondwana: kannemeyeriids, shansiodontids, dinodontosaurids, and stahleckeriids, whereas only the last two families are known in the Ladinian. In Laurasia, shansiodontids, dinodontosaurids and, perhaps, kannemeyeriids (Maisch 2001) are represented in the Russian ?Late Anisian/Ladinian (Shishkin *et al.* 2000) and in the Middle Triassic of China.

The only record of rhynchosaur in the Middle Triassic of Brazil is suggestive of a putative Anisian age for some beds of the Santa Maria Formation (Fig. 1). Rhynchosaurs are recorded in the Anisian of Gondwana (e.g. India and Tanzania) and particularly well represented in Anisian faunas from the United Kingdom (Benton *et al.* 1994). It is remarkable that this group is not represented at all in the rich Ladinian faunas from Argentina and Brazil, although it is known from a partially coeval fauna from Madagascar (Langer *et al.* 2000).

With the record of parareptiles and several archosauriforms, along with therapsids (Table 2), the Ladinian faunas from Argentina and Brazil document an increase in diversity compared with those from the Anisian. Representatives of the latter are always dominant: traversodontid cynodonts in Chañares and Santa Cruz do Sul and dicynodonts in the *Dinodontosaurus* AZ (Table 2). Archosauriforms show a remarkable diversification in the Ladinian of South America, including endemic proterochampsids, raiuisuchians, and dinosauromorphs, the latter two groups with a respectable diversity.

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