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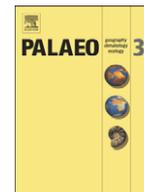
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Distribution and diversity patterns of Triassic cynodonts (Therapsida, Cynodontia) in Gondwana

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ABSTRACT

Cynodonts are an important component of Triassic tetrapod faunas and are frequently one of the dominant groups. A summary of their record during the Triassic of Gondwana is presented. Cynodonts are represented by 63 species/57 genera in Gondwana with diversification peaks occurring during the Late Anisian (particularly in Africa) and the Carnian of South America and India. Data on the number of faunas of each age and the duration (in millions of years) estimated for these faunas were integrated with cynodont generic diversity values. One of the most important turnovers in cynodonts occurred at the Late Olenekian–Anisian, involving changes in two directions: a) the record of complex bucco-lingually expanded (gomphodont) postcanines, with traversodontid cynodonts already representing an important group at the end of the Anisian; b) the record, particularly during the Anisian, of significantly large-sized cynodonts (e.g. *Cynognathus* and *Diademodon* with basal skull length between 30 to 40 cm). Considering that the global maximum peak of cynodont diversity is during the Norian–Rhaetian, the diversity of Gondwanan cynodonts for that time, eight taxa, is remarkably low.

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1. Introduction

The early Mesozoic is one of the most significant periods in the history of life because represents the recovery of the Permo/Triassic (P/T) extinction event, the largest of its kind and one that brought all life on the Earth dangerously close to an end (Erwin, 1994; Benton, 1995). It is also in early Mesozoic times when several important amniote groups appear, among others turtles (Li et al., 2008), dinosaurs (Sereno et al., 1993; Langer et al., 1999), proto-crocodyles (Clark et al., 2004) and mammaliaforms (Luo, 2007).

Also represented in this age are mammal-like therapsids, a group of fossil forms that includes the ancestor of living mammals (Rubidge and Sidor, 2001; Luo, 2007). Therapsids were particularly successful in the Permian, but were severely affected by the P/T extinction (Kemp, 2005). Amongst the six main therapsid lineages, dinocephalians became extinct at the end of the Middle Permian, whereas biarmosuchians and the large carnivorous gorgonopsians were victims of the P/T extinction. The three remaining therapsid lineages survived the end-Permian extinction in different ways. Anomodonts (including dicynodonts), the most abundant and diverse therapsid lineage in the Permian (Kemp, 2005), were severely decimated by the extinction event, but recovered in diversity towards the Middle Triassic (Fröbisch, 2008). Representatives of therocephalians, a lineage with a disputed monophyly (Botha et al., 2007; Abdala, 2007; Huttenlocker, 2009), survived the P–T boundary

but with reduced diversity and they disappeared by the Middle Triassic (Abdala et al., 2008).

Cynodonts, the youngest therapsid lineage first recorded in the early Late Permian of South Africa (Botha et al., 2007), experienced a first phase of diversification towards the end of the Permian. This decreased only slightly after the P/T event, and this was followed by a remarkable Middle Triassic diversification (Abdala, 2004). Cynodonts, or, in particular, non-mammaliaform cynodonts, are the only therapsids whose main taxonomic diversification occurred in the Triassic (Abdala, 2007). Here we present a summary of the Triassic record of cynodonts in Gondwana and discuss the diversification pulses of this group during that age. For this, we consider number of taxa at the level of genus, represented in each temporal assemblage, but also integrate data on the number of contemporaneous faunas in which the group is represented and the temporal interval corresponding to each recorded fauna.

2. Material and methods

There are approximately 63 taxonomic entities included in the dataset analyzed (see Appendix A): 55 nominated species, three unpublished taxa, and five with tentative identifications at the level of genus, family and as a non-mammaliaform cynodont. If we consider the dataset at the level of genus (including also unpublished cases and tentative identifications) then the number of entities is 57. Considering the small difference between numbers of taxa at genus and specific level, the analysis of diversity presented below was undertaken considering genus.

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Eight terrestrial geological formations, including 10 different faunas in South America; 10 formations with eight, or perhaps nine, faunas in Africa and two and four faunas in Antarctica and India respectively, document the record of cynodonts in the Triassic of Gondwana.

The Geologic Time Scale 2004 (Gradstein and Ogg, 2004; Ogg, 2004; Fig. 1A) was used for correlation purposes and to establish temporal intervals included in the analysis of diversity. It is important to mention that the Triassic time scale is the subject of intense debate (Muttoni et al., 2004, 2010; Furin et al., 2006; Lehrmann et al., 2006; Ovtcharova et al., 2006), resulting in a proposal widely different from that of Gradstein and Ogg (2004). Major differences in the modified time scale are a temporal extension of the Norian up to 228 Ma (this age represents the Carnian/Ladinian limit of Gradstein and Ogg, 2004), and of the Carnian to 235 Ma (an age that is near the Ladinian/Anisian limit on the Gradstein and Ogg, 2004 scale). These changes imply a much-extended temporal range for the Late Triassic which is approximately two-thirds (67%) of the total Triassic time (Gallet et al., 2003; Fig. 1B). As examples of contrast between these different temporal proposals, the Ladinian and Early Carnian South American faunas in the Gradstein and Ogg (2004) scheme will be Early to Late Carnian, respectively in the alternative proposal by Muttoni et al. (2004; see also Ogg et al. 2008: 102).

Subdivision of stages (lower, upper; see Figs. 7–9) was judged the minimum temporal units allowing the analysis of cynodont genera occurrences without committing big errors with the data. Even though there is a general consensus on the age of several Gondwanan Triassic faunas, we are aware that some decisions concerning the age of particular faunas are arbitrary at this point (for example, the interpretation of the Isalo II fauna from Madagascar as upper Ladinian instead of upper Ladinian–lower Carnian, Flynn et al., 2000). Another problem with the Triassic ages portrayed in this analysis is the lack of agreement to allocate

Gondwanan faunas in subdivisions of the particularly long stages Carnian and Norian. Differences in absolute dates on levels of the base (227.8 ± 0.3 Ma: Rogers et al., 1993) and top (217.0 ± 1.7 Ma: Currie et al., 2009) of the Ischigualasto Formation indicate a temporal range of 10.8 Ma for this unit. There is however no evidence that the fauna were extended throughout the complete Formation. Temporal restriction of this fauna to the Lower Carnian is based on Rogers et al. (1993) who interpreted a rapid accumulation, 1 to 4 Ma, of the section of the Ischigualasto Formation including fossils forms (see also Langer, 2005).

The youngest faunas from the Los Colorados and lower Elliot formations in Argentina and South Africa have been temporally interpreted in different ways (i.e., Upper Triassic, Norian, Late Norian or even Rhaetian; see Lucas, 1998; Knoll, 2004), and there is a growing consensus that they are contemporaneous. In an attempt to reduce their temporal range, the lower Elliot, and by faunal similarity the Los Colorados faunas are here considered Late Norian to Rhaetian following Knoll and Battail (2001) and Knoll (2004). In addition, the *Ictidosaur* AZ from the Caturrita Formation, largely interpreted as Early Norian (Rubert and Schultz, 2004; Bonaparte and Sues, 2006), is here also included in the Late Norian–Rhaetian age. This is based in sister group relationship of *Irajatherium* to tritheledontids from the Los Colorados, lower and upper Elliot formations, along with the record of *Riograndia* which has a more basal placement among tritheledontids (Martinelli and Rougier, 2007). Another line of evidence for this interpretation is the sister group relationship of brasilodontids with Early Jurassic Mammaliaformes (Martinelli and Rougier, 2007) and the report of the sphenodontian *Clevosaurus* from the *Riograndia* AZ (Bonaparte and Sues, 2006), a taxon known from the Rhaetian and Lower Jurassic. Recent findings of theropod dinosaur tracks also suggest a younger age (Rhaetian–Lower Jurassic) for this fauna (Silva et al., 2009). It is important to mention that in this analysis the *Riograndia* AZ does not include the fauna with *Jachaleria* and phytosaurids which are also known from the Caturrita Formation (see Langer et al., 2007: Fig. 3).

We have not used the Land Vertebrate Faunachrons (LVF; Lucas, 1998; Lucas et al., 2007) in this study as they remain a contested topic. Problems in the use of Nonesian and Perovkian LVFs for Gondwanan faunas were mentioned in Abdala et al. (2005a). Langer (2005) extensively discussed problems with Carnian LVFs (Otischalkian and Adamanian) for global correlation, whereas Rayfield et al. (2005; see also Rayfield et al., 2009) presented serious objections to the use of the LVFs for the establishment of a biochronological scheme between Triassic faunas from North America and Western Europe. For us, the most problematic issue with the LVFs, simply stems from an extremely liberal use of index taxa, with several cases in which the material representing the index taxon in the faunas has a disputed taxonomy. In summary, the idea of a terrestrial vertebrate biozonation as originally proposed by Lucas (1998) is indeed an important step for Triassic continental correlation, but the alpha taxonomy of several index taxa (or perhaps the use of alternative index taxa) needs to be clarified to improve the reliability of a global terrestrial biozonation scheme.

Considering that the sample units are not independent (as different temporal intervals may record the same cynodont genus, and taxa of different ages are linked by phylogeny) Mantel randomization tests were used to analyze correlations between cynodont genera, faunas with cynodonts, and time intervals (Manly, 2007). A final and obvious point to bear in mind is the provisional state of this proposal as improved knowledge of the fossil record, dating of fossil host rocks and temporal scale fine-tuning (as is currently the case of the Triassic temporal scale, see Ogg et al., 2008) will certainly modify the results presented here.

3. Palaeogeography and climate of faunas from Gondwana including cynodonts

The majority of Triassic vertebrate faunas including cynodonts from Gondwana are located between the 40° to 60° South palaeolatitude,

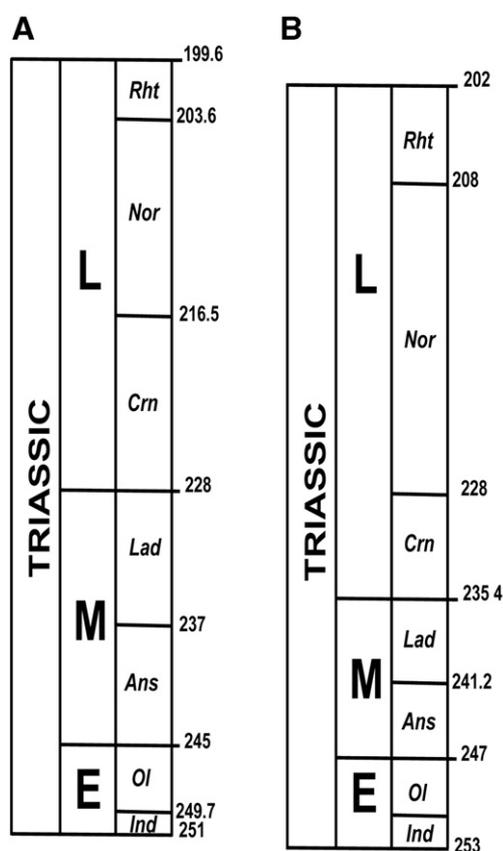


Fig. 1. Triassic time scales. (A) Geologic Time Scale 2004 (Gradstein and Ogg, 2004); (B) time scale after Muttoni et al. (2004 and reference cited therein), except for the Anisian lower age, after Lehrmann et al. (2006). Abbreviations: Ans, Anisian; Crn, Carnian; E, Early; Ind, Induan; Lad, Ladinian; L, Late; M, Middle; Nor, Norian; Ol, Olenekian; Rht, Rhaetian.

being the only exception the Fremouw faunas from Antarctica which have been positioned around 68° or 85° South (Sidor et al., 2008a). Five geographic areas with faunas having cynodonts are known in Africa, four in South America, three in India and one in Antarctica. The South African Karoo was located approximately 60°S in the Early Triassic, between 50° and the 60° S in the Middle Triassic (Fig. 2), and around 50° S in the Late Triassic. This northward migration also happened with all the other Gondwanan localities. During the Middle Triassic, the majority of Gondwanan faunas with cynodonts were located between 45° and 50° S (Fig. 2), whereas in the Late Triassic most of them were placed between 40° and 45° S.

The Paleozoic–Mesozoic transition represented one of the most intense Hothouse intervals without evidence of polar ice in Gondwana from the Middle Permian to the Jurassic (Scotese et al., 1999). The Triassic was one of the hottest periods in the Earth's history, in which there is no record of glacial activity (Frakes et al., 1992). The biome of higher latitudes in the Early Triassic, that includes all the deposits having cynodonts, is interpreted as cool temperate (cool winters and warm summers; Sellwood and Valdes, 2006). This biome also included the far south fauna from Antarctica, which indicate that this was a very hot period (Scotese, 2000) with high levels of CO₂ in the atmosphere that led to the expansion of deciduous forests in the polar regions of the southern Hemisphere (Woods, 2005). During the Middle Triassic (see Fig. 2) the Karoo Basin and the upper Fremouw Formation faunas continued to have a temperate regime, whereas the remaining Middle Triassic African terrestrial localities were arid (Scotese, 2000). An arid regime is also interpreted for the South American Ischigualasto–Villa Union and Paraná Basins and for the Pranhita–Godavari Basin in India. In contrast, Middle Triassic localities at the Cuyo Basin and, particularly, at the San Rafael Basin in Argentina, were in the area separating arid from warm temperate regimes (Scotese, 2000). During the Late Triassic the regime for the areas of Gondwana where cynodonts are represented (South Africa, South America and India) is interpreted as warm temperate by Scotese (2000), and as a mixture of warm temperate humid and cool temperate by Sellwood and Valdes (2006; Fig. 2B). Climatic conditions in Norian localities of South America, usually interpreted as arid and dry (e.g., the Los Colorados Formation in the Ischigualasto–Villa Unión Valley), were more recently reinterpreted as humid-temperate to subhumid, with a probable alternating dry station, based in sedimentological and faunal analyses (Caselli et al., 2001). Holz and Scherer (2000; see also Pires et al., 2005) also proposed an increase of humidity towards the Upper Triassic of Gondwana with the Brazilian

Norian Caturrita Formation being considered far more humid than in previous studies.

4. Palaeoecology and palaeobiology of cynodonts from Gondwana

Earliest Triassic cynodonts manifest the same skull size variation as those of the Late Permian (skull length between 6–14 cm), and all of them are sectorial toothed insectivores to carnivores (Abdala et al., 2006a). However, the most common Late Permian form, *Procynosuchus delaharpeae* shows a skull length above 10 cm (until 14 cm), whereas *Thrinaxodon liorhinus*, the most common Early Triassic cynodont (Fig. 3A), shows a skull length below 10 cm (maximum skull length around 9 cm, with the majority of individuals presenting between 6 and 7 cm). The latter taxon grew rapidly in early ontogeny and slowed down at an older age, apparently unaffected by the seasonal environment (Botha and Chinsamy, 2005). There is strong evidence that some species (and considering their relatively small body size, perhaps all of them) lived in burrows (Damiani et al., 2003; Abdala et al., 2006a). Vertebrate burrows have also been recognized in the lower Fremouw Formation (Sidor et al., 2008b), suggesting a similar behaviour for Early Triassic amniotes from South Africa and Antarctica. This behaviour, known in other small to medium-sized Early Triassic vertebrates, is interpreted as a possible advantage for survival of the end-Permian crisis (Smith and Botha-Brink, 2009). Burrowing is also represented in small late Early Triassic trirachodontid gomphodonts from the base of the Burgersdorp Formation (Groenewald et al., 2001; Botha and Chinsamy, 2004).

One of the most important faunal turnovers in Gondwanan cynodonts occurred between the end of the Early Triassic and the beginning of the Middle Triassic, and resulted in two directions of change. One innovation was the first record of large individuals with both carnivorous and herbivorous forms having a skull length of up to 30 to 40 cm (Fig. 3B), being among the largest Triassic cynodonts. The second innovation was the development of complex dentition with bucco-lingually expanded postcanines (gomphodont), the earliest record of which is known at the end of the Olenekian (Subzone A of the *Cynognathus* AZ). The large herbivorous *Diademodon tetragonus* showed a cyclical bone growth pattern, whereas in the large carnivorous *Cynognathus crateronotus* it was sustained and rapid (Botha and Chinsamy, 2000). Omnivorous/herbivorous traversodontid cynodonts appeared suddenly in the Late Anisian of Gondwana. This group presented gomphodont postcanines with transverse crests and deep occlusal basins (Fig. 4A, B), and were able to process food orally. The Anisian traversodontid *Pascualgnathus* present hypertrophied canines

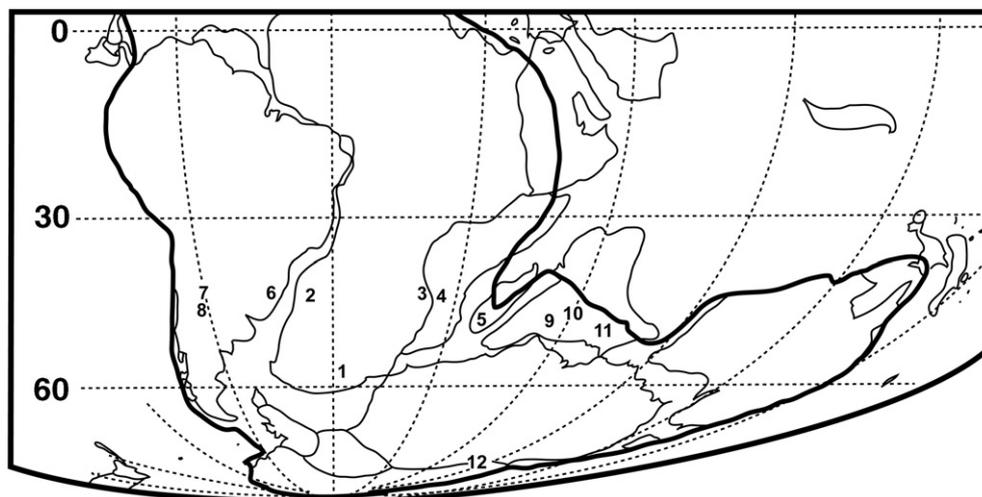


Fig. 2. Palaeogeography of Triassic deposits in Gondwana. Map is based on paleocoastline map of the Middle Triassic (Smith et al., 1994). 1. Karoo Basin, South Africa; 2. Otiwarongo Basin, Namibia; 3. Luangwa Basin, Zambia; 4. Ruhuhu Basin, Tanzania; 5. Isalo II, Madagascar; 6. Triassic deposits of the Parana Basin, Brazil; 7. Ischigualasto–Villa Union Basin, Argentina; 8. Uspallata Group of the Cuyo Basin and Puesto Viejo Group from the San Rafael Basin, Argentina; 9. Pranhita–Godavary Basin, India; 10. Son–Mahanadi Basin, India; 11. Damodar Basin, India; 12. Fremouw faunas, Antarctica.

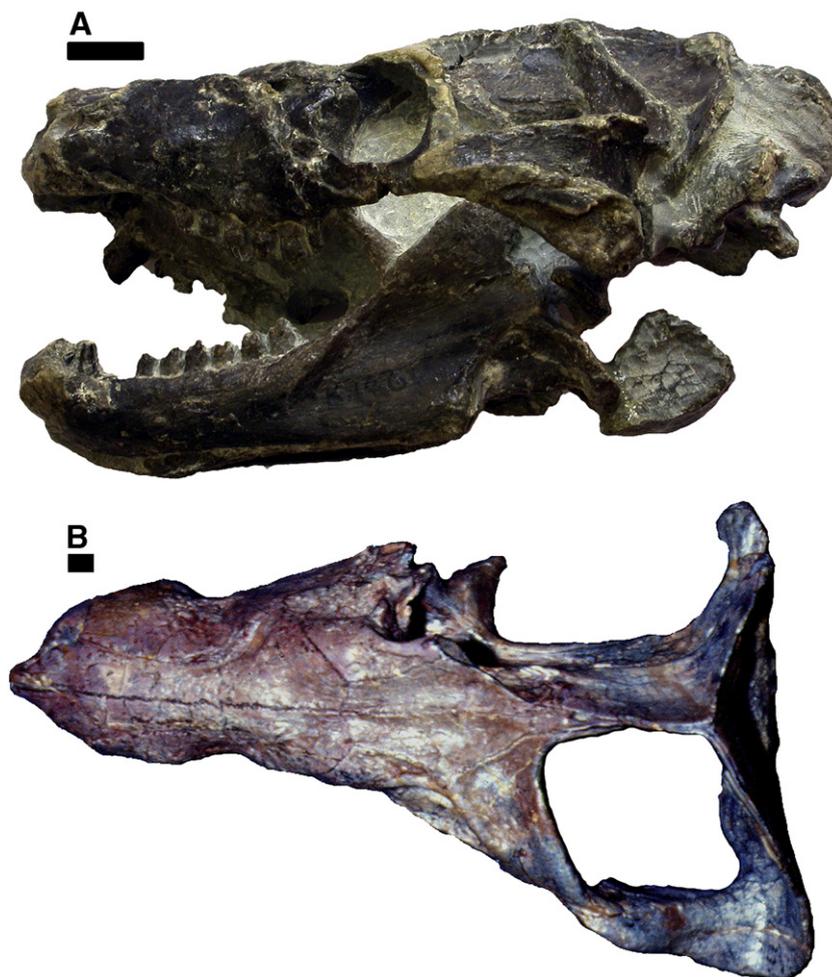


Fig. 3. Sectorial toothed cynodonts. A, lateral view of skull and lower jaw of one of the larger specimens of *Thrinaxodon liorhinus* known from the Lower Triassic of the Karoo Basin. B, dorsal view of the skull of *Cynognathus crateronotus* from the Middle Triassic of the Karoo Basin. Scale bar represent 1 cm.

(Bonaparte, 1967) probably used for intraspecific display and as defence against predators. The presence of a thickened bone wall in the femur of the Middle Triassic traversodont *Andescynodon* was interpreted as suggestive of a fossorial lifestyle (Chinsamy and Abdala, 2008), even though this taxon was not found in association with burrows. Traversodontids were the most successful Triassic cynodonts, and survived in Gondwana for around 40 Ma. They were frequently the dominant taxon of their faunas, especially in the Middle Triassic (Abdala et al., 2009).

In Late Triassic cynodonts there was a predominance of small to medium-sized animals, except for some large traversodontids (Fig. 4B). The earliest record of Tritheledontidae was in Norian faunas dominated by large herbivorous dinosaurs, where this small insectivorous/carnivorous cynodonts (skull length from 4–6 cm) were poorly represented. Tritheledontids however, were abundant in Norian Brazilian faunas mostly characterized by small-sized animals (Fig. 5A). Important members of these faunas were also the tiny insectivorous/faunivorous brasilodontids (Bonaparte et al., 2005; Fig. 5B). Another group of small to medium-sized carnivores were the enigmatic dromatherids from the Late Triassic Tiki Formation of India (Datta et al., 2004), which are only known elsewhere in Laurasia. This is one of the few Triassic Gondwanan faunas in which the record of cynodonts is restricted to isolated teeth.

5. Cynodonts from the Triassic of Gondwana

Cynodonts have different representation in the subcontinents of Gondwana. They are well documented in Triassic faunas from South

America and Africa, with 29 and 26 genera respectively, which provide most of the information on the evolution of this group in Triassic time in Gondwana. The record of cynodonts is remarkably sparse in India (seven taxa), whereas the group has a fair representation in the restricted outcrops of Antarctica (four taxa). Australia is the only Gondwanan subcontinent without any evidence of Triassic cynodonts.

We present below a summary of the record of Gondwanan cynodonts during the Triassic (see also Appendix A).

5.1. South American cynodonts

In western Argentina and southern Brazil, non-mammaliaform cynodonts are found only in Triassic rocks. The oldest record of this group from the south of the Parana Basin in Rio Grande do Sul State, Brazil, comprises of fragmentary postcranial material of uncertain taxonomic affinity from the Lower Triassic Sanga de Cabral Formation (Abdala et al., 2002b; Fig. 6).

The Middle and Late Triassic record of non-mammaliaform cynodonts in Brazil is richer and four different faunas (or assemblage zones; AZ) are recognized in the Santa Maria and Caturrita formations (Fig. 6).

The traversodontid cynodont *Luangwa sudamericana* is from an unknown locality in the Santa Maria Formation (Abdala and Teixeira, 2004). As this taxon is closely related to the congeneric taxa from the Anisian of Zambia and Namibia (Kemp, 1980; Abdala and Smith, 2009), Abdala and Teixeira (2004) suggested an Anisian age for some levels of the Santa Maria Formation. However, additional material from this

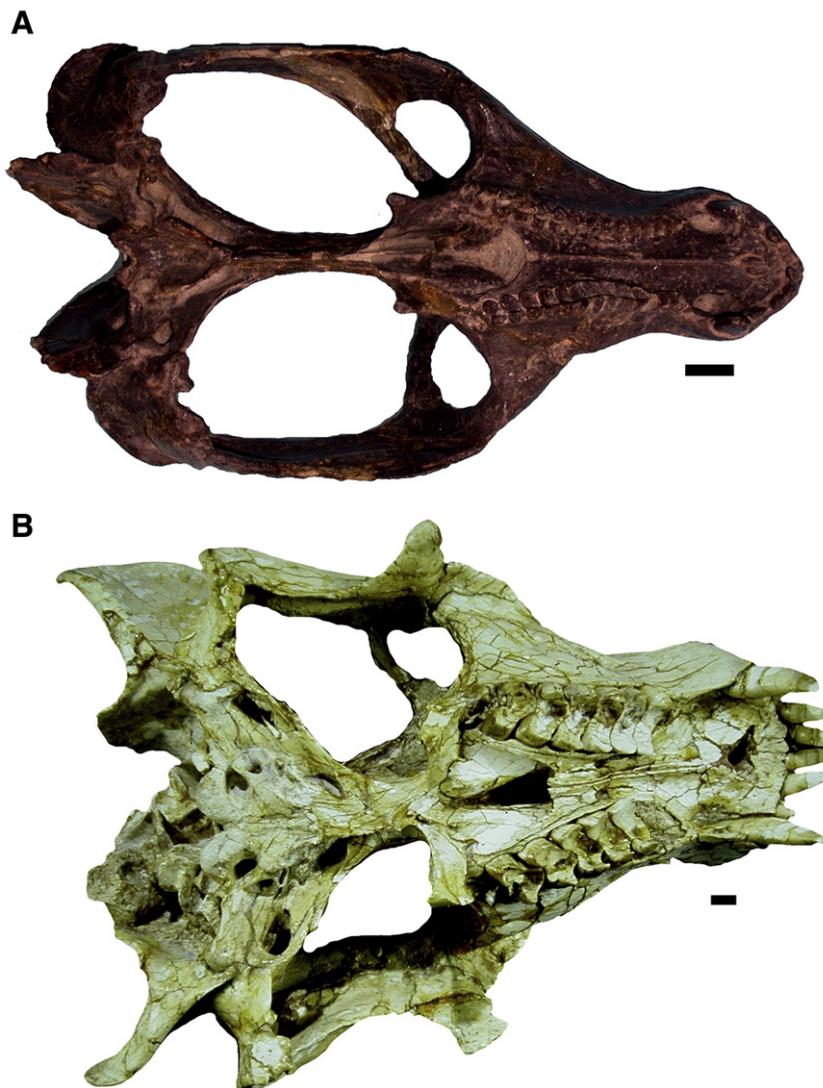


Fig. 4. Traversodontid cynodonts. A, ventral view of *Massetognathus pascuali* from the Middle Triassic of Argentina; B, ventral view of *Exaeretodon riograndensis* from the Upper Triassic of Brazil. Note the remarkable differences in morphology of the bucco-lingually expanded postcanines. Scale bar represent 1 cm.

taxon was found more recently in a locality of the *Dinodontosaurus* AZ, which is considered as Ladinian (Da Silva and Cabreira, 2009).

Six cynodonts are known from the *Dinodontosaurus* AZ of the Santa Maria Formation; four traversodontids, *Luangwa sudamericana*, *Massetognathus ochagaviae*, *Traversodon stahleckeri* and *Protuberum cabralensis* (von Huene, 1936; Barberena, 1974, 1981; Liu et al., 2008; Reichel et al., 2009); the chiniquodontid *Chiniquodon theotonicus* (von Huene, 1936; Teixeira, 1982; Abdala and Giannini, 2002), and the recently described *Protheriodon estudianti* (Bonaparte et al., 2006), represented only by the holotype, a juvenile specimen.

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 (Abdala et al., 2001). Among these, there are three different traversodontids: *Santacruzodon hopsoni* (Abdala and Ribeiro, 2003); *Menadon* sp. (Melo et al., 2009); and *Massetognathus* (Schultz and Langer, 2007). Carnivorous cynodonts are represented by three specimens of *Chiniquodon* sp. (Abdala et al., 2001) and a tiny mandibular fragment with a tooth preliminary assigned to cf. *Probainognathus* (Soares and Abdala, 2008; Soares, pers. comm., 2009). This fauna is usually considered as transitional between the Early Ladinian and Carnian Brazilian faunas (Abdala et al., 2001; Abdala and Ribeiro, 2003; Langer et al., 2007), but Lucas (2002) considers it as part of the *Dinodontosaurus* AZ.

The *Hyperodapedon* AZ is considered Carnian (Langer et al., 2007) and includes traversodontid cynodonts. These are the rare *Gomphodontosuchus brasiliensis* (von Huene, 1928; Hopson, 1985), and the common *Exaeretodon riograndensis* (Abdala et al., 2002a; Oliveira et al., 2007a; Fig. 4B). Sectorial toothed cynodonts from this fauna are *Therioherpeton carnini*, *Prozostrodon brasiliensis* and *Charruodon tetracuspidatus* (Bonaparte and Barberena, 1975; Barberena et al., 1987; Abdala and Ribeiro, 2000; Bonaparte and Barberena, 2001; Oliveira, 2006), all of them represented by a single specimen. There is also a new, as yet undescribed, carnivorous cynodont from this assemblage zone (Langer et al., 2007; Oliveira et al., 2007b).

The most recently discovered Norian faunas from the Caturrita Formation (Bonaparte et al., 2001) present a differentiated fauna of small cynodonts including the tritheledontids (= ictidosaur) *Riograndia guaibensis* (Fig. 5A) and *Irajatherium hernandezii* (Bonaparte et al., 2001; Martinelli et al., 2005) and the brasilodontids *Brasilodon quadrangularis* and *Brasilitherium riograndensis* (Bonaparte et al., 2003, 2005; Fig. 5B). These faunas were referred to as Ictidosaur Cenozoone/AZ (Rubert and Schultz, 2004; Langer et al., 2007) and Mammalianomorpha Cenozoone (Schultz and Soares, 2006; Schultz and Langer, 2007).

In Argentina the two older faunas with cynodonts are considered to be Anisian (Fig. 6). The traversodontid *Pascualgnathus polanskii*, the carnivorous *Cynognathus crateronotus* and the recently discovered



Fig. 5. Late Triassic sectorial cynodonts. A, lateral view of the lower jaw of *Riograndia guaibensis*; B, lateral view of the skull of *Brasilitherium riograndensis*. Scale bar represent 1 cm.

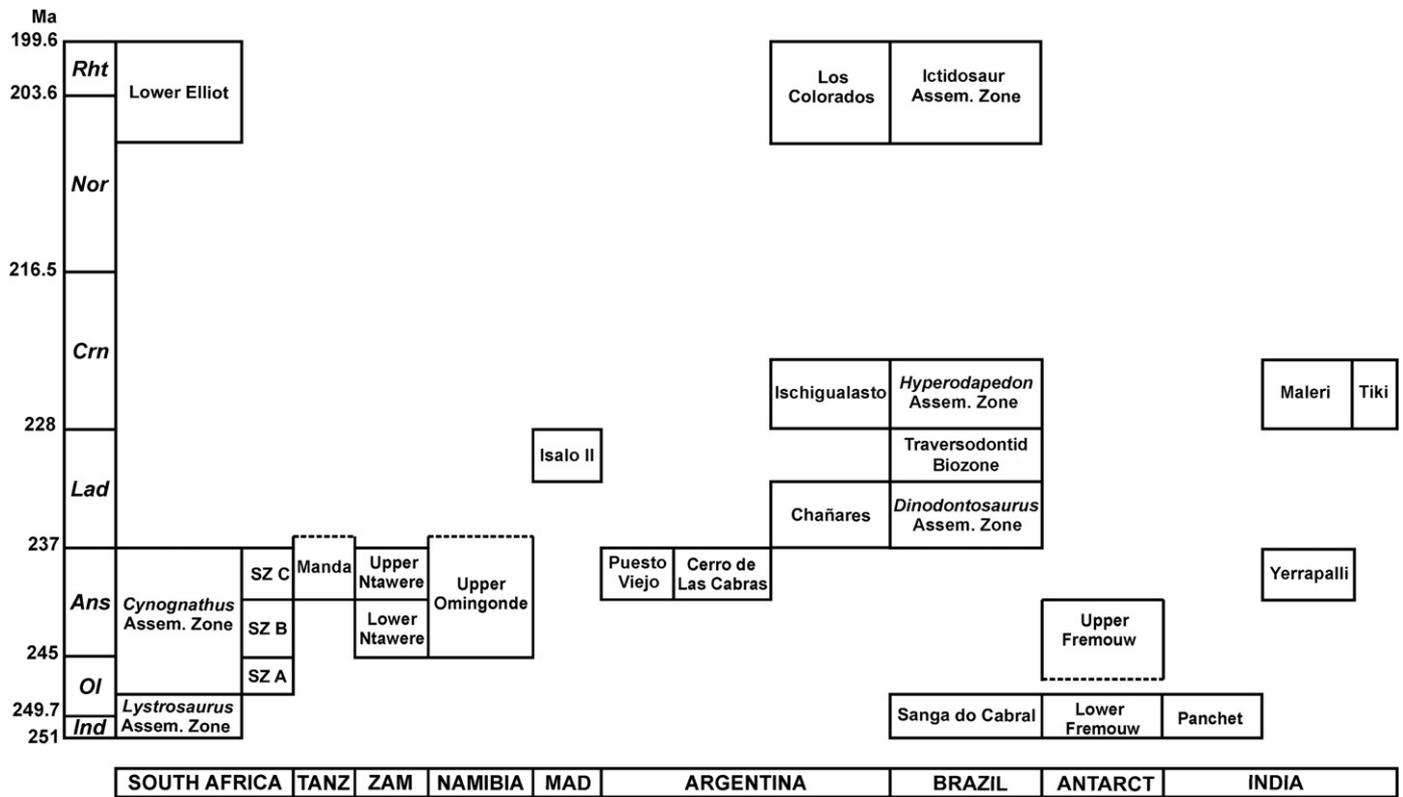


Fig. 6. Biostratigraphic chart of terrestrial Triassic faunas from Gondwana including cynodonts. Faunal correlations based on Hancox (2000); Knoll and Battail (2001); Stipanovic and Marsicano (2002); Abdala and Ribeiro (2003); Abdala and Teixeira (2004); Knoll (2004); Abdala et al. (2005a); Rubidge (2005), Langer et al. (2007), Bandyopadhyay and Sengupta (2006), Sidor et al. (2008a), Abdala and Smith (2009); Martinelli et al. (2009); and references cited therein. Geological Time Scale based on Gradstein and Ogg (2004). Abbreviations: Ans, Anisian; Antarct, Antarctica; Assem, Assemblage; Crn, Carnian; Ind, Induan; Lad, Ladinian; Low, lower; Mad, Madagascar; Nor, Norian; Oi, Olenekian; Rht, Rhaetian; SZ, Subzone; Tanz, Tanzania; Up, upper; Zam, Zambia.

gomphodont *Diademodon tetragonus* (Bonaparte 1967, 1969a, 1982; Abdala, 1996; Martinelli et al., 2009) are from the Rio Seco de la Quebrada Formation (Puesto Viejo Local Fauna, Bonaparte, 1982; Stipanovic et al., 2007; Fig. 6) of the San Rafael Basin, Mendoza Province. The second Anisian fauna is that from the Cerro de Las Cabras Formation, Cuyo Basin, north of the Mendoza Province (Fig. 6). Here cynodonts are represented by the traversodontids *Andescynodon mendozensis* and *Rusconiodon mignonei*, and the sectorial toothed *Cromptodon mamiferoides* represented by only a tiny lower jaw (Bonaparte, 1969b, 1972, 1982). The presence of traversodontid cynodont in these two Argentinean faunas was considered as suggestive of a Late Anisian age (Martinelli et al., 2009).

Faunas from the Ladinian to the Norian are known from the Ischigualasto–Villa Union Basin between La Rioja and San Juan Provinces, central-western Argentina. The Ladinian fauna is from concretions at the base of the volcanoclastic Chañares Formation (Rogers et al., 2001; Fig. 6) and includes the traversodontid cynodont *Masseognathus pascuali* (the most abundant taxon; Fig. 4A), and the sectorial toothed *Probainognathus jenseni*, and *Chiniquodon theotonicus* (Romer, 1969, 1970, 1972; Abdala and Giannini, 2000, 2002).

In the Carnian Ischigualasto Formation (Fig. 6) traversodontid cynodonts are represented by *Exaeretodon argentinus* and *Ischignathus sudamericanus* (Bonaparte 1962, 1963; Abdala 2000; Liu, 2007 consider the latter taxon a junior synonym of *E. argentinus*, a proposal which is not agreed to by FA). Carnivorous forms are represented by *Chiniquodon sanjuanensis* and *Ecteninion lunensis* (Martinez et al., 1996; Martinez and Forster, 1996) and a tiny skull identified as cf. *Probainognathus* (Bonaparte and Crompton, 1994).

The youngest non-mammaliaform cynodont from Argentina is the tritheledontid *Chalimonia musteloides* (Bonaparte, 1980; Martinelli and Rougier, 2007) from the Upper Norian Los Colorados Formation (Fig. 6). Fragmentary postcranial remains assigned to tritylodontids are known from the same unit (Bonaparte, 1971), but which we consider here as taxonomically indeterminate.

5.2. African cynodonts

The most extensive African cynodont record is from the main Karoo Basin of South Africa (Fig. 6). This is one of the few places in the world in which it is possible to follow a succession of terrestrial faunas from the Permian to the Triassic (Rubidge, 2005).

The earliest Permian cynodonts from the Karoo are from the *Tropidostoma* AZ and three different genera are present in the *Dicynodon* AZ at the end of the Permian, with *Procynosuchus delaharpeae* being the most abundant (Botha et al., 2007). The oldest fauna of the *Lystrosaurus* AZ is represented in levels of the Palingkloof Member of the Balfour Formation and encompasses the P/T boundary (Groenewald and Kitching, 1995; Botha and Smith, 2006). Three cynodonts are present in these beds: the abundant *Thrinaxodon liorhinus* (Fig. 3A), *Galesaurus planiceps*, and the rare *Progalesaurus lootsbergensis* (van Heerden, 1988; Abdala, 2003, 2007; Sidor and Smith, 2004). The only record of the fourth cynodont, *Platycraniellus elegans*, is from the Harrismith Member of the Normandien Formation (Haughton, 1924; Abdala, 2007), in the north of the Basin, which is considered coeval to the Palingkloof Member (see Rubidge et al., 1995; Fig. 3). These units are overlain by the Katberg Formation, from which only *T. liorhinus* and *G. planiceps* are known. The first species occurs throughout the entire stratigraphic range of the Katberg Formation, whereas *G. planiceps* is restricted to the lower portion of the unit (Botha and Smith, 2006).

The *Cynognathus* AZ fauna (Upper Olenekian–Anisian; Fig. 6) is represented in levels of the Burgersdorp Formation (Kitching, 1977, 1995). This AZ is informally divided into three subzones (Hancox et al., 1995; Hancox, 2000; Neveling et al., 2005; Fig. 2); in Subzone A, there are remains of the carnivorous *Cynognathus crateronotus* an unpublished sectorial toothed cynodont (Abdala et al., 2005b), the gomphodont

cynodont *Langbergia modisei* (Abdala et al., 2006b) and a taxon represented by isolated teeth with haramiyid-like crowns (Abdala et al., 2007b). Subzone B has remains of the abundant *Diademodon tetragonus* and *Cynognathus crateronotus* (Fig. 3B), whereas *Trirachodon berryi* is also well represented (Kitching, 1995). More rare are the sectorial toothed *Bolotrilon kannemeyeri*, *Cistecynodon parvus* and *Lumkuia fuzzi* (the last two represented only by their holotypes; Brink and Kitching, 1953; Hopson and Kitching, 2001), and there is a possible record of *Cricodon metabolus* (Abdala et al., 2006b). Hopson (2005) described a juvenile trirachodontid apparently from levels of the Subzone B, with a crown morphology well differentiated from that of other member of the group. In the younger Subzone C, *C. metabolus* is the most abundant cynodont, and there are also remains of *C. crateronotus* and *D. tetragonus* (Abdala et al., 2005a).

There is a gap in the record of amniote body fossils in the Karoo Basin for the Ladinian–Carnian interval. However, this stratigraphic interval has an outstanding record of fossil plants in the Carnian Molteno Formation, where some insects are also known (Anderson and Anderson, 1984; Anderson et al., 1998). The next record of amniote fossils is from the Upper Norian–Rhaetian lower Elliot Formation (Lucas and Hancox, 2001; Knoll and Battail, 2001; Knoll, 2004; Fig. 6). Cynodonts from this stratigraphic interval include at least eight specimens of the last Gondwanan traversodontid *Scalenodontoides macrodotes* (Crompton and Ellenberger, 1957; Battail, 2005), the recently described tritheledontid *Elliotherium kersteni* (Sidor and Hancox, 2006), and a fragmentary lower jaw that was tentatively assigned to Diademodontidae (Abdala et al., 2007a).

Outside South Africa, Late Permian cynodonts are represented by *Procynosuchus* in the Ruhuhu Basin in Tanzania and the Madumabisa Mudstones of the Luangwa Valley in Zambia (Abdala and Allinson, 2005; Weide et al., 2009). The record is resumed in the Late Anisian Lifua Member of the Ruhuhu Basin, Tanzania (Wopfner, 2002; Fig. 6), where the traversodontids *Scalenodon angustifrons*, *S. hirschsoni*, *S. attridgei* and *S. charigi* (Parrington, 1946; Crompton, 1955, 1972) are represented. Phylogenetic analyses found that *S. angustifrons* and *S. hirschsoni* were not part of the same monophyletic group (Hopson and Kitching, 2001; Abdala et al., 2006b; Kammerer et al., 2008), suggesting that the genus *Scalenodon* is polyphyletic. In addition, Abdala and Ribeiro (2003) pointed out that the traversodontids *S. attridgei* and *S. charigi* may prove to be the same taxon. Also present in the Lifua Member are *Aleodon brachyrhamphus*, the trirachodontid *Cricodon metabolus* and *Diademodon tetragonus*, represented by an isolated postcanine (Crompton, 1955). Cynodonts from the Anisian are also represented in the Luangwa Basin of Zambia (Drysdall and Kitching, 1963; Kitching, 1963; Fig. 6) with the gomphodont *Diademodon tetragonus* from the lower Ntawere Formation (Brink, 1963), and the traversodontid *Luangwa drysdalli* from the upper Ntawere Formation (Brink, 1963; Kemp, 1980).

Middle Triassic Anisian and even possibly Ladinian age rocks are represented in the upper Omingonde Formation of the Otiwarongo Basin in Namibia (Keyser, 1973a,b; Smith and Swart, 2002; Fig. 6). This unit present one of the most diverse cynodont faunas from Gondwana and includes the large carnivorous *Cynognathus crateronotus*, the gomphodonts *Diademodon tetragonus*, *Titanogomphodon crassus* and *Trirachodon berryi* (Keyser, 1973a,b) and the recently described *Luangwa* sp., an undetermined traversodontid, *Aleodon* sp. and *Chiniquodon* sp. Abdala and Smith (2009) suggested that faunas of two different ages might be represented in the upper Omingonde Formation. The older fauna included *Diademodon*, *Cynognathus* and *Trirachodon*, whereas the putative younger one included the two traversodontids, *Aleodon*, *Chiniquodon* and perhaps also *Titanogomphodon*.

The fauna from the Isalo II beds in the south of Madagascar is considered as Late Ladinian–Early Carnian in age (Flynn et al., 1999, 2000). The cynodonts in the Isalo II fauna include two traversodontids *Menadon besairei* and *Dadadon isaloii* and also chiniquodontids (Flynn et al., 2000; Flynn and Wyss, 2002; Kammerer et al., 2008). Based on

similarities of these cynodonts with those from the Brazilian Traversodontid Biozone (Fig. 6) we consider this fauna to be Late Ladinian.

5.3. Antarctic cynodonts

Continental rocks of the Early and Middle Triassic are represented in this portion of Gondwana and include cynodonts (Fig. 6). From the lower Fremouw Formation, considered as coeval with the *Lystrosaurus* AZ of the South African Karoo, are known several specimens of *Thrinaxodon liorhinus* and a couple of individual considered cynodontia *incertae sedis* (Colbert and Kitching, 1977). Carnivorous *Cynognathus* and a large diademodontid tentatively identified as *Titanogomphodon* (Hammer, 1995) were recovered from the upper Fremouw Formation, a unit correlated with the *Cynognathus* AZ of South Africa and of an age interpreted as being Late Olenekian or Anisian (Sidor et al., 2008a).

5.4. Indian cynodonts

Even though Triassic deposits containing vertebrates are known throughout the India, cynodonts have a remarkably poor record in this portion of Gondwana. The only Lower Triassic cynodont known from India is *Thrinaxodon bengalensis* from the Lower Triassic Panchet Formation, Damodar Basin (Satsangi, 1987; Bandyopadhyay et al., 2002; Fig. 6). In the Anisian Yerrapalli Formation of the Pranhita–Godavari Basin there are records of undescribed isolated teeth of trirachodontids (Bandyopadhyay and Sengupta, 1999, 2006), the only out-of-Africa record of this group in Gondwana. An isolated and fragmentary record of the traversodontid *Exaeretodon statisticae* is known from the Carnian beds of the lower Maleri Formation (Chatterjee, 1982; Bandyopadhyay and Sengupta, 2006; Fig. 6). More recently, Nath and Yadagiri (2007) reported five tiny (approximately 1 mm in mesio-distal length) isolated sectorial teeth in the Maleri Formation, interpreted as of non-mammaliaform cynodonts and one of them was assigned to the new species *Deccanodon maleriensis*. Finally, the isolated tooth of *Gondwanadon tapani* (Datta and Das, 2001), considered, with some doubts, as the oldest morganucodontid mammaliaform (Kielan-Jaworowska et al., 2004), several teeth of the dromatherid *Rewaconodon tikiensis* (Datta et al., 2004), and the transversely expanded upper molar of *Tikitherium copei* (Datta, 2005) were recorded from the Carnian Tiki Formation of the Son–Mahanadi Basin.

6. Shared cynodonts between Triassic faunas from Gondwana

Several similar cynodonts are shared by faunas from nowadays the same continent, but there are also several cynodont genera which occur in assemblages on different Gondwana subcontinents.

In South America the traversodontid *Massetognathus* and the chiniquodontid *Chiniquodon* are known in the Argentinean Chañares Formation and the Brazilian *Dinodontosaurus* AZ, and the Traversodontid Biozone. *Chiniquodon* is also represented in the Carnian Ischigualasto Formation of Argentina, whereas the presence of *Exaeretodon* is a similarity between the later and the Brazilian *Hyperodapedon* AZ (the record of *Exaeretodon major* in the *Dinodontosaurus* AZ should be considered with caution, Abdala et al., 2002a). In addition, a new, unnamed, sectorial toothed cynodont from the *Hyperodapedon* AZ is similar to *Ecteninion* from the Ischigualasto fauna (Oliveira et al., 2007b). *Probainognathus* is known from the Chañares fauna whereas forms having some similarities in the dentition identified as Cf. *Probainognathus* are known from the Argentinean Ischigualasto Formation and from the Brazilian Traversodontid Biozone (Bonaparte and Crompton, 1994; Soares and Abdala, 2008; Soares, comm. pers. 2009).

In Africa, *Diademodon*, *Cynognathus* and *Trirachodon* are present in the *Cynognathus* AZ of the Karoo Basin and at the base of the upper Omingonde Formation in Namibia. *Diademodon* is also represented in the lower Ntawere Formation of Zambia and, through an isolated postcanine, in the Lifua Member of the Manda beds of Tanzania (Crompton, 1955). The trirachodontid *Cricodon* is known from the Subzone C of the *Cynognathus* AZ in South Africa and the Manda beds of Tanzania (Abdala et al., 2005a). Amongst the recently described fauna from the top of the upper Omingonde Formation, are the traversodontid *Luangwa*, also known from the upper Ntawere Formation of Zambia, and the probainognathian *Aleodon*, which is also recorded in the Lifua Member of the Manda beds (Crompton, 1955).

Cynodonts also show evidence of association between terrestrial faunas from different continents during the Triassic. In the Early Triassic, *Thrinaxodon*, the commonest cynodont from the *Lystrosaurus* AZ of the Karoo Basin, is also represented in the lower Fremouw fauna from Antarctica and the Panchet fauna from India, indicating a widespread distribution of the taxa across Gondwana. At the end of the Early Triassic and in the Anisian, the typical southern African cynodonts *Cynognathus* and *Diademodon* are also known in the Argentinean Rio Seco de la Quebrada Formation (=Puesto Viejo Formation; Bonaparte, 1969a; Martinelli et al., 2009) and *Cynognathus* is also represented in the upper Fremouw fauna in Antarctica (Hammer, 1995; Sidor et al., 2008a). From outcrops of the Santa Maria Formation in Brazil were described *Luangwa*, a traversodontid cynodont previously represented in the upper Ntawere Formation of Zambia (Brink, 1963; Kemp, 1980) and most recently discovered at the top levels of the upper Omingonde Formation (Abdala and Smith, 2009). The carnivorous cynodont *Chiniquodon*, which is known from Ladinian and Carnian faunas from Brazil and Argentina, was also present in the fauna from the top of the upper Omingonde Formation which is considered upper Anisian. Because of the presence of *Chiniquodon* in the last unit, Abdala and Smith (2009) suggested that Ladinian rocks may be present in Namibia. If the fauna from the top of the upper Omingonde is indeed Anisian, then *Chiniquodon* will be one of the longest-living cynodonts, first represented in the Late Anisian and last in the Early Carnian, spanning around of 9 Ma. Recent findings confirmed the presence of *Menadon*, a traversodontid cynodont typical from Madagascar, in the Late Ladinian Traversodontid Biozone of the Santa Maria Formation, Brazil (Melo et al., 2009). Finally, the traversodontid *Exaeretodon*, known from Argentinean and Brazilian Carnian faunas is also represented in the lower Maleri fauna from India (Chatterjee, 1982).

7. Cynodont diversity changes in South America

The lowest diversity of cynodonts in South America is in the Induan–Early Olenekian, represented by the Brazilian Sanga do Cabral Formation. In this case the evidence is limited to fragmentary postcranial remains of a small-sized cynodont (Abdala et al., 2002b) which are conservatively interpreted as being one taxon. Taxonomic diversity increases progressively from the Early Triassic to the Carnian, the latter age including ten genera, the highest diversity of South American cynodonts (Fig. 7). Diversity decreases during the Norian, where the number of cynodont genera is the same as that in the Late Ladinian. In South America most of the temporal units having cynodonts are represented by two faunal associations: two Anisian faunas from Argentina, whereas the Early Ladinian, Carnian and Middle–Late Norian are documented by one Brazilian and one Argentinean fauna. The Induan–Early Olenekian (Sanga do Cabral Formation) and the Late Ladinian (Traversodontid Biozone, Santa Maria Formation) intervals are represented only by one faunal assemblage each (Fig. 7A).

In the Brazilian Santa Maria Formation, where 15 cynodont genera, are known, there are three faunal associations, whose proposed ages are based in correlations with Argentinean and Madagascan faunas

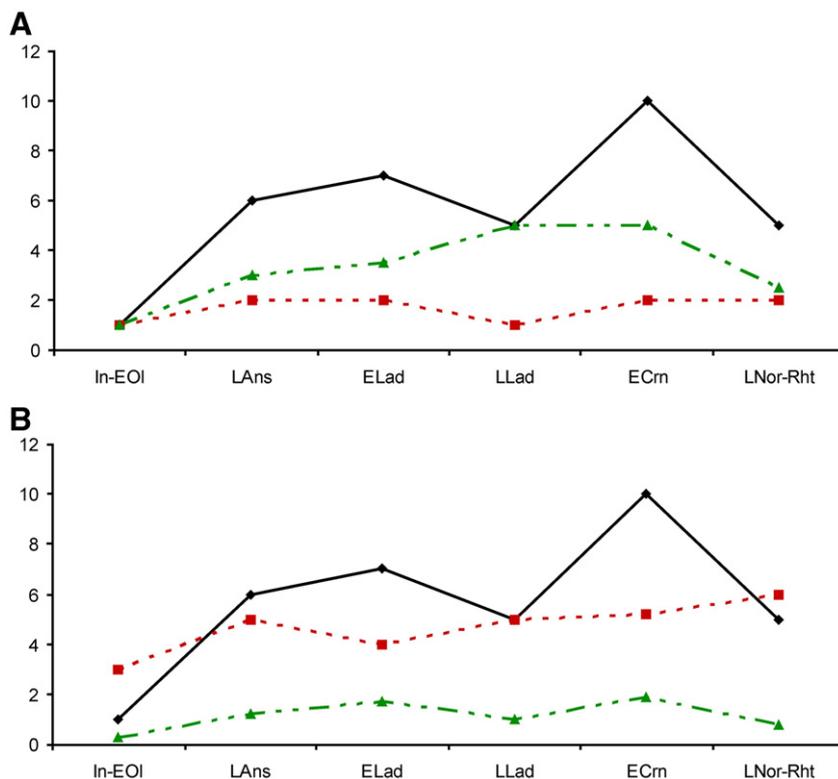


Fig. 7. Diversity of South American cynodonts during the Triassic in relation to number of faunas (A) and temporal range in millions of years (B). Diamonds linked by a continuous line (in black) represent the number of cynodont genera in each interval; squares linked by dashed line (in red) represent the number of faunas having cynodonts in A, and temporal range of stages in millions of years with cynodonts in B; triangles linked by dashed line (in green) represent the ratio between number of cynodont genera and number of fauna having cynodonts in A, and between number of cynodont genera and temporal range in B. Abbreviations: ECrn, Early Carnian; ELad, Early Ladinian; In-EOI, Induan–Early Olenekian; LAns, Late Anisian; LLad, Late Ladinian; LNor–Rht, Late Norian–Rhaetian. Mantel correlation tests indicate significant correlation between the number of cynodont genera (cg) and the ratio cg/temporal range ($r: 0.96; p: 0.002$) and cg and the ratio cg/number of faunas having cynodonts ($r: 0.78; p: 0.04$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Schultz et al., 2000; Schultz and Langer, 2007). The oldest of these is the *Dinodontosaurus* AZ, dated as Early Ladinian, which has six taxa; the Traversodontid Biozone, considered Late Ladinian, has five, and the Carnian *Hyperodapedon* AZ also has six cynodonts. The diversity of cynodont genera therefore, remains relatively constant in the three faunas from the Santa Maria Formation. It is important to note that the Traversodontid Biozone is known from a single outcrop, whereas the other two assemblage zones are represented by several localities (Langer et al., 2007).

Traversodontids, the most diverse group of Triassic cynodonts, first appear in the Anisian of South America and remain as an important group until the Carnian. Their diversity remains constant during different ages: three taxa during the Anisian, the Late Ladinian and the Carnian and four in the Early Ladinian. Traversodontids are the dominant taxa in several faunal associations: *Andescynodon mendozensis* in the Anisian Cerro de Las Cabras Formation, *Massetognathus pascualii* in the Early Ladinian Chañares Formation and *Santacruzodon hopsoni* in the Late Ladinian Traversodontid Biozone (Abdala et al., 2009).

Trends between the temporal range in millions of years and cynodont genera (Fig. 7B, solid line linked by diamonds and dashed line linked by squares) do not exhibit a statistically significant correlation. However, a significant correlation ($r: 0.96, p: 0.002$) exists between number of cynodont genera and the ratio between number of cynodont genera and temporal range (Fig. 7B, solid line linked by diamonds and dashed line linked by triangles).

8. Cynodont diversity changes in Africa

In the African faunas, the cynodont generic diversity increases steadily from the Early Triassic to the Early Anisian and doubles

during the Late Anisian (Fig. 8). The lowest cynodont Triassic diversity is during the Late Norian–Rhaetian, where only three genera are known. The remarkable increase in diversity of African cynodonts in the Late Anisian is probably related to the fact that four of the five African geographical localities (i.e., countries) or four of the nine Triassic faunal assemblages which include cynodonts are represented in this interval (Fig. 8A). A Mantel correlation test shows significant correlation between the number of cynodont genera and the number of faunas in Africa ($r: 0.77; p: 0.02$).

In the South African Burgersdorp Formation ten cynodont genera are present, the greatest diversity in a single stratigraphic unit. However, if this is broken up into the three subzones recently proposed for the *Cynognathus* AZ, five cynodonts are known from the Late Olenekian Subzone A (= *Kestrosaurus* AZ of Neveling, 2004), seven from the Early Anisian Subzone B and only three from the Late Anisian Subzone C.

Traversodontids are first represented in the Late Anisian of Africa and are responsible for the diversity explosion at that time (Fig. 8), with five different taxa. Interestingly, this group is documented in Namibia, Tanzania and Zambia, but there is not a single record in the supposedly contemporaneous levels of the highly fossiliferous Burgersdorp Formation of the Karoo Basin. Abdala and Smith (2009) point out the southerly location of the Karoo Basin in relation to the other African faunas (Fig. 2) and suggested that the recorded sparseness of this group in the Karoo Basin can be an indication of less tolerance to cold environments in the earliest traversodontids. The youngest Gondwanan record of this group is present in the Upper Triassic lower Elliot Formation of the Karoo Basin. Traversodontids are also represented by two taxa in the Upper Ladinian–Lower Carnian Makay Formation from Madagascar (Kammerer et al., 2008). It is

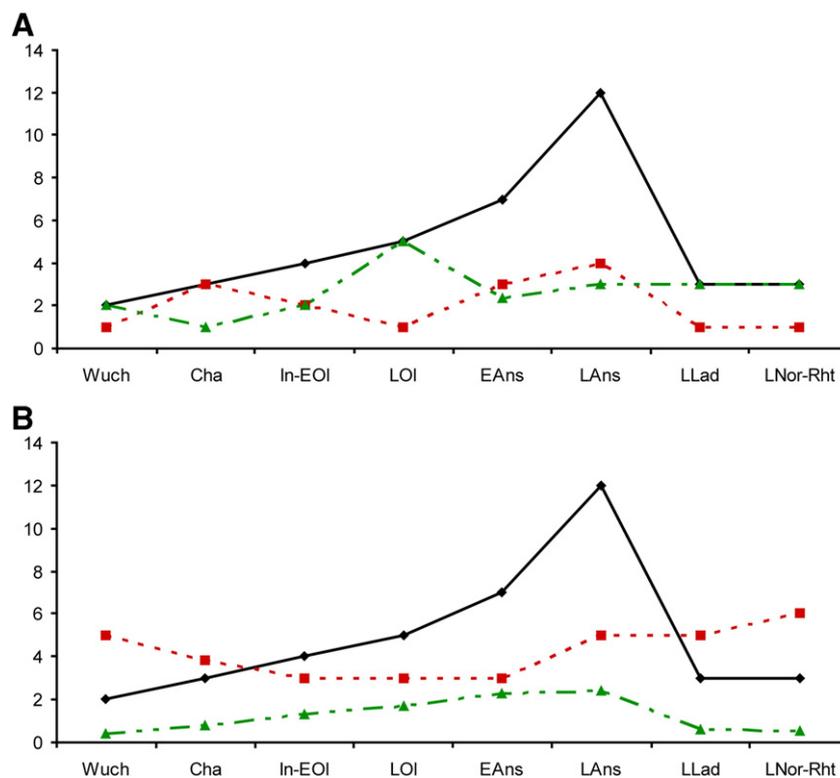


Fig. 8. Diversity of African cynodonts during the Permo-Triassic. See Fig. 7 for abbreviations and symbols. Additional abbreviations: Cha, Changhsingian; EAns, Early Anisian; Wuch, Wuchiapingian; LOI, Late Olenekian. A Mantel correlation test indicate significant correlation between the number of cynodont genera (cg) and number of faunas ($r: 0.77; p: 0.021$) and between cg and the ratio cg/interval range ($r: 0.89, p: 0.001$).

important to note that the last traversodontids in the Carnian of South America (i.e., *Exaeretodon* and *Ischnathus*) and the Norian of Africa (*Scalenodontoides*) are the largest representatives of the group, suggesting a trend to increasing size in Upper Triassic Gondwanan members of the family.

There is no correlation between cynodont genera diversity and interval range with cynodonts in Africa (Fig. 8B, solid line linked by diamonds and dashed line linked by squares). However, as in the case of South American faunas, a significant correlation ($r: 0.89; p: 0.001$) exists between cynodont genera and the ratio between number of cynodont genera and temporal range (Fig. 8B, solid line linked by diamonds and dashed line linked by triangles).

9. Discussion

The cynodonts from the earliest Triassic faunas are similar in size, dentition and occlusal system to those of the Latest Permian, thus suggesting that the Permo-Triassic transition did not have a great effect on Gondwanan cynodonts. This similarity between Late Permian and Early Triassic faunas also appears to characterize other therapsids. A recent study on anomodont-bearing faunas using cluster analysis showed that Early Triassic (*Lystrosaurus*-dominated) dicynodont faunas grouped with those from the Late Permian, and were independent of the remaining Triassic faunas (Fröbisch, 2009). The lowest generic diversity of Gondwanan cynodonts represented in the Early Triassic (four genera) is one genus more than the record from the Late Permian (Fig. 9). Considering that Early Triassic cynodonts are documented in vertebrate faunas from Africa, South America, Antarctica and India, the record of only four genera appears remarkably low. All are represented in the South African Karoo, with *Thrinaxodon* having a 'Gondwanopolitan' distribution, also known in Antarctica and India.

Cynodont generic diversity steadily increases until the Early Anisian, and by the Late Anisian there is a diversity explosion to 15 genera, reflecting changes represented particularly in African faunas. However, it is during the Late Olenekian and Early Anisian when cynodonts show remarkable variations in size and feeding system, producing a clear contrast with the previous record of the group. During this time cynodonts attained their largest body size in both herbivorous and carnivorous forms and developed complex bucco-lingually expanded postcanines. Traversodontids with postcanines bearing transverse crests and deep occlusal basins (Fig. 4A, B) appeared suddenly in the Late Anisian of Gondwana, making more evident the Middle Triassic turnover. At that time, seven of the 15 Gondwanan cynodont genera were members of the Traversodontidae. Other herbivorous tetrapods with bucco-lingually expanded postcanines not closely related to gomphodont cynodonts, such as bauriidae thercephalians and procolophonids are also known from this time (Gow, 1978). The latter group is the earliest, and the only one presenting expanded postcanines in the *Lystrosaurus* AZ, but several forms of this lineage with complex bucco-lingually expanded crowns are also known from younger faunas (Cisneros, 2008a). In addition, terrestrial representatives of different tetrapod groups reached greater size during the Anisian (e.g. *Cynognathus* AZ) than in the Induan–Early Olenekian (e.g. *Lystrosaurus* AZ), reflecting perhaps a recovery from the Lilliput effect post end-Permian extinction (Twichett, 2007). Apart from cynodonts, this is true for dicynodonts (e.g. *Kannemeyeria*; King, 1988; Fröbisch, 2009), archosauriforms (e.g. *Erythrosuchus*; Gower, 2003) and procolophonids (e.g. *Teratophon spinigensis*; Cisneros, 2008b).

The independent origin of the occlusal system in different amniote groups, the renaissance in diversity and abundance of dicynodonts in the Middle Triassic (Fröbisch, 2008, 2009) and the tendency to produce large size animals in comparison with those of the earliest Triassic, is suggestive of critical changes in the latest Olenekian to

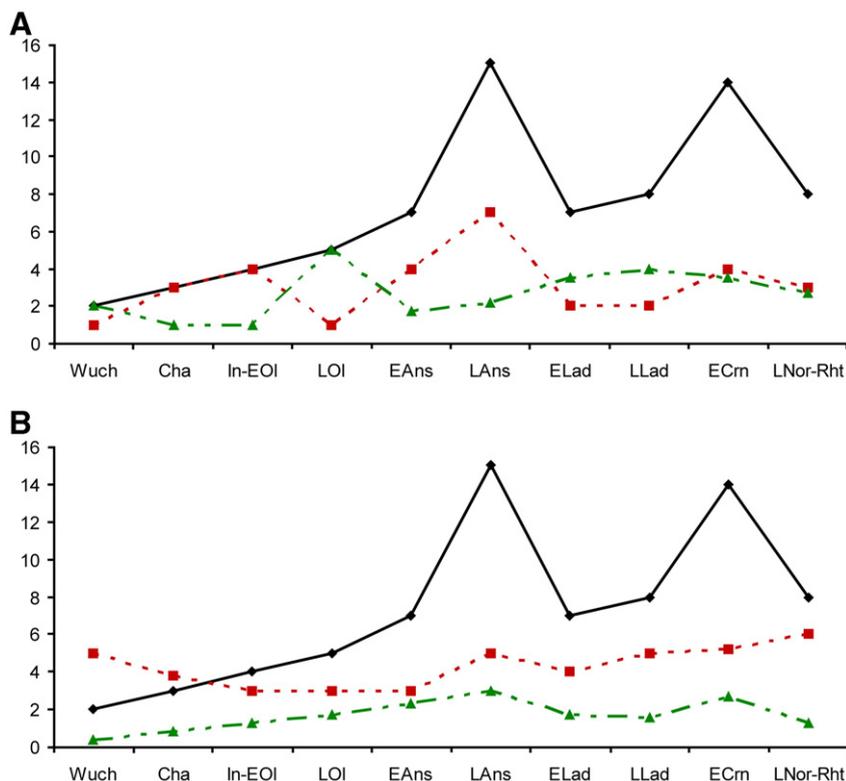


Fig. 9. Diversity of Gondwana cynodonts during the Permo-Triassic. See Figs. 7 and 8 for abbreviations and symbols. A Mantel correlation test indicate significant correlation between the number of cynodont genera (cg) and number of faunas ($r: 0.70, p: 0.026$) and between cg and the ratio cg/interval range ($r: 0.90, p: 0.001$).

Early Anisian environment. Palynomorphs are also suggestive of this trend, as Early Triassic pollen associations are not significantly different from those of the latest Permian, whereas important qualitative changes in the associations occur in the Middle Triassic (Traverse, 2008). Changes in the vertebrate faunas of the Anisian are perhaps related to the huge diversification of conifers in the Triassic (Tiffney, 1997; Willis and McElwain, 2002), particularly Voltziacean and primitive Podocarpacean (Wing and Sues, 1992).

In the Early Ladinian, represented only in South America, cynodont genera decrease from 14 to seven, the same number as in the Early Anisian. Diversity increases again in the Carnian, with 14 cynodont genera represented in South America and India, and then decreases in the Late Norian–Rhaetian where only eight taxa are known. This later reduction of cynodont diversity in Gondwana is in notable contrast with the Laurasian record, where Norian–Rhaetian cynodonts are represented by at least 20 genera. In fact, is in the Norian–Rhaetian Age where the highest diversity of cynodonts is recorded in the Triassic.

Considering monophyletic groups, advanced cynodonts (Eucynodontia) are represented in the Gondwanan Triassic faunas by 26 genera included in Cynognathia (sensu Abdala and Ribeiro, 2003), and 17 in Probainognathia (sensu Martinelli and Rougier, 2007, also including *Aleodon* following Hopson and Kitching, 2001, and by similarity with the latter, *Cromptodon*). *Cynognathus*, the oldest representative of Cynognathia is known from the Late Olenekian, whereas *Lumkuia*, the oldest Probainognathia, is recorded from the early Anisian, and the two lineages are represented in Ladinian, Carnian and Norian faunas from Gondwana. The herbivorous/omnivorous traversodontids, which are members of Cynognathia, are the most diverse group of Gondwanan cynodonts, being represented by 19 genera (see Appendix A) from the Late Anisian to the Late Norian. There is a demise of traversodontids, represented by only

one genus in the Late Norian–Rhaetian. In contrast, there are six members of the Probainognathia at this time: four included in Tritheledonta and two successive sister-groups of Mammaliaformes (see Martinelli and Rougier, 2007: Fig. 4).

The explosion of cynodont diversity in the Late Anisian seems to reflect the fact that seven faunas from Gondwana have cynodont representatives. A Mantel correlation test between cynodont genera and faunas indicate significant correlation between these variables ($r: 0.70; p: 0.022$; Fig. 9A, solid line linked by diamonds and dashed line linked by squares). Number of cynodont genera (cg) is also strongly correlated with the ratio between cg/interval range ($r: 0.90, p: 0.001$; Fig. 9B, solid line linked by diamonds and dashed line linked by triangles). These correlations are suggestive of a taphonomic bias in the record of cynodont diversity. Correlations between fossil-bearing units and global taxic diversity were also found amongst anomodonts and dinosaurs (Fröbisch, 2008; Barret et al., 2009), and interpreted in the latter, as a probable reflection of the amount of fossil-bearing rock preserved through time. Close inspection of the generic diversity and the number of faunas with cynodonts (Fig. 9A) highlights some differences between these trends. Cynodonts from the Late Olenekian, represented by only one fauna (*Cynognathus* AZ, Subzone A) show more diversity than the Induan–Early Olenekian, in which at least four different faunas are known. Induan to Late Olenekian is the only time range in which faunal and cynodont trends are opposing (Fig. 9A). This is also evident in the trend reflecting the ratio of the number of cynodont genera/number of fauna with cynodonts (Fig. 9A, dashed line linked by triangles) in which the largest diversity is represented in the Late Olenekian instead. A remarkably low diversity is also recognized in the global record of Induan anomodonts, which are known from several geological formations (Fröbisch, 2008). Low diversity in the well represented Induan record, when compared with the single Late Olenekian fauna

having several cynodonts, represents a landmark event when analyzing diversity changes in the group. In addition to this, the recovery from the Lilliput effect during the Anisian is also an important factor characterizing the post-Permian extinction in some therapsid lineages that survived that event.

10. Conclusion

Most therapsid lineages evolved predominantly during the Permian. Cynodontia, however, the last therapsid to appear in the fossil record, show the most important morphological changes during their early evolution in the Triassic. Gondwanan cynodont generic diversity in the post-extinction earliest Triassic was only slightly greater than that of the Latest Permian, without major ecological and size differences between cynodonts of these ages. In contrast, a very different morphotype appeared at the end of the Early Triassic in the form of gomphodont cynodonts (i.e., with bucco-lingually expanded postcanines), and in the Anisian both carnivorous and herbivorous forms reach their greatest size. This turnover is reaffirmed with the explosive appearance of traversodontid cynodonts in the faunas of both South America and Africa at the end of the Anisian. This group remained as an important and usually dominant component of Ladinian and Carnian faunas of Gondwana. In the Norian–Rhaetian is the last record of large Gondwanan traversodontids, together with the first record of the small-sized insectivorous tritheledontids, a lineage that is also represented in the Early Jurassic. The diversity of Gondwanan cynodonts during the Norian–Rhaetian is remarkably low considering that the maximum Triassic global diversity of this group occurs precisely at this time. Cynodonts remain an important component of Early Jurassic faunas, in the form of mammaliaforms and the remarkably diverse herbivorous tritylodontids, but are best represented in Laurasia at this time.

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Appendix A

List of cynodont taxa represented in Gondwanan faunas. The numbers following each continent represent the number of genera/species in each of them. Abbreviations: It, isolated teeth; M, mandible; pSk, isolated postcranial remains; S, skull; SF, skull fragment; Sk, skeleton; Tr, Traversodontidae. Number in Arabic indicates known specimens. *Recent new discovery (Oliveira et al., 2009) not considered in the analysis.

SOUTH AMERICA (30/36)

Brazil

Induan Faunas

Sanga do Cabral Formation, Paraná Basin

Cynodont of small size, pSk, ?2

Ladinian Faunas

Dinodontosaurus Assemblage Zone, Santa Maria Formation, Paraná Basin

Basin

Luangwa sudamericana, S-M, 3, Tr

Massetognathus ochagaviae, S-M, 20, Tr

Protuberum cabralensis, S-Sk, ?2, Tr

Traversodon stahleckeri, S-pSk, 4, Tr

Chiniquodon theotonicus, S-Sk, 10

Protheriodon estudianti, S-M, 1

*New unnamed taxon, M, 1

Santacruzodon Assemblage Zone, Santa Maria Formation, Paraná Basin

Basin

Santacruzodon hopsoni, S-Sk, 6, Tr

Menadon sp., S-Sk, 6, Tr

Massetognathus sp., S-M, ?, Tr

Chiniquodon sp., S-M, 3

Cf. *Probainognathus* sp., M, 1

Carnian Faunas

Hyperodapedon Assemblage Zone, Santa Maria Formation, Paraná Basin

Basin

Exaeretodon riograndensis, S-Sk, 7, Tr

Gomphodontosuchus brasiliensis, S-M, 1, Tr

Therioherpeton cargnini, S-Sk, 1

Prozostrodon brasiliensis, S-Sk, 1

Charruodon tetracuspidatus, M, 1

Ecteninion-like, S-Sk, 1

Norian Faunas

Riograndia Assemblage Zone, Caturrita Formation, Paraná Basin

Riograndia guaibensis, S-M, more than 20

Irajatherium hernandezi, S-pSk, 1

Brasilodon quadrangularis, S-pSk, 4

Brasilitherium riograndensis, S-M, 8

Argentina

Anisian Faunas

Cerro de Las Cabras Formation, Cuyo Basin

Cromptodon mamiferoides, M, 1

Andescynodon mendozensis, S-Sk, more than 10, Tr

Rusconiiodon mignonei, S-Sk, 7, Tr

Rio Seco de la Quebrada Formation, San Rafael Basin

Cynognathus crateronotus, S-pSk, 1

Diademodon tetragonus, SF-M, 1

Pascualgnathus polanskii, S-Sk, 3, Tr

Ladinian Faunas

Chañares Formation, Ischigualasto–Villa Unión Basin

Massetognathus pascuali, S-Sk, more than 40, Tr

Chiniquodon theotonicus, S-Sk, more than 20

Probainognathus jenseni, S-Sk, more than 20

Carnian Faunas

Ischigualasto Formation, Ischigualasto–Villa Unión Basin

Exaeretodon argentinus, S-Sk, more than 30, Tr

Ischignathus sudamericanus, S-M, 2, Tr

Chiniquodon sanjuanensis, S-M, 4

Ecteninion lunensis, S-M, 4

Cf. *Probainognathus*, S-M, 1

Norian Faunas

Los Colorados Formation, Ischigualasto–Villa Unión Basin

Chalimnia musteloides, S-M, 2

AFRICA (31/33)

South Africa

Induan Faunas

Lystrosaurus Assemblage Zone, Palingkloof Member of the Balfour Formation, Harrismith Member of the Normandien Formation, base of the Katberg Formation, Karoo Basin

Progalesaurus lotbergensis, S-pSk, 1

Galesaurus planiceps, S-Sk, 20

Platycraniellus elegans, S-M, 2

Thrinaxodon liorhinus, S-Sk, more than 40

Olenekian Faunas

Lystrosaurus Assemblage Zone, top of the Katberg Formation, Karoo Basin

Thrinaxodon liorhinus, S-Sk, common
 Cynognathus Assemblage Zone, SubZone A, Burgersdorp Formation, Karoo Basin
Cynognathus sp., It, 2
Langbergia modisei, S-Sk, 14
Trirachodon berryi, S-M It, 2
 Allotheria-like teeth, It, ?1
 Unnamed sectorial toothed cynodont, S-M, 4
 Anisian Faunas
 Cynognathus Assemblage Zone, SubZone B, Burgersdorp Formation, Karoo Basin
Diademodon tetragonus, S-Sk, more than 50
Trirachodon berryi, S-Sk, more than 20
 Trirachodontidae, S-M, 1
Cynognathus crateronotus, S-Sk, more than 20
Lumkuia fuzzi, S-Sk, 1
Cistecynodon parvus, S-M, 1
Bolotridon frerensis, S-M, 3–4
 Cynognathus Assemblage Zone, SubZone C, Burgersdorp Formation, Karoo Basin
Diademodon sp. M, 2
Cynognathus sp., S-M, 1
Cricodon metabolus, S-M, 5
 Norian Faunas
 Lower Elliot Formation, Karoo Basin (also in Lesotho)
Scalenodontoides macrodentes, S-pSk, 6, Tr
Elliotherium kersteni, S, 1
 ?Diademodontidae, M, 1
 Namibia
 Anisian Faunas
 Upper Omingonde Formation, Otiwarongo Basin
Diademodon, S-Sk, 5
Titanogomphodon crassus, S, 1
Cynognathus, S-M, 3
Trirachodon berryi, S-Sk, 1
Luangwa sp., S-Sk, 7, Tr
 Traversodontidae, S-M, 1, Tr
Aleodon sp., S, 1
Chiniquodon sp, S-Sk, 1
 Tanzania
 Anisian Faunas
 Lifua Member of the Manda beds, Ruhuhu Basin
Aleodon brachyrhamphus, S-M, 7
Scalenodon angustifrons, S-M, 12, Tr
 'Scalenodon' *hirschsoni*, S, 1, Tr
 'Scalenodon' *attridgei* (= ?*S. charigi*), S, ?2, Tr
Cricodon metabolus, S-pSk, 1
Diademodon sp., It, 1
 Zambia
 Anisian Faunas, Luangwa Basin
 Lower Ntawere Formation, Luangwa Basin
Diademodon tetragonus, S-M, 1
 Upper Ntawere Formation, Luangwa Basin
Luangwa drysdalli, S-M, 3, Tr
 Madagascar
 ?Ladinian Faunas
 Makay Formation, Morondava Basin
Dadadon isaloi, S, 2, Tr
Menadon besairiei, S-Sk, 4, Tr
 Chiniquodontid cynodont, S-Sk, ?

ANTARCTICA (4/4)
 Induan Faunas
 Lower Fremouw Formation
Thrinaxodon liorhinus, S-Sk, 15
Cynodontia incertae sedis, S-M, 1

Anisian Faunas
 Upper Fremouw Formation
Cynognathus sp., M, 3
 Diademodontidae, ?*Titanogomphodon*, SF, 1

INDIA (7/7)

Induan Faunas
 Panchet Formation, Damodar Basin
Thrinaxodon bengalensis, S-M, 1
 Anisian Faunas
 Yerrapalli, Formation, Pranhita–Godavari Basin
 Trirachodontidae teeth, It, ?1
 Carnian Faunas
 Maleri Formation, Pranhita–Godavari Basin
Exaeretodon statisticae, SF, 1
Deccanodon maleriensis, It, 1
 Tiki Formation, Son–Mahanadi Basin
Rewacondon tikiensis, It, ?1
Gondwanadon tapani, It, 1
Tikitherium copei, It, 1

References

- Abdala, F., 1996. Redescrpción del cráneo y reconsideración de la validez de *Cynognathus minor* (Eucynodontia–Cynognathidae) del Triásico Inferior de Mendoza. *Ameghiniana* 33, 115–126.
- Abdala, F., 2000. Catalogue of non-mammalian cynodonts in the Vertebrate Paleontology Collection of the Instituto Miguel Lillo. Universidad Nacional de Tucumán, with comments on species. *Ameghiniana* 37, 463–475.
- Abdala, F., 2003. Galesaurid cynodonts from the Early Triassic of South Africa: another example of conflicting distribution of characters in non-mammalian cynodonts. *South African Journal of Science* 99, 95–96.
- Abdala, F., 2004. Abundance and diversity of non-mammaliaform cynodonts in the South African Karoo. *Geosciences Africa* 2004, University of the Witwatersrand, Johannesburg, Abstract volume 1, 1.
- Abdala, F., 2007. Redescription of *Platycraniellus elegans* (Therapsida, Cynodontia) from the Lower Triassic of South Africa, and the cladistic relationships of eutheriodonts. *Palaeontology* 50, 591–618.
- Abdala, F., Allinson, M., 2005. The taxonomic status of *Parathrinaxodon proops* (Therapsida: Cynodontia), with comments on the morphology of the palate in basal cynodonts. *Palaeontologia Africana* 41, 45–52.
- Abdala, F., Giannini, N.P., 2000. Gomphodont cynodonts of the Chañares Formation: the analysis of an ontogenetic sequence. *Journal of Vertebrate Paleontology* 20, 501–506.
- Abdala, F., Giannini, N.P., 2002. Chiniquodontid cynodonts: systematic and morphometric considerations. *Palaeontology* 45, 51–1170.
- Abdala, F., Ribeiro, A.M., 2000. A new therioherpetid cynodont from the Santa Maria Formation (middle Late Triassic), southern Brazil. *Geodiversitas* 22, 589–596.
- Abdala, F., Ribeiro, A.M., 2003. A new traversodontid cynodont from the Santa Maria Formation (Ladinian–Carnian) of southern Brazil, with a phylogenetic analysis of Gondwanan traversodontids. *Zoological Journal of the Linnean Society* 139, 529–545.
- Abdala, F., Smith, R.M.H., 2009. A middle Triassic cynodont fauna from Namibia and its implications for the biogeography of Gondwana. *Journal of Vertebrate Paleontology* 29, 837–851.
- Abdala, F., Teixeira, A.M.S., 2004. A traversodontid cynodont of African affinity in the South American Triassic. *Palaeontologia Africana* 40, 11–22.
- Abdala, F., Ribeiro, A.M., Schultz, C.L., 2001. A rich cynodont fauna of Santa Cruz do Sul, Santa Maria Formation (Middle–Late Triassic), southern Brazil. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 2001, 669–687.
- Abdala, F., Barberena, M.C., Dornelles, J., 2002a. A new species of the traversodontid cynodont *Exaeretodon* from the Santa Maria Formation (Middle/Late Triassic) of southern Brazil. *Journal of Vertebrate Paleontology* 22, 313–325.
- Abdala, F., Dias-da-Silva, S., Cisneros, J.C., 2002b. First record of nonmammalian cynodonts (Therapsida) in the Sanga do Cabral Formation (Early Triassic) of southern Brazil. *Palaeontologia Africana* 38, 93–98.
- Abdala, F., Hancox, P.J., Neveling, J., 2005a. Cynodonts from the uppermost Burgersdorp Formation, South Africa, and their bearing on the biostratigraphy and correlation of the Triassic *Cynognathus* Assemblage Zone. *Journal of Vertebrate Paleontology* 25, 192–199.
- Abdala, F., Neveling, J. and Rubidge, B.S., 2005b. A new cynodont from the base of the *Cynognathus* Assemblage Zone (Lower Triassic) of the Karoo Basin: wrong teeth or wrong skull? In: Pankhurst, R.J. and Veiga, G.D. (eds.) *Gondwana 12: Geological and biological heritage of Gondwana, Abstracts, Academia Nacional de Ciencias, Cordoba, Argentina*, p. 31.
- Abdala, F., Cisneros, J.C., Smith, R.M.H., 2006a. Faunal aggregation in the Early Triassic Karoo Basin: earliest evidence of shelter-sharing among tetrapods? *Palaiois* 21, 507–512.
- Abdala, F., Neveling, J., Welman, J., 2006b. A new trirachodontid cynodont from the lower levels of the Burgersdorp Formation (Lower Triassic) of the Beaufort Group, South Africa and the cladistic relationships of Gondwanan gomphodonts. *Zoological Journal of the Linnean Society* 147, 383–413.

- Abdala, F., Damiani, R., Yates, A., Neveling, J., 2007a. A non-mammaliaform cynodont from the Upper Triassic of South Africa: a therapsid Lazarus taxon? *Palaeontologia Africana* 42, 17–23.
- Abdala, F., Mocke, H., Hancox, P.J., 2007b. Lower Triassic postcanine teeth with allotherian-like crowns. *South African Journal of Science* 103, 245–247.
- Abdala, F., Rubidge, B.S., van den Heever, J., 2008. The oldest therocephalians (Therapsida, Eutheriodontia) and the early diversification of Therapsida. *Palaeontology* 51, 1011–1024.
- Abdala, F., Martinelli, A.G., Soares, M.B., de la Fuente, M., Ribeiro, A.M., 2009. South American Middle Triassic continental faunas with amniotes: biostratigraphy and correlation. *Palaeontologia Africana* 44, 83–87.
- Anderson, J.M., Anderson, H.M., 1984. The fossil content of the Upper Triassic Molteno Formation, South Africa. *Palaeontologia Africana* 25, 39–59.
- Anderson, J.M., Anderson, H.M., Cruickshank, A.R.I., 1998. Late Triassic ecosystem of the Molteno/Elliott biome of southern Africa. *Palaeontology* 41, 387–421.
- Bandyopadhyay, S., Sengupta, D.P., 1999. Middle Triassic vertebrates of India. *Journal of African Earth Sciences* 29, 233–241.
- Bandyopadhyay, S., Sengupta, D.P., 2006. Vertebral faunal turnover during the Triassic–Jurassic transition: and Indian scenario. In: Harris, J.D., Lucas, S.G., Spielman, J.A., Lockley, M.G., Milner, A.R.C., Kirkland, J.I. (Eds.), *The Triassic–Jurassic Terrestrial Transition: New Mexico Museum of Natural History and Science, Bulletin*, vol. 37, pp. 77–85.
- Bandyopadhyay, S., RoyChowdhury, T.K., Sengupta, D.P., 2002. Taphonomy of some Gondwana vertebrate assemblages of India. *Sedimentary Geology* 147, 219–245.
- Barberena, M.C., 1974. Contribuição ao conhecimento dos cinodontes gonfodontes (Cynodontia, Tritylodontoidea) do Brasil. Tese para obtenção do título de Livre Docente inédita. Ministério de Educação e Cultura, Universidade Federal do Rio Grande do Sul. 194 pp.
- Barberena, M.C., 1981. Novos materiais de *Traversodon stahleckeri* da Formação Santa Maria (Triássico do Rio Grande do Sul). *Pesquisas* 14, 149–162.
- Barberena, M.C., Bonaparte, J.F., Teixeira, A.M.S., 1987. *Thrinaxodon brasiliensis* sp. nov., a primeira ocorrência de cinodontes galesauros para o Triássico do Rio Grande do Sul. *Anais do X Congresso Brasileiro de Paleontologia*. Rio de Janeiro 1, 67–74.
- Barret, P.M., McGowan, A.J., Page, V., 2009. Dinosaur diversity and the rock record. *Proceedings of the Royal Society B* 276, 2667–2674.
- Battail, B., 2005. Late Triassic traversodontids (Synapsida: Cynodontia) in southern Africa. *Palaeontologia Africana* 41, 67–80.
- Benton, M.J., 1995. Diversification and extinction in the history of life. *Science* 268, 52–58.
- Bonaparte, J.F., 1962. Descripción del cráneo y mandíbula de *Exaeretodon frenguelli*, Cabrera, y su comparación con *Diademodontidae*, *Tritylodontidae* y los cinodontes sudamericanos. *Publicaciones del Museo Municipal de Ciencias Naturales y Tradición Mar del Plata* 1, 135–202.
- Bonaparte, J.F., 1963. Descripción de *Ischnognathus sudamericanus* n. gen. n. sp., nuevo cinodonte gonfodonte del Triásico Medio superior de San Juan, Argentina. *Acta Geologica Lilloana* 4, 111–118.
- Bonaparte, J.F., 1967. New vertebrate evidence for a southern transatlantic connection during the Lower or Middle Triassic. *Palaeontology* 10, 554–563.
- Bonaparte, J.F., 1969a. *Cynognathus minor* n. sp. (Therapsida–Cynodontia). Nueva evidencia de vinculación faunística Afro-Sudamericana a principios del Triásico. *Gondwana Stratigraphy, I.U.G.S. Coloquio Mar del Plata* 1967, 273–281.
- Bonaparte, J.F., 1969b. Dos nuevas “faunas” de reptiles triásicos de Argentina. *Gondwana Stratigraphy, I.U.G.S. Coloquio Mar del Plata* 1967, 283–302.
- Bonaparte, J.F., 1971. Los tetrapódos del sector superior de la Formación Los Colorados, La Rioja, Argentina (Triásico Superior). I Parte. *Opera Lilloana* 22, 1–183.
- Bonaparte, J.F., 1972. *Cromptodon mamiferoides*, Galesauridae de la Formación Río Mendoza, Mendoza, Argentina (Therapsida–Cynodontia). *Ameghiniana* 9, 343–353.
- Bonaparte, J.F., 1980. El primer ictiosaurio (Reptilia–Therapsida) de América del Sur, *Chalimnia musteloides*, del Triásico Superior de La Rioja, República Argentina. *Actas II Congreso Argentino de Paleontología y Bioestratigrafía y I Congreso Latinoamericano de Paleontología*. Buenos Aires Tomo 1, 123–133.
- Bonaparte, J.F., 1982. Faunal replacement in the Triassic of South America. *Journal of Vertebrate Paleontology* 2, 362–371.
- Bonaparte, J.F., Barberena, M.C., 1975. A possible mammalian ancestor from the Middle Triassic of Brazil (Therapsida–Cynodontia). *Journal of Paleontology* 49, 931–936.
- Bonaparte, J.F., Barberena, M.C., 2001. On two advanced carnivorous cynodonts from the Late Triassic of southern Brazil. *Bulletin of the Museum of Comparative Zoology* 156, 59–80.
- Bonaparte, J.F., Crompton, A.W., 1994. A juvenile probainognathid cynodont skull from the Ischigualasto Formation and the origin of mammals. *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia* 5, 1–12.
- Bonaparte, J.F., Sues, H.-D., 2006. A new species of *Clevoosaurus* (Lepidosauria: Rhynchocephalia) from the Upper Triassic of Rio Grande do Sul, Brazil. *Palaeontology* 49, 917–923.
- Bonaparte, J.F., Ferigolo, J., Ribeiro, A.M., 2001. A primitive Late Triassic ‘ictidosaur’ from Rio Grande do Sul, Brazil. *Palaeontology* 44, 623–635.
- Bonaparte, J.F., Martinelli, A.G., Schultz, C.L., Rubert, R., 2003. The sister group of mammals: small cynodonts from the Late Triassic of southern Brazil. *Revista Brasileira de Paleontologia* 5, 5–27.
- Bonaparte, J.F., Martinelli, A.G., Schultz, C.L., 2005. New information on *Brasilodon* and *Brasilitherium* (Cynodontia, Probainognathia) from the Late Triassic of southern Brazil. *Revista Brasileira de Paleontologia* 8, 25–46.
- Bonaparte, J.F., Schultz, C.L., Soares, M.B., 2006. A new non-mammalian cynodont from the Middle Triassic of southern Brazil and its implications for the ancestry of mammals. *Bulletin of the New Mexico Museum of Natural History and Science* 37, 599–607.
- Botha, J., Chinsamy, A., 2000. Growth patterns deduced from the bone histology of the cynodonts *Diademodon* and *Cynognathus*. *Journal of Vertebrate Paleontology* 20, 705–711.
- Botha, J., Chinsamy, A., 2004. Growth and life habits of the Triassic cynodont *Trirachodon*, inferred from bone histology. *Acta Paleontologica Polonica* 619–627.
- Botha, J., Chinsamy, A., 2005. Growth patterns of *Thrinaxodon liorhinus*, a non-mammalian cynodont from the Lower Triassic of South Africa. *Palaeontology* 48, 385–394.
- Botha, J., Smith, R.M.H., 2006. Rapid vertebrate recuperation in the Karoo Basin of South Africa following the End-Permian extinction. *Journal of African Earth Sciences* 45, 502–514.
- Botha, J., Abdala, F., Smith, R., 2007. The oldest cynodont: new clues on the origin and diversification of the Cynodontia. *Zoological Journal of the Linnean Society* 149, 477–492.
- Brink, A.S., 1963. Two cynodonts from the Ntawere Formation in the Luangwa valley of Northern Rhodesia. *Palaeontologia Africana* 8, 77–96.
- Brink, A.S., Kitching, J.W., 1953. On some new *Cynognathus* Zone specimens. *Palaeontologia Africana* 1, 29–48.
- Caselli, A.T., Marsicano, C.A., Arcucci, A.B., 2001. Sedimentología y paleontología de la Formación Los Colorados, Triásico Superior (provincias de La Rioja y San Juan, Argentina). *Revista de la Asociación Geológica Argentina* 56, 173–188.
- Chatterjee, S., 1982. A new cynodont reptile from the Triassic of India. *Journal of Paleontology* 56, 203–214.
- Chinsamy, A., Abdala, F., 2008. Palaeobiological implications of the bone microstructure of South American traversodontids (Therapsida: Cynodontia). *South African Journal of Science* 104, 225–230.
- Cisneros, J.C., 2008a. Phylogenetic relationships of procolophonid parareptiles with remarks on their geological record. *Journal of Systematic Palaeontology* 6, 345–366.
- Cisneros, J.C., 2008b. Taxonomic status of the reptile genus *Procolophon* from the Gondwanan Triassic. *Palaeontologia Africana* 43, 7–17.
- Clark, J.M., Xu, X., Forster, C.A., Wang, Y., 2004. A Middle Jurassic ‘sphenosuchian’ from China and the origin of the crocodylian skull. *Nature* 430, 1021–1024.
- Colbert, E.H., Kitching, J.W., 1977. Triassic cynodont reptiles from Antarctica. *American Museum Novitates* 2611, 1–30.
- Crompton, A.W., 1955. On some Triassic cynodonts from Tanganyika. *Proceedings of the Zoological Society of London* 125, 617–669.
- Crompton, A.W., 1972. Postcanine occlusion in cynodonts and tritylodonts. *Bulletin of the British Museum (Natural History)*. Geology 21, 29–71.
- Crompton, A.W., Ellenberger, F., 1957. On a new cynodont from the Molteno Beds and the origin of the tritylodontids. *Annals of the South African Museum* 44, 1–13.
- Currie, B.S., Colombi, C.E., Tabor, N.J., Shipman, T.C., Montañez, I.P., 2009. Stratigraphy and architecture of the Upper Triassic Ischigualasto Formation, Ischigualasto Provincial Park, San Juan, Argentina. *Journal of South American Earth Sciences* 27, 74–87.
- Da Silva, L.R., Cabreira, S.F., 2009. Novo achado de *Luangwa sudamericana* Abdala & Teixeira, 2004 do Triássico Médio da Formação Santa Maria, Rio Grande do Sul, Brasil. *Palaeontologia em Destaque* 24, 23–24.
- Damiani, R., Modesto, S., Yates, A., Neveling, J., 2003. Earliest evidence of cynodont burrowing. *Proceedings of the Royal Society of London B* 270, 1747–1751.
- Datta, P.M., 2005. Earliest mammal with transversely expanded upper molar from the Late Triassic (Carnian) Tiki Formation, South Rewa Gondwana Basin, India. *Journal of Vertebrate Paleontology* 25, 200–207.
- Datta, P.M., Das, D.P., 2001. *Indozostrodon simpsoni*, Gen. et sp. nov., an early Jurassic megazostrodonid mammal from India. *Journal of Vertebrate Paleontology* 21, 528–534.
- Datta, P.M., Das, D.P., Luo, Z., 2004. A Late Triassic dromatheriid (Synapsida: Cynodontia) from India. *Annals of Carnegie Museum* 73, 72–84.
- Drysdall, A.R., Kitching, J.W., 1963. A re-examination of the Karoo succession and fossil localities of part of the Upper Luangwa Valley. *Memoire of the Geological Survey of Northern Rhodesia* 1, 1–62.
- Erwin, D.H., 1994. The Permo-Triassic extinction. *Nature* 367, 231–236.
- Flynn, J.J., Wyss, A.R., 2002. Madagascar’s Mesozoic secrets. *Scientific American* February, pp. 42–51.
- Flynn, J.J., Parrish, J.M., Rakotosamimanana, B., Simpson, W.F., Whatley, R.L., Wyss, A.R., 1999. A Triassic fauna from Madagascar, including early dinosaurs. *Science* 286, 763–765.
- Flynn, J.J., Parrish, J.M., Rakotosamimanana, B., Ranivoharimanana, L., Simpson, W.F., Wyss, A.R., 2000. New traversodontids (Synapsida: Eucynodontia) from the Triassic of Madagascar. *Journal of Vertebrate Paleontology* 20, 422–427.
- Frakes, L.A., Francis, J.E., Syktus, J.I., 1992. *Climate Models of the Phanerozoic*. Cambridge University Press, Cambridge. 274 pp.
- Fröbisch, J., 2008. Global taxonomic diversity of anomodonts (Tetrapoda, Therapsida) and the terrestrial rock record across the Permian–Triassic boundary. *PLoS ONE* 3 (11), e3733 doi:10.1371/journal.pone.0003733.
- Fröbisch, J., 2009. Composition and similarity of global anomodont-bearing tetrapod faunas. *Earth-Science Reviews* doi:10.1016/j.earscirev.2009.04.001.
- Furin, S., Preto, N., Rigo, M., Roghi, G., Gianolla, P., Crowley, J.L., Bowring, S.A., 2006. High-precision U–Pb zircon age from the Triassic of Italy: implications for the Triassic time scale and the Carnian origin of calcareous nannoplankton and dinosaurs. *Geology* 34, 1009–1012.
- Gallet, Y., Krystyn, L., Besse, J., Marcoux, J., 2003. Improving the Upper Triassic numerical time scale from cross-correlation between Tethyan marine sections and the continental Newark basin sequence. *Earth and Planetary Science Letters* 212, 255–261.
- Gow, C.E., 1978. The advent of herbivory in certain reptilian lineages during the Triassic. *Palaeontologia Africana* 133–141.
- Gower, D.J., 2003. Osteology of the early archosaurian reptile *Erythrosuchus africanus* Broom. *Annals of the South African Museum* 110, 1–84.
- Gradstein, F.M., Ogg, J.G., 2004. *Geologic Time Scale 2004 – why, how, and where next!* *Lethaia* 37, 175–181.
- Groenewald, G.H., Kitching, J.W., 1995. Biostratigraphy of the *Lystrosaurus* Assemblage Zone. In: Rubidge, B.S. (Ed.), *Biostratigraphy of the Beaufort Group (Karoo Supergroup): Biostratigraphic Series 1*, South African Committee for Stratigraphy, Pretoria, pp. 35–39.
- Groenewald, G.H., Welman, J., MacEachern, J.A., 2001. Vertebrate burrow complexes from the Early Triassic Cynognathus Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa. *Palaio* 16, 148–160.

- Hammer, W.R., 1995. New therapsids from the upper Fremouw Formation (Triassic) of Antarctica. *Journal of Vertebrate Paleontology* 15, 105–112.
- Hancox, P.J., 2000. The Continental Triassic of South Africa. *Zentralblatt für Geologie und Paläontologie Teil I, Heft 11–12*, 1998, 1285–1324.
- Hancox, P.J., Shishkin, M.A., Rubidge, B.S., Kitching, J.W., 1995. A threefold subdivision of the *Cynognathus* Assemblage Zone (Beaufort Group, South Africa) and its palaeogeographic implications. *South African Journal of Science* 91, 143–144.
- Haughton, S.H., 1924. On Cynodontia from the middle Beaufort beds of Harrismith, Orange Free State. *Annals of the Transvaal Museum* 11, 74–92.
- Holz, M. and Scherer, C.M.S., 2000. Sedimentological and paleontological evidence of paleoclimatic change during the South Brazilian Triassic: the register of a global trend towards humid paleoclimate. *Zentralblatt für Geologie und Paläontologie Teil 1*. 1998, Heft 11–12, 1589–1609.
- Hopson, J.A., 1985. Morphology and relationships of *Gomphodontosuchus brasiliensis* von Huene (Synapsida, Cynodontia, Tritylodontoidea) from the Triassic of Brazil. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1985, 285–299.
- Hopson, J.A., 2005. A juvenile gomphodont cynodont specimen from the *Cynognathus* Assemblage Zone of South Africa: implications for the origin of gomphodont postcanine morphology. *Palaeontologia Africana* 41, 53–66.
- Hopson, J.A., Kitching, J.W., 2001. A probainognathian cynodont from South Africa and the phylogeny of nonmammalian cynodonts. *Bulletin of the Museum of Comparative Zoology* 156, 5–35.
- Huttenlocker, A., 2009. An investigation into the cladistic relationships and monophyly of thercephalian therapsids (Amniota: Synapsida). *Zoological Journal of the Linnean Society* 157, 865–891.
- Kammerer, C.F., Flynn, J.J., Ranivoharimanana, L., Wyss, A.R., 2008. New material of *Menadon besairei* (Cynodontia: Traversodontidae) from the Triassic of Madagascar. *Journal of Vertebrate Paleontology* 28, 445–462.
- Kemp, T.S., 1980. Aspects of the structure and functional anatomy of the Middle Triassic cynodont *Luangwa*. *Journal of Zoology* 191, 193–239.
- Kemp, T.S., 2005. *The Origin and Evolution of Mammals*. Oxford University Press, Oxford. 331 pp.
- Keyser, A.W., 1973a. A new Triassic vertebrate fauna from South West Africa. *Palaeontologia Africana* 16, 1–15.
- Keyser, A.W., 1973b. New Triassic vertebrate fauna from South West Africa. *South African Journal of Sciences* 69, 113–115.
- Kielan-Jaworowska, Z., Cifelli, R.L., Luo, Z.-X., 2004. *Mammals from the Age of Dinosaurs: Origin, Evolution and Structure*. Columbia University Press, New York, NY. 630 pp.
- King, G.M., 1988. Anomodontia. *Encyclopedia of Paleoherpology*. Gustav Fischer Verlag, Stuttgart. 174 pp.
- Kitching, J.W., 1963. The fossil localities and mammal-like reptiles of the upper Luangwa Valley, northern Rhodesia. *South African Journal of Science* 59, 259–264.
- Kitching, J.W., 1977. The distribution of the Karoo vertebrate fauna. *Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Memoir 1*, pp. 1–131.
- Kitching, J.W., 1995. Biostratigraphy of the *Cynognathus* Assemblage Zone. In: Rubidge, B.S. (Ed.), *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*, Biostratigraphic Series 1. South African Committee for Stratigraphy, Pretoria, pp. 40–45.
- Knoll, F., 2004. Review of the tetrapod fauna of the “Lower Stormberg Group” of the main Karoo Basin (southern Africa): implications for the age of the Lower Elliot Formation. *Bulletin de la Societe géologique de France* 175, 73–83.
- Knoll, F., Batail, B., 2001. New ornithischian remains from the upper Elliot Formation (Lower Jurassic) of Lesotho and stratigraphical distribution of southern African fabrosaurids. *Geobios* 34, 415–421.
- Langer, M.C., 2005. Studies on continental Late Triassic tetrapod biochronology. II. The Ischigualastian and a Carnian global correlation. *Journal of South American Earth Sciences* 19, 219–239.
- Langer, M.C., Abdala, F., Richter, M., Benton, M.J., 1999. A sauropodomorph dinosaur from the Upper Triassic (Carnian) of southern Brazil. *Comptes Rendus de l'Académie des Sciences, serie II, fascicule A, Sciences de la Terre e des Planetes* 329, 511–517.
- Langer, M.C., Ribeiro, A.M., Schultz, C.L., Ferigolo, J., 2007. The continental tetrapod-bearing Triassic of south Brazil. *Bulletin of the New Mexico Museum of Natural History and Science* 41, 201–218.
- Lehrmann, D.J., et al., 2006. Timing of recovery from the end-Permian extinction: geochronologic and biostratigraphic constraints from South China. *Geology* 34, 1053–1056.
- Li, C., Wu, X.-C., Rieppel, O., Wang, L.-T., Zhao, L.-J., 2008. An ancestral turtle from the Late Triassic of southwestern China. *Nature* 456, 497–501.
- Liu, J., 2007. The taxonomy of the traversodontid cynodonts *Exaeretodon* and *Ischignathus*. *Revista Brasileira de Paleontologia* 10, 133–136.
- Liu, J., Soares, M.B., Reichel, M., 2008. *Massetognathus* (Cynodontia, Traversodontidae) from the Santa Maria Formation of Brazil. *Revista Brasileira de Paleontologia* 11, 27–36.
- Lucas, S.G., 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 143, 347–384.
- Lucas, S.G., 2002. A new dicynodont from the Triassic of Brazil, and the tetrapod biochronology of the Brazilian Triassic. *Bulletin of the New Mexico Museum of Natural History and Science* 21, 131–141.
- Lucas, S.G., Hancox, P.J., 2001. Tetrapod-based correlation of the nonmarine Upper Triassic of southern Africa. *Albertiana* 25, 5–9.
- Lucas, S.G., Hunt, A.P., Heckert, A.B., Spielman, J.A., 2007. Global Triassic tetrapod biostratigraphy and biochronology: 2007 status. *Bulletin of the New Mexico Museum of Natural History and Science* 41, 229–240.
- Luo, Z.-X., 2007. Transformation and diversification in early mammal evolution. *Nature* 450, 1011–1019.
- Manly, B.F.J., 2007. *Randomization, Bootstrap and Monte Carlo Methods in Biology*, 3rd Edition. Chapman & Hall/CRC, Boca Raton, Florida. 455 pp.
- Martinelli, A.G., Rougier, G.W., 2007. On *Chalimnia musteloides* (Eucynodontia: Trithelodontidae) from the Late Triassic of Argentina, and a phylogeny of Ictidosauria. *Journal of Vertebrate Paleontology* 27, 442–460.
- Martinelli, A.G., Bonaparte, J.F., Schultz, C.L., Rubert, R., 2005. A new trithelodontid (Therapsida, Eucynodontia) from the Late Triassic of Rio Grande do Sul (Brazil) and its phylogenetic relationships among carnivorous non-mammalian eucynodonts. *Ameghiniana* 42, 191–208.
- Martinelli, A.G., de la Fuente, M., Abdala, F., 2009. *Diademodon tetragonus* Seeley, 1894 (Therapsida: Cynodontia) in the Triassic of South America and its biostratigraphic implications. *Journal of Vertebrate Paleontology* 29, 852–862.
- Martinez, R.N., Forster, C.A., 1996. The skull of *Probesodon sanjuanensis*, sp. nov., from the Late Triassic Ischigualasto Formation of Argentina. *Journal of Vertebrate Paleontology* 16, 285–291.
- Martinez, R.N., May, C.L., Forster, C.A., 1996. A new carnivorous cynodont from the Ischigualasto Formation (Late Triassic, Argentina), with comments on eucynodont phylogeny. *Journal of Vertebrate Paleontology* 16, 271–284.
- Melo, T.P., Soares, M.B. and Oliveira, T.V. 2009. Primeiro registro do traversodontídeo *Menadon* sp. (Flynn et al. 2000) na Biozona de Traversodontídeos da Formação Santa Maria, Triássico Médio do Rio Grande do Sul, Brasil. *Paleo 2009, Reunião Anual da Sociedade Brasileira de Paleontologia, Rio Grande do Sul*, p. 16.
- Muttoni, G., Kent, D.V., Olsen, P.E., Di Stefano, P., Lowrie, W., Bernasconi, S.M., Hernández, F.M., 2004. Tethyan magnetostratigraphy from Pizzo Mondello (Sicily) and correlation to the Late Triassic Newark astrochronological polarity time scale. *Geological Society of America Bulletin* 116, 1043–1058.
- Muttoni, G., Kent, D.V., Jadoul, F., Olsen, P.E., Rigo, M., Galli, M.T., Nicora, A., 2010. Rhaetian magneto-biostratigraphy from the Southern Alps (Italy): constraints on Triassic chronology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 285, 1–16.
- Nath, T.T., Yadagiri, P., 2007. A new mammal-like reptile (cynodont) from Upper Triassic Maleri Formation of Pranhita–Godavari Valley, Andhra Pradesh. *Journal of the Geological Society of India* 69, 57–60.
- Neveling, J., 2004. Stratigraphic and sedimentological investigation of the contact between the *Lystrosaurus* and the *Cynognathus* assemblage zones (Beaufort Group: Karoo Supergroup). *Council for Geoscience Bulletin* 137, 1–165.
- Neveling, J., Hancox, P.J., Rubidge, B.S., 2005. Biostratigraphy of the lower Burgersdorp Formation (Beaufort Group; Karoo Supergroup) of South Africa – implications for the stratigraphic ranges of early Triassic tetrapods. *Palaeontologia Africana* 41, 81–87.
- Ogg, J.G., 2004. The Triassic Period. In: Gradstein, F.M., Ogg, J.G., Smith, A.G. (Eds.), *A Geologic Time Scale 2004*. Cambridge University Press, pp. 271–306.
- Ogg, J.G., Ogg, G., Gradstein, F.M., 2008. *The Concise Geologic Time Scale*. Cambridge University Press. 177 pp.
- Oliveira, E.V., 2006. Reevaluation of *Therioherpeton carnini* Bonaparte and Barberena, 1975 (Probainognathia, Therioherpetidae) from the Upper Triassic of Brazil. *Geodiversitas* 28, 447–465.
- Oliveira, T.V., Schultz, C.L., Soares, M.B., 2007a. O esqueleto pós-craniano de *Exaeretodon riograndensis* Abdala et al. (Cynodontia, Traversodontidae), Triássico do Brasil. *Revista Brasileira de Paleontologia* 10, 79–94.
- Oliveira, T.V., Schultz, C.L., Soares, M.B., 2007b. Un nuevo cinodonte carnívoro (Eucynodontia, Probainognathia) del Triásico tardío de Brasil (Cuenca de Paraná, Formación Santa Maria, Cuenca de Rhyncosauria). 23rd Jornadas Argentinas de Paleontología de Vertebrados, Programa de Comunicaciones Científicas y Libro de Resúmenes. Trelew, Argentina, p. 10.
- Oliveira, T.V., Soares, M.B., Schultz, C.L., 2009. Um novo e peculiar cinodonte do mesotriássico sul-brasileiro (Formação Santa Maria). *Paleo 2009, Reunião Anual da Sociedade Brasileira de Paleontologia, Rio Grande do Sul*, p. 15.
- Ovtcharova, M., Bucher, H., Schaltegger, U., Galfetti, T., Brayard, A., Guex, J., 2006. New Early to Middle Triassic U–Pb ages from South China: calibration with ammonoid biochronozones and implications for the timing of Triassic biotic recovery. *Earth and Planetary Science Letters* 243, 463–475.
- Parrington, F.R., 1946. On the cranial anatomy of cynodonts. *Proceedings of the Zoological Society of London* 116, 181–197.
- Pires, E.F., Guerra-Sommer, M., Scherer, C.M.S., 2005. Late Triassic climate in southernmost Parana Basin (Brazil): evidence from dendrochronological data. *Journal of South American Earth Sciences* 18, 213–221.
- Rayfield, E.J., Barrett, P.M., McDonnell, R.A., Willis, K.J., 2005. A geographical information system (GIS) study of Triassic vertebrate biochronology. *Geological Magazine* 142, 327–354.
- Rayfield, E.J., Barrett, P.M., Milner, A.R., 2009. Utility and validity of Middle and Late Triassic ‘Land Vertebrate Faunachrons’. *Journal of Vertebrate Paleontology* 29, 80–87.
- Reichel, M., Schultz, C.L., Soares, M.B., 2009. A new traversodontid cynodont (Therapsida, Eucynodontia) from the Middle Triassic Santa Maria Formation of Rio Grande do Sul, Brazil. *Palaeontology* 52, 229–250.
- Rogers, R.R., Swisher III, C.C., Sereno, P.C., Monetta, A.M., Forster, C.A., Martinez, R.N., 1993. The Ischigualasto tetrapod assemblage (Late Triassic, Argentina) and ⁴⁰Ar/³⁹Ar dating of dinosaurs origins. *Science* 260, 794–797.
- Rogers, R.R., Arcucci, A.B., Abdala, F., Sereno, P.C., Forster, C.A., May, C.L., 2001. Paleoenvironment and taphonomy of the Chañares Formation tetrapod assemblage (Middle Triassic), north-western Argentina: spectacular preservation in volcano-genic concretions. *Palaios* 16, 461–481.
- Romer, A.S., 1969. The Chañares (Argentina) Triassic reptile fauna. V. A new chiniquodontid cynodont, *Probesodon lewisi*. *Cynodont ancestry*. *Breviora* 333, 1–24.
- Romer, A.S., 1970. The Chañares (Argentina) Triassic reptile fauna. VI. A chiniquodontid cynodont with an incipient squamosal-dentary jaw articulation. *Breviora* 344, 1–18.
- Romer, A.S., 1972. The Chañares (Argentina) Triassic reptile fauna. XVII. The Chañares gomphodonts. *Breviora* 396, 1–9.
- Rubert, R.R., Schultz, C.L., 2004. Um novo horizonte de correlação para o Triássico Superior do Rio Grande do Sul. *Pesquisas em Geociências* 31, 71–88.

- Rubidge, B.S., 2005. Re-uniting lost continents – fossil reptiles from the ancient Karoo and their wanderlust. *South African Journal of Geology* 108, 135–172.
- Rubidge, B.S., Sidor, C.A., 2001. Evolutionary patterns among Permo-Triassic therapsids. *Annual Review of Ecology and Systematics* 32, 449–480.
- Rubidge, B.S., Johnson, M.R., Kitching, J.W., Smith, R.M.H., Keyser, A.W., Groenewald, G. H., 1995. An introduction to the biozonation of the Beaufort Group. In: Rubidge, B.S. (Ed.), *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*, Biostratigraphic Serie 1. South African Committee for Stratigraphy, Pretoria, pp. 1–2.
- Satsangi, P.P., 1987. The vertebrate faunas from the Permian and the Lower Triassic Gondwana sequences of India. *Geological Survey of India Special Publication* 11, 165–178.
- Schultz, C.L., Langer, M.C., 2007. Tetrapodes triassicos do Rio Grande do Sul, Brasil. *Paleontologia: Cenários de vida* 277–290.
- Schultz, C.L., Soares, M.B., 2006. Proposta de nova denominação para a Cenozona de Ictidosauria do Triássico Superior (Formação Caturrita) do Rio Grande do Sul. V Simposio Brasileiro de Paleontologia de Vertebrados, Ciência e Natura. Universidade Federal de Santa Maria, Rio Grande do Sul, Brazil. 41 pp.
- Schultz, C.L., Scherer, C.M.S., Barberena, M.C., 2000. Biostratigraphy of southern Brazilian Middle–Upper Triassic. *Revista Brasileira de Geociências* 30, 495–498.
- Scotese, C.R., 2000. Climate history. Paleomap Project, Department of Geology, University of Texas at Arlington. Available at <http://www.scotese.com>. Accessed December 10, 2008.
- Scotese, C.R., Boucrot, A.J., Mckerrow, W.S., 1999. Gondwanan palaeogeography and palaeoclimatology. *Journal of African Earth Sciences* 28, 99–114.
- Sellwood, B.W., Valdes, P.J., 2006. Mesozoic climates: general circulation models and the rock record. *Sedimentary Geology* 190, 269–287.
- Sereno, P.C., Forster, C.A., Rogers, R.R., Monetta, A.M., 1993. Primitive dinosaur skeleton from Argentina and the early evolution of the Dinosauria. *Nature* 361, 64–66.
- Sidor, C.A., Hancox, P.J., 2006. *Elliotherium kersteni*, a new tritheledontid from the Lower Elliot Formation (Upper Triassic) of South Africa. *Journal of Paleontology* 80, 333–342.
- Sidor, C.A., Smith, R.M.H., 2004. A new galesaurid (Therapsida: Cynodontia) from the Lower Triassic of South Africa. *Palaeontology* 47, 535–556.
- Sidor, C.S., Damiani, R., Hammer, W.R., 2008a. A new Triassic temnospondyl from Antarctica and a review of Fremouw Formation biostratigraphy. *Journal of Vertebrate Paleontology* 28, 656–663.
- Sidor, C.S., Miller, M.F., Isbell, J.L., 2008b. Tetrapod burrows from the Triassic of Antarctica. *Journal of Vertebrate Paleontology* 28, 277–284.
- Silva, R., Bardoni, R., Godoy, M., Binotto, R., 2009. Pegadas de um grande dinossauro terópode no sítio Linha São Luiz (Faxinal do Soturno, Rio Grande do Sul) e implicações sobre a idade da Formação Caturrita. *Paleo 2009, Reunião Anual da Sociedade Brasileira de Paleontologia*, Rio Grande do Sul, pp. 21–22.
- Smith, R.M.H., Botha-Brink, J., 2009. Burrowing as a survival strategy in the earliest Triassic Karoo Basin, South Africa. *Journal of Vertebrate Paleontology* 29, 183A.
- Smith, R.M.H., Swart, R., 2002. Changing fluvial environments and vertebrate taphonomy in response to climatic drying in a Mid-Triassic rift valley fill: the Omingonde Formation (Karoo Supergroup) of central Namibia. *Palaios* 17, 249–267.
- Smith, A.G., Smith, D.G., Funnell, B.M., 1994. *Atlas of Mesozoic and Cenozoic coastlines*. Cambridge University Press. 99 pp.
- Soares, M.B., Abdala, F., 2008. The first record of *Probainognathus* Romer, 1970 (Therapsida, Cynodontia) in the Triassic of Rio Grande do Sul, Brazil. *Paleontologia em Destaque* 23, Boletim de Resumos VI Simpósio Brasileiro de Paleontologia de Vertebrados, Ribeirão Preto, pp. 189–190.
- Stipanovic, P.N. and Marsicano, C.A., 2002. Léxico estratigráfico de la Argentina, Volumen VIII. Triásico. Asociación Geológica Argentina, Serie “B” (Didáctica y Complementaria) 26, 370 pp.
- Stipanovic, P.N., González Díaz, E., Zavattieri, A.M., 2007. Grupo Puesto Viejo *nom. transl.* por Formación Puesto Viejo González Díaz, 1964, 1967: nuevas interpretaciones paleontológicas, estratigráficas y cronológicas. *Ameghiniana* 44, 759–761.
- Teixeira, A.M.S., 1982. Um novo cinodonte carnívoro (*Probesodon kitchingi*, sp. nov.) do Triássico do Rio Grande do Sul, Brasil. *Comunicações do Museu de Ciências PUCRS* 24, 1–31.
- Tiffney, B.H., 1997. Land plants as food habitat in the age of dinosaurs. In: Farlow, J.O., Brett-Surman, M.K. (Eds.), *The Complete Dinosaur*. Indiana University Press, pp. 352–370.
- Traverse, A., 2008. *Paleopalynology*, Second Edition. Springer, Dordrecht. 813 pp.
- Twichett, R.J., 2007. The Lilliput effect in the aftermath of the end-Permian extinction event. *Palaeogeography, Palaeoclimatology, Palaeoecology* 252, 132–144.
- Van Heerden, J., 1988. Distribution and synonymy of the cynodont reptile, *Thrinaxodon liorhinus*. *South African Journal of Science* 84, 130–131.
- von Huene, F., 1928. Ein Cynodontier aus des Trias Brasilien. *Centralblatt für Mineralogie, Geologie und Paläontologie* 1928B, 251–270.
- von Huene, F., 1936. Die fossilen Reptilien des südamerikanischen Gondwanalandes. *Ergebnisse der Sauriergrabungen in Südbrasilien 1928–29: Lieferung 2*. Verlag Franz F. Heine, Tübingen, 93–159.
- Weide, D.M., Sidor, C.A., Angielczyk, K.D., Smith, R.M.H., 2009. A new record of *Procyonuchus delaharpeae* (Therapsida, Cynodontia) from the Upper Permian Usili Formation, Tanzania. *Palaeontologia Africana* 44, 21–26.
- Willis, K.J., McElwain, J.C., 2002. *The Evolution of Plants*. Oxford University Press. 378 pp.
- Wing, S.L., Sues, H.-D., 1992. Mesozoic and Early Cenozoic terrestrial ecosystems. In: Behrensmeier, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.-D., Wings, S.L. (Eds.), *Terrestrial Ecosystem through Time. Evolutionary Paleocology of Terrestrial Plants and Animals*. University Chicago Press, pp. 327–416.
- Woods, A.D., 2005. Paleoclimatographic and paleoclimatic context of Early Triassic time. *Compte Rendus Palevol* 4, 463–472.
- Wopfner, H., 2002. Tectonic and climatic events controlling deposition in Tanzanian Karoo basins. *Journal of African Earth Sciences* 34, 167–177.