

A new traversodontid cynodont from the Santa Maria Formation (Ladinian-Carnian) of southern Brazil, with a phylogenetic analysis of Gondwanan traversodontids

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The Traversodontidae is a Triassic family of nonmammalian cynodonts, recorded worldwide, characterized by its bucco-lingually expanded postcanines. A recently discovered fauna in the locality of Santa Cruz do Sul, corresponding to the Santa Maria Formation of the Brazilian Middle/Upper Triassic (Ladinian/Carnian), is made up exclusively of nonmammalian cynodonts with an abundance of traversodontids. A new taxon, *Santaacruzodon hopsoni* gen. et sp. nov., the most commonly recorded traversodontid cynodont in the fauna, is described here. It is diagnosed by an autapomorphy, a very large posterolabial cusp in the upper postcanine, representing more than half of the labial crest, and a suite of traits present in other traversodontids. Among these features are the descendent flange of the jugal developed as a ball-shaped projection, also known in the Madagascan traversodontid *Dadadon isaloi*, and the presence of symmetrical incisors with numerous mesial and distal marginal cuspules, feature shared with the North American taxon *Arctotraversodon plemmyridon*. A phylogenetic analysis of traversodontids from Gondwana, based on a data matrix of 28 characters (mostly dental) and 15 terminals (13 traversodontids, including the new species, plus *Diademodon* and *Trirachodon*) was performed. The new traversodontid appears as the sister taxon of *Dadadon*. A monophyletic Carnian group composed of *Exaeretodon*, *Menadon* and *Scalenodontoides*, with the Carnian *Gomphodontosuchus*, and the Ladinian *Massetognathus* as successive outgroups is also supported. In line with a recent phylogenetic hypothesis, a nonmonophyletic relationship for *Scalenodon* 'species' from the Anisian Manda beds also results from our analysis. Based on the cladogram obtained, morphological trends of change in the dentition of traversodontids throughout the Triassic are suggested. © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2003, 139, 529–545.

ADDITIONAL KEYWORDS: dental evolution – Gondwana – Middle/Upper Triassic – phylogeny – Traversodontidae.

INTRODUCTION

Traversodontid cynodonts have proven to be one of the most diverse and dominant groups in South American Triassic faunas. Huene (1928, 1936) first documented the family in southern Brazil, describing three species, including the enigmatic *Gomphodontosuchus brasiliensis* Huene, 1928. The family has a long stratigraphic history in Argentina, with four distinct faunas

ranging from the Late Scythian-Early Anisian to the Carnian (Abdala, 2000). Eight to nine different species, some of them dominant (e.g. *Massetognathus pascuali* Romer, 1967 in the Chañares Formation; Rogers *et al.*, 2001), represent the vast diversity of the traversodontids in South America. This diversity is also paralleled worldwide with at least five species in eastern and southern Africa (Crompton, 1972; Kemp, 1980; Gow & Hancox, 1993), two recently described from Madagascar (Flynn *et al.*, 2000), one in India (Chatterjee, 1982), three in North America (Hopson, 1984; Sues & Olsen, 1990; Sues, Hopson & Shubin, 1992; Sues, Olsen & Kroehler 1994; Sues, Olsen & Carter,

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1999) and possibly four or five in Europe (Tatarinov, 1973; Hahn, Lepage & Wouters, 1988; Godefroit & Battail, 1997).

Traversodontids thus constitute a hallmark of many Triassic faunas, and their success in Triassic ecosystems may be credited to the system of crown-to-crown postcanine occlusion (Crompton, 1972; Hopson, 1984), predating the precise bilateral occlusion later developed by mammals. Members of the Family Traversodontidae show differences in cranial, dental, and even postcranial morphology. Thus, *Pascualgnathus* of the Late Scythian-Early Anisian of Argentina, displays a hypertrophied canine and, consequently, a paracanine fossa perforating the muzzle dorsally (Bonaparte, 1966). However, canines in the Ladinian *Massetognathus* of Argentina and Brazil (Romer, 1967; Barberena, 1981a) are small. Notable differences among traversodontids in the postcranial skeleton are the presence/absence of costal plates and the morphology of the iliac plate (Jenkins, 1970).

The Brazilian Triassic has provided further contributions to the South American traversodontid record. The recently discovered fauna of Santa Cruz do Sul, preliminarily reported by Abdala, Ribeiro & Schultz (2001), documented only nonmammalian cynodonts (henceforth referred to as cynodonts). Traversodontid cynodonts are diversely represented in this fauna, with four different types (three of them previously unrecorded) that differ mainly in postcanine morphology. In addition, a few remains of chiniquodontid cynodonts have also been recovered. We present here a comparative description of a new species of a traversodontid cynodont from the Santa Cruz do Sul fauna. With the aim of exploring the interrelationships of the new species with remaining traversodontid cynodonts, we compiled a character data matrix considering mostly dental, but also some cranio-mandibular, characters. The analysis is also useful for suggesting morphological trends in the development of traversodontid dentitions.

INSTITUTIONAL ABBREVIATIONS

BMNH	Natural History Museum, London
BP	Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg
BS	Bayerische Staatssammlung für Paläontologie und historische Geologie, München
FMNH	Field Museum of Natural History, Chicago
GPIT	Institut und Museum für Geologie und Paläontologie der Universität Tübingen
HMN	Humboldt Museum für Naturkunde, Berlin
MACN	Museo Argentino de Ciencias Naturales, Buenos Aires

MCN-PV	Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil
MCP-PV	Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MLP	Museo de La Plata, Argentina
OUMNH	Oxford University Museum of Natural History
PULR	Museo de Antropología, Universidad Nacional de La Rioja, Argentina
PV	Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil
PVL	Colección Palaeontología de Vertebrados Lillo, Universidad Nacional de Tucumán, Argentina
PVSJ	Museo de Ciencias Naturales, Universidad Nacional de San Juan, Argentina
SAM	South African Museum, Cape Town
UA	University of Antananarivo, Madagascar

SYSTEMATIC PALAEONTOLOGY

SYNAPSIDA EUCYNODONTIA TRAVERSODONTIDAE *SANTACRUZODON HOPSONI* GEN. ET SP. NOV.

Holotype. MCN PV 2768: fragmentary skull with lower jaws (Fig. 1).

Referred specimens. MCN PV 2751, MCN PV 2752 (Fig. 2B,C), MCP 4044 PV: three lower jaws; MCN PV 2770: incomplete maxilla with postcanines (Fig. 2A); MCP 4034 PV: fragmentary skull and lower jaw with postcanines.

Age. The Santa Cruz do Sul cynodonts most closely resemble predominantly Carnian forms such as *Exaeretodon*, and Ladinian forms such as *Massetognathus*; thus a Late Ladinian age is assumed for the Santa Cruz do Sul Fauna of the Santa Maria Formation (Abdala *et al.*, 2001).

Etymology. Named after the city of Santa Cruz do Sul, where the new species was discovered, plus *don* (tooth; Greek) and *hopsoni* in honour of Dr James A. Hopson, in recognition of his vast contribution to our knowledge of nonmammalian therapsids.

Diagnosis. *Santacruzodon hopsoni* exhibits a combination of features observed in other traversodontid cynodonts and an autapomorphy. It features a ball-shaped ventrally projecting suborbital process such as occurs in *Dadadon isaloi* Flynn *et al.*, 2000; the incisors are flattened bucco-lingually as in *Massetognathus pascuali*, but showing a series of 7–9 marginal cuspules as in *Arctotraversodon plemmyridon* (Hopson, 1984); the upper postcanines present an

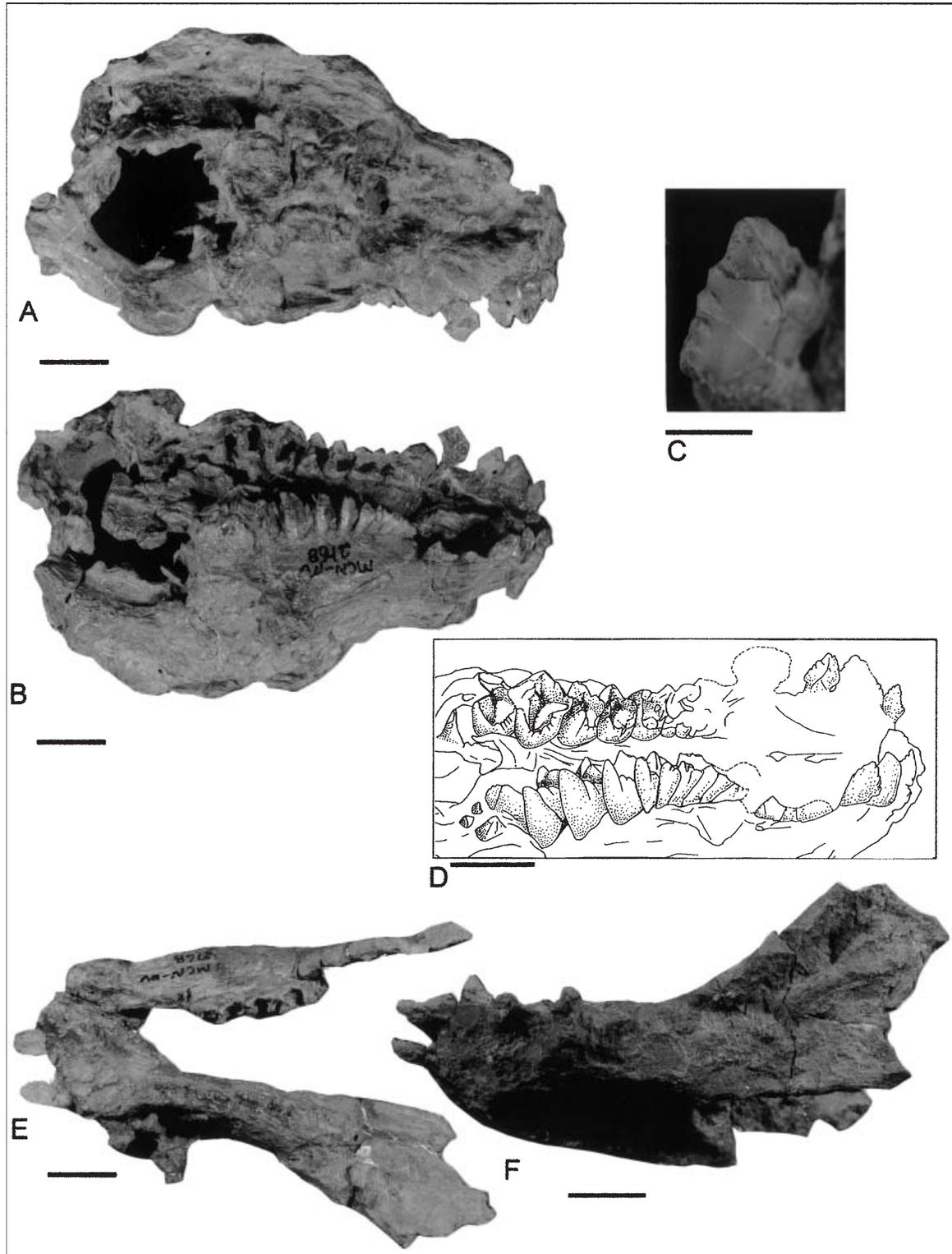


Figure 1. *Santacruzodon hopsoni* gen et sp. nov. Holotype (MCN PV 2768). Skull in (A) latero-dorsal, (B) latero-ventral views. (C) Close-up showing the upper incisor structure. (D) Drawing of the upper dentition; Lower jaw in (E) dorsal, (F) lateral views. Scale bars: A, B, D, E, F = 10 mm; C = 2 mm.

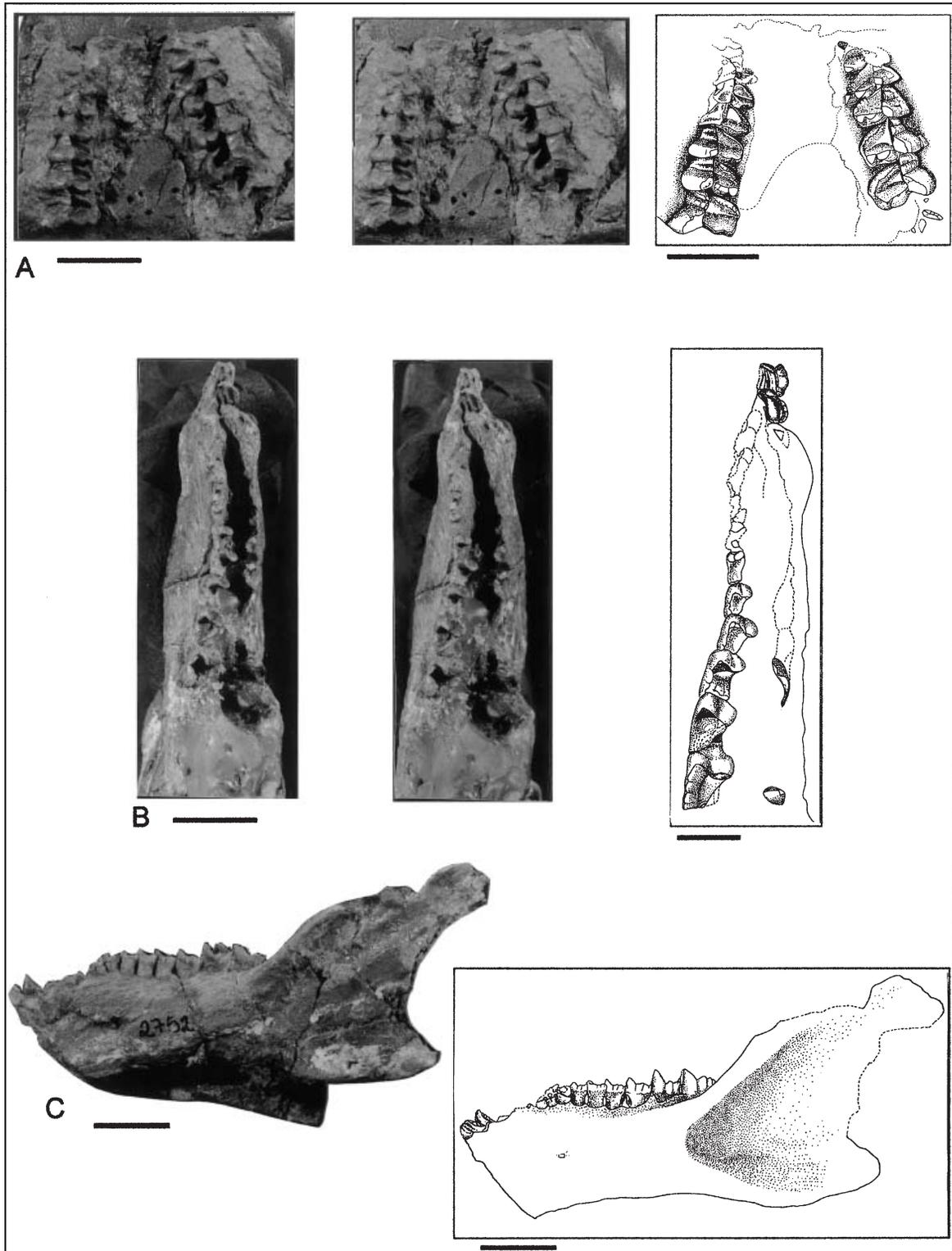


Figure 2. *Santacruzodon hopsoni* gen et sp. nov. (A) Stereopair of upper postcanine series (MCN PV 2770) in occlusal view; Lower jaw (MCN PV 2752) in (B) dorsal (stereopair) and (C) lateral views. Scale bars = 10 mm.

anterior small crest conformed by a series of cingular cusps as in '*Scalenodon*' *attridgei* Crompton, 1972. As in many other cynodonts (e.g. *Massetognathus*, *Exaeretodon*), *S. hopsoni* features three labial cusps in the upper postcanines, but showing as autapomorphy the posterior cusp very large, representing more than half the length of the labial crest.

Description. Most of the material is poorly preserved, providing little information on bone sutures. The skull fragment of the holotype includes the rostrum and orbital region, but lacks the temporal portion (Fig. 1A). Measurements of the specimen are presented in Table 1. The estimated skull length of this specimen is 80 mm. The rostrum is crushed dorsoventrally, without preservation of the dorsal surface, but with remnants of the ascending process of the premaxilla. A distinctive feature of the skull is a rounded, ventrally well-projected suborbital process of the jugal (Fig. 1A). A platform of the maxilla is present lateral to the postcanine series (Figs 1B, 2A).

There are four arrowhead-shaped upper incisors, flattened labio-lingually with 9–11 marginal cusps (Fig. 1B, C). The external aspect of the incisor is flat, whereas the internal face is more convex. A diastema is present between incisors and canine. The canine is

poorly preserved, but seems to have been small in size. There is no diastema between the canine and postcanines. The postcanines are morphologically heterogeneous and vary from seven to ten in number on the different specimens (Fig. 1B). The anterior teeth are mostly triangular in occlusal outline, whereas the posterior ones become more enlarged bucco-lingually (Figs 2A, 3A). These last teeth are proportionally more developed anteroposteriorly than in other traversodontids and present a deep occlusal basin. The labial crest shows three cusps, the large posterior one representing more than half the length of the crest (Fig. 3A). The posterior transverse crest bears three cusps, with the lingual and middle ones positioned very close together and with a basin separating them from the labial cusp (Fig. 3A). In addition, there is an anterior cingular crest less developed in height than the posterior crest, formed by a series of cingular cusps (at least eight or nine; Fig. 3A).

The lower jaws present a shallow mandibular ramus with a fused symphysis (Figs 1E, 1F, 2C). The masseteric fossa extends anteriorly to the level of postcanine 7 to 9; the last two postcanines are covered laterally by the ascending coronoid process.

Three procumbent and labio-lingually flattened lower incisors are present, each with 11 marginal cusps. These teeth are larger than the upper incisors,

Table 1. Skull and dentition measurements of *Santacruzodon hopsoni* gen et sp. nov. (in mm)

	MCN PV 2768 (Holotype)	MCN PV 2752
Rostrum	49.6	
Orbital region	24.5	
Orbital diameter	22.4	
2nd upper incisor length	4.1	
4th upper incisor length	3.6	
Upper canine length	5.3	
Upper postcanine length	29.2	
1st upper postcanine length	2.1	
1st upper postcanine width	2.2	
Last upper postcanine length	3.9	
Last upper postcanine width	5.4	
Height of the preserved portion of the ascendant ramus of the mandible	28.2	32.1
Mandibular length (incomplete)		69.2
Length from the tip of the mandible to the angle	65.1	60.3
2nd lower incisor length	4	2.9
Lower canine length	74.4	
Lower postcanine length	27.6	25.5
Last lower postcanine length	5.6	5.3
Last lower postcanine width	4.0	3.8

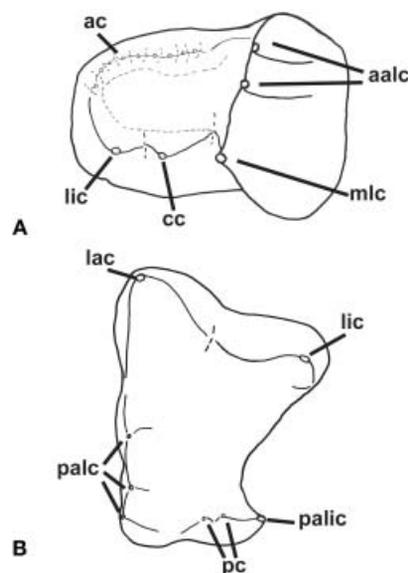


Figure 3. *Santacruzodon hopsoni* gen et sp. nov. (A) Upper postcanine in occlusal view. Labial, right; anterior top. (B) Lower postcanine in occlusal view. Labial, left; anterior, top. **Abbreviations:** aalc, anterior accessory labial cusps; ac, anterior cingular crest; cc, central cusp; lac, labial cusp; lic, lingual cusp; mlc, main labial cusp; palc, posterior accessory labial cusps; palic, posterior accessory lingual cusp; pc, posterior cingular crest.

and spoon-shaped, being convex labially, whereas its lingual face is remarkably concave (Figs 1E, 2B, 2C). A wide vertical ridge separating two shallow depressions is present on the lingual face of the lower incisors. The canine is relatively small and there is a short diastema between the canine and the first postcanine. There are 9–10/11 lower postcanines, with the anterior transverse crest formed by two cusps: the higher labial cusp lies slightly anterior to the wider lingual cusp (Fig. 3B). In addition, the postcanines feature a labial crest with 2–3 cusps following the main anterior one (Fig. 3B), and a posterior cingular crest being, in some cases, as high as the anterior transverse crest.

Comparison. *Santacruzodon hopsoni* resembles the Madagascan traversodontid *Dadadon isaloi* (Flynn *et al.*, 2000) in the rounded suborbital process, and the differentiation between the triangular occlusal outline of the anterior and the more rectangular posterior upper postcanines (a feature also recorded in *Gomphodontosuchus*; Hopson, 1985: fig. 3). The high number of postcanines, the overall structure of the upper posterior postcanines, including a slightly developed shouldering are also seen in *Dadadon* and the South American Ladinian *Massetognathus*. Other similarities (i.e. the presence of three cusps in the posterior transverse crest of the upper postcanines, and the close spacing of the central and the lingual cusps) shared by *Santacruzodon*, *Dadadon* and *Massetognathus* are plesiomorphies, also occurring in more basal traversodontids (see Phylogenetic analysis below). A synapomorphy shared by *Santacruzodon*, *Massetognathus* and other late traversodontids is the presence of three cusps in the sectorial labial border of the upper postcanines (*Dadadon* shows two cusps instead). As in many late traversodontids (i.e. *Dadadon* and *Massetognathus*), *Santacruzodon* features a remarkably enlarged postero-external upper cusp. The incisors of *Santacruzodon*, are flattened buccolingually, as in *Massetognathus*, but overall incisor morphology more closely matches that of *Arctotraversodon plemmyridon* of Nova Scotia, Canada (Sues *et al.*, 1992; = ?*Scalenodontoides plemmyridon* of Hopson, 1984), also showing cuspules along their edges.

PHYLOGENETIC ANALYSIS

A data matrix with 28 cranio-dental characters and 15 taxa, including *Diademodon* (used for rooting the cladograms), *Trirachodon* and 13 traversodontids was assembled (Appendix 3). Most characters scored in the data matrix were examined first-hand on material housed at the institutions mentioned above (see Appendix 1 for the list of material). In addition, the following references were consulted for each taxon: *Diademodon* (Seeley, 1894; Broili & Schröder, 1935a;

Brink, 1955; Hopson, 1971), *Trirachodon* (Seeley, 1895; Broili & Schröder, 1935b); *Scalenodon* (Crompton, 1955, 1972); *Luangwa* (Brink, 1963; Kemp, 1980); *Scalenodontoides* (Crompton & Ellenberger, 1957; Hopson, 1984; Gow & Hancox, 1993); *Massetognathus* (Romer, 1967, 1972; Crompton, 1972; Abdala & Giannini, 2000); *Exaeretodon* (Bonaparte, 1962; Chatterjee, 1982; Hopson, 1984, 1985; Abdala, Barberena & Dornelles, 2002); *Gomphodontosuchus* (Huene, 1928; 1936; Hopson, 1985); *Traversodon* (Huene, 1936; Barberena, 1974, 1981b); *Andescynodon* (Bonaparte, 1969; Goñi, 1986; Goñi & Goin, 1988); *Pascualgnathus* (Bonaparte, 1966); *Menadon* and *Dadadon* (Flynn *et al.*, 2000).

Some caution should be introduced to our analysis and its resulting cladograms. The data matrix is focused on dental characters (21 features vs. seven of cranium and mandible; see list of characters in Appendix 2), because teeth provide most of the information in *Santacruzodon*. Characters of postcranium or even of the cranium/mandible, which might influence hypotheses of relationship in the group, fell outside the scope of this analysis. No less important are some aspects related to topographic identity in gomphodont postcanine teeth that make primary homology assessment difficult (De Pinna, 1991; Hawkins, 2000). Gomphodont cynodonts (a group that includes diademodontids, trirachodontids and traversodontids; Diademodontidae *sensu* Hopson & Kitching, 1972) show transversely enlarged teeth, with occlusion between the upper and lower postcanines. The homology of the tooth portions in these three groups, however, is not easy to assess. The sectorial border of the postcanines in *Diademodon* seems to be homologous with the sectorial postcanines of nongomphodont cynodonts, such as galesaurids and chiniquodontids (Broom, 1919; Abdala & Giannini, 2002). This implies that the enlarged medial portion of the postcanine in *Diademodon* would be the result of the expansion of the lingual cingulum, and thus, that entire portion would be a new structure (Fig. 4A). The same explanation was proposed for the origin of the traversodontid tooth in *Andescynodon*, starting from a sectorial tooth and passing through an intermediate condition represented by *Cromptodon* (Fig. 4B), a cynodont with sectorial teeth with a wide lingual cingulum (Goñi & Goin, 1987). On the other hand, *Trirachodon* complicates this scenario inasmuch as its transversely enlarged lower postcanines seem to result from the rotation of the posterior sectorial tooth of the series. Thus, the last teeth of the lower postcanine series remain with their cusps aligned longitudinally, whereas the anterior postcanines rotate so that the sectorial cusps became transversely aligned (Rowe, 1986: fig. 27; SAM K171; Fig. 4C). This indicates that two hypotheses of primary homology are possible to

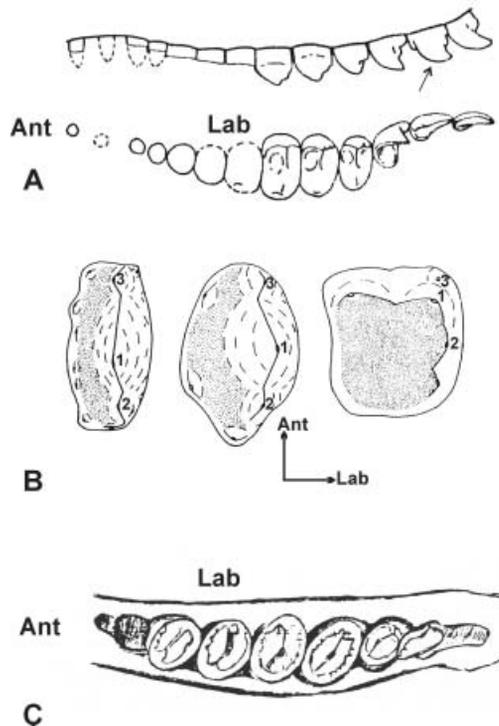


Figure 4. (A) Upper postcanine series of *Diademodon* in labial (above) and occlusal (below) views. Arrow indicates sectorial tooth. (B) Lower postcanine of *Thrinaxodon* (left), *Cromptodon* (middle) and *Andescynodon* (right). (C) Lower postcanine series in *Trirachodon*. (A) after Hopson (1971); (B) after Goñi & Goin (1987); (C) after Rowe (1986). Numbers: 1, main cusp; 2, posterior accessory cusp; 3, anterior accessory cusp.

account for gomphodont teeth. We apply the first here; a more exhaustive analysis than is possible here would be necessary to address this issue more completely.

There is currently an intense debate centred on the monophyly of Traversodontidae and, in a wider context, of gomphodont cynodonts (Sues, 1985; Hopson & Barghusen, 1986; Rowe, 1986, 1988, 1993; Battail, 1991; Hopson, 1991, 1994; Wible, 1991; Hopson & Kitching, 2001). In this study, Traversodontidae is considered monophyletic, following the results of cladistic analyses of eucynodonts (Abdala, 1996) and of nonmammalian cynodonts (F. Abdala, unpubl. data). In both analyses, Tritylodontidae is not closely related with Traversodontidae (as proposed by Sues, 1985; Hopson, 1991, 1994; more recently Hopson & Kitching, 2001), and a close relationship between Tritylodontidae and Mammaliaformes appears strongly supported instead (as advanced by Kemp, 1983; Rowe, 1988, 1993 and Wible, 1991, among others).

Two main objectives are pursued with the phylogenetic analysis presented here: the first is to identify the relationships of *Santacruzodon hopsoni* among

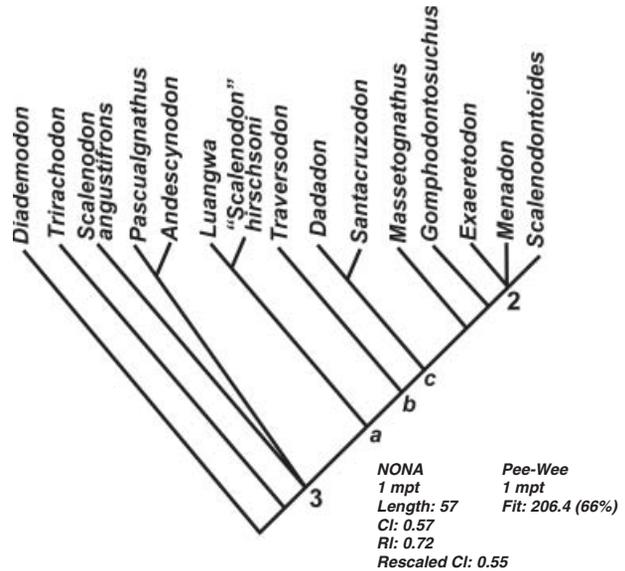


Figure 5. Cladogram based on parsimony analyses on data matrix in Appendix 3. Numbers indicate branch support for the nodes. Letters used to name nodes.

other Gondwanan traversodontids; the second is to examine the patterns of transformation experienced by the dentition of traversodontid cynodonts during the Triassic.

Cladistic analyses were performed with NONA and Pee-Wee (Goloboff, 1993a). The first searches for trees that minimize steps according to prior weights defined by the user (all characters having equal weights in our runs). The second performs cladistic analysis under implied weights, considering the fit of the characters as a concave function of the homoplasy, which resolves conflict between characters in favour of those that have less homoplasy on the trees, implying that the average weight for the character is as high as possible (Goloboff, 1993b).

For tree searching, the option 'mswap+' was used in both programs. This command, a multiple swapper, produces an exact solution, clipping a tree of T taxa at T-3 points (Goloboff, 1993a). The runs were performed with the 'ambiguous-' option that collapses nodes with ambiguous support. This is why some groups may appear as polytomous even when the analysis results in a single most parsimonious tree. Three multistate characters (6, 16 and 25) were treated as additive and one (10) as nonadditive. Statistics and topology of the tree obtained are depicted in Figure 5.

PHYLOGENETIC INTERRELATIONSHIPS OF TRAVERSODONTID CYNODONTS

One most parsimonious tree (MPT) was obtained with both programs. The cladogram with the branch

support of the nodes is shown in Figure 5. The best-supported monophyletic groups are Traversodontidae and the clade [*Menadon*, *Scalenodontoides*, *Exaeretodon*]. Bremer support (i.e. extra steps required to collapse a branch in the consensus tree of near-most-parsimonious trees; Bremer, 1994) for traversodontids is three steps, while for the clade [*Menadon*, *Scalenodontoides*, *Exaeretodon*] it is two steps. The remaining clades collapse with one extra step (Fig. 5). These low values of branch support imply that monophyletic groups presented here should be considered with some caution.

In the MPT (Figs 5, 6; see Appendix 4 for synapomorphies), *Scalenodon angustifrons* (Parrington, 1946) and a clade including *Pascualgnathus* and *Andescynodon* represent the most basal traversodontids. This is followed by a monophyletic group comprising *Luangwa* and '*Scalenodon*' *hirschsoni*, and a later clade including the Ladinian/Carnian traversodont-

tids. Among the Ladinian/Carnian forms, *Traversodon* is the most basal member and *Dadadon* and *Santacruzodon* form a monophyletic group. Finally, a clade formed by *Scalenodontoides*, *Exaeretodon* and *Menadon* is present, followed by *Gomphodontosuchus* and *Massetognathus* as successive outgroups in relation to that clade.

'*Scalenodon*' *hirschsoni* and *Traversodon* are the more ambiguous taxa in character distribution. In the former taxon, features of incisor/canine ally it to the *Gomphodontosuchus*[*Menadon*, *Scalenodontoides*, *Exaeretodon*] clade (which is supported by many characters of the anterior dentition), whereas the presence of the cingular cusp in advance of the transverse crest in the lower postcanines is a condition shared only with basal traversodontids such as *S. angustifrons*, *Luangwa* and *Andescynodon*. *Traversodon* shares three synapomorphies with late (Ladinian/Carnian) traversodontids: three cusps in the

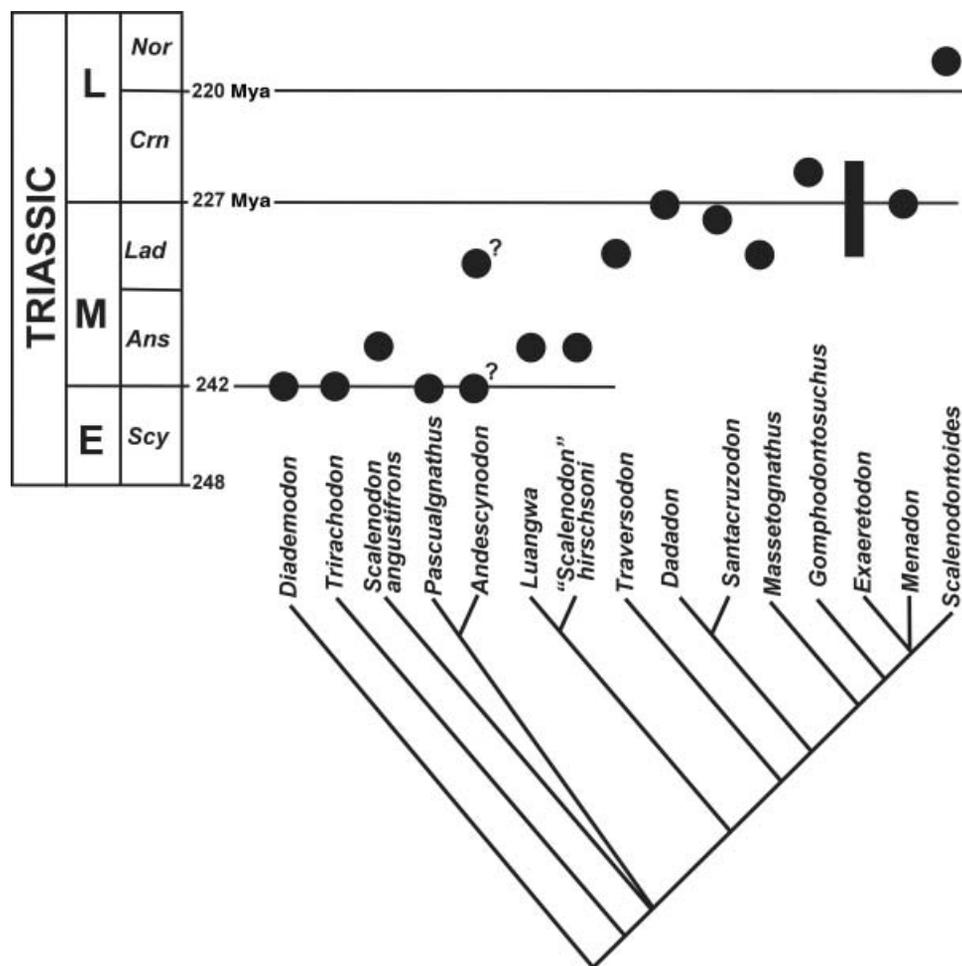


Figure 6. MPT obtained and temporal distribution of the taxa. Abbreviations: Scy, Scythian; Ans, Anisian; Lad, Ladinian; Crn, Carnian; Nor, Norian. Different ages were proposed for the Rio Mendoza Formation where *Andescynodon* was found (see Abdala, 2000). Time-scale based on Gradstein & Ogg (1996).

sectorial border of the upper postcanines; the inclination of the last upper postcanines in relation to the longitudinal axis of the skull; and the absence of a cingular cusp anterior to the transverse crest on the lower postcanines. Sympleisomorphies shared with basal traversodontids are the absence of shouldering in the upper postcanines; the presence of a posterior cingulum in the upper postcanines; and the labial cusp lower than the lingual cusp in the lower postcanines.

The phylogeny depicted here is congruent with Hopson's (1984, 1985) hypothesis of a close relationship between *Exaeretodon* and *Scalenodontoides*, with *Gomphodontosuchus* as the plesiomorphic out-group (Fig. 7A). A traversodontid phylogeny based on upper postcanine features and a large number of taxa, albeit hand-generated, was published by Godefroit & Battail (1997). Differences between that study and ours include a more basal placement of *Traversodon* and a more deeply nested position for *Scalenodon* (Fig. 7B), although there is no indica-

tion of which species of *Scaledon* they consider in their hypothesis. Our analysis is consistent with the cladogram by Flynn *et al.* (2000) with respect to the phylogenetic position of *Menadon* (Fig. 7C), although we cannot support a sister-group relationship between *Scalenodontoides* and *Exaeretodon*, and *Dadadon* seems to diverge earlier than suggested by these authors (Flynn *et al.*, 2000: 426). In a recent phylogenetic analysis of nonmammalian cynodonts, Hopson & Kitching (2001) included seven traversodontid taxa (Fig. 7D). Differences with our phylogeny include: (1) *Pascualgnathus* is among the most basal 'traversodontids' (we have identified no single earliest diverging form); (2) *Massetognathus* appears as more plesiomorphic than '*S.* *hirschsoni*'. Certainly, a major difference in Hopson & Kitching's (2001) hypothesis is the paraphyletic nature of traversodontids, with '*S.* *hirschsoni*' as a sister taxon of Tritylodontidae (see above), whereas in our cladogram '*S.* *hirschsoni*' forms a monophyletic group with *Luangwa*.

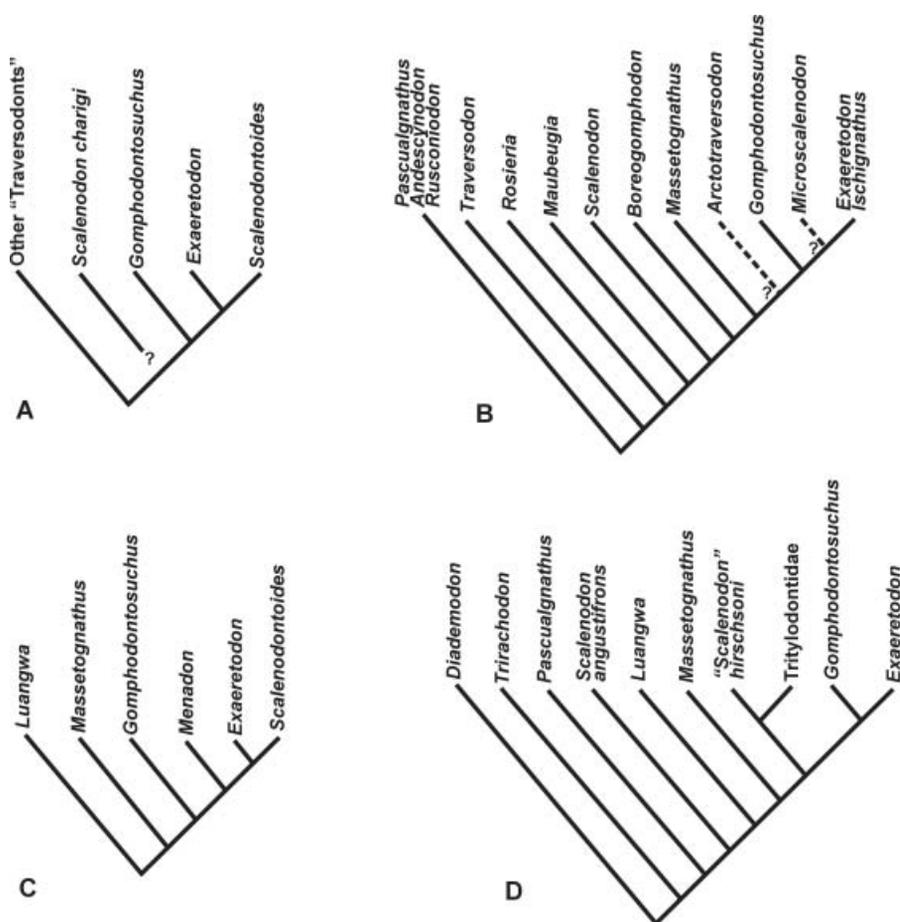


Figure 7. Previous phylogenetic hypotheses on traversodontid interrelationships. (A) after Hopson (1985); (B) after Godefroit & Battail (1997); (C) after Flynn *et al.* (2000); (D) after Hopson & Kitching (2001). Dashed lines and question marks indicate uncertain relationships.

PATTERN OF CHANGES IN TRAVERSODONTID DENTITION

The resulting cladogram is employed here as a framework to discuss several aspects of morphological changes in the dentition of traversodontids throughout the Triassic.

The presence of three enlarged upper incisors is a synapomorphy shared by *Exaeretodon*, *Scalenodontoides* and *Menadon* and acquired convergently by '*S.*' *hirschsoni*, a species that is also distinguished by the presence of two lower incisors, an autapomorphy among traversodontids. Two lower incisors are also present in some probainognathian cynodonts (such as *Aleodon brachyramphus* Crompton, 1955), some tritheledontids, and tritylodontids (Hopson & Kitching, 2001). *Pascualgnathus* also has three upper incisors, but they are small and widely separated. The paracanine fossa in relation to the upper canine changes from an anteromedial position, widely distributed among traversodontids (and in other sectorial-toothed cynodonts), to a medial position in *Massetognathus* and *Gomphodontosuchus* and to a posteromedial position in *Exaeretodon* and *Scalenodontoides* (Fig. 8). This migration may be related to the absence of a diastema between the incisors and canines in taxa having the fossa medial and posteromedial to the

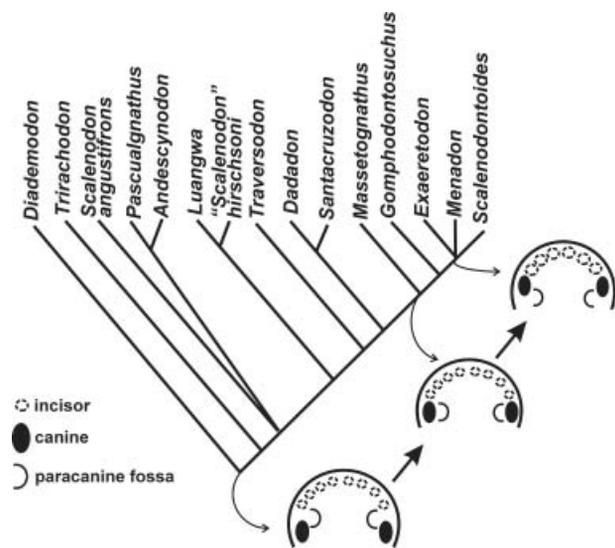


Figure 8. Changing pattern in the anterior dentition of traversodontids. The basal condition (widely distributed among cynodonts) is the presence of four upper incisors, a diastema between the last incisor and the canine, and the antero-medial location of the paracanine fossa with respect to the canine; an intermediate condition is the loss of diastema and the medial location of the paracanine fossa; the derived pattern is represented by three large incisors, and a posteromedial paracanine fossa. See text for more details.

upper canine. The changes in position in the last two genera also seem connected to the remarkably small size of the lower canine (J. A. Hopson, pers. comm.), the reduced number of upper incisors, and the remarkable degree of procumbency of the lower incisors.

Typical features of traversodontid postcanines include the outlines of the upper and lower postcanines in crown view, and the development of the transverse and sectorial crests. All traversodontids have roughly rectangular upper postcanines and quadrate lowers in occlusal view (Fig. 9). Both morphologies are clearly distinct from the oval upper and circular lower postcanines of *Diademodon* and the more ellipsoid teeth of *Trirachodon* and *Cricodon*. Apparently more susceptible to modification, the upper postcanines show a triangular occlusal outline in the Carnian-aged *Boreogomphodon*, and in the anterior postcanines of *Dadadon*, *Gomphodontosuchus* and *Santacruzodon*. Recently erupted postcanines in *Exaeretodon* are also roughly triangular in occlusal view, but become more rectangular with wear (Abdala *et al.*, 2002).

The transverse crest is one of the typical characters present on both upper and lower postcanines of traversodontids. The way in which it develops in upper and lower postcanines differs, however. Its anterior position on the lower postcanines is a synapomorphy that clearly diagnoses Traversodontidae (Fig. 9). In addi-

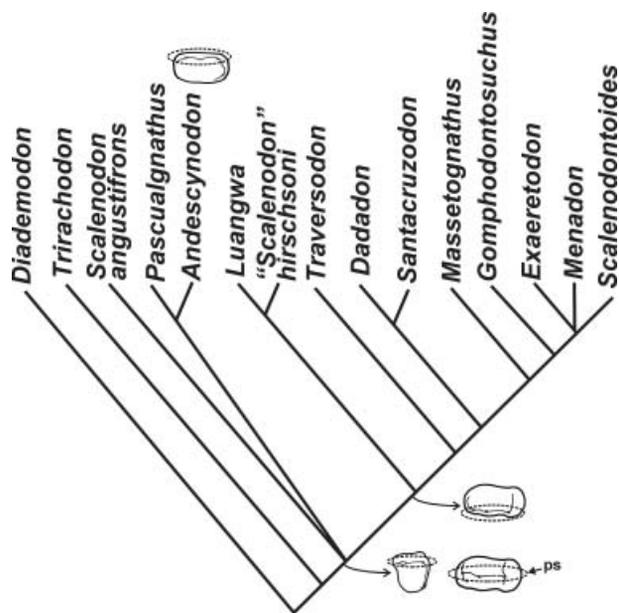


Figure 9. Changing pattern in the postcanines of traversodontids. The central position of the transverse crest in the upper postcanines (arrow, ps) is plesiomorphic for Traversodontidae because it is also present in *Trirachodon* and *Diademodon*. The anterior position of the transverse crest is an autapomorphy of *Andescynodon*. See text for more details.

tion, the crest of most traversodontids is formed by two cusps. The only exceptions are *Boreogomphodon* (Sues *et al.*, 1994), an undescribed lower postcanine from Germany (Sues *et al.*, 1992) and, with caution, *Arctotraversodon* (see Hopson, 1984: 196), with three cusps (see below). Its position on the upper postcanines is less conservative. A central placement, the plesiomorphic condition, occurs in older traversodontids such as *Pascualgnathus* (Late Scythian/Early Anisian; Fig. 10A) and *S. angustifrons* (Anisian; Fig. 10B). *Andescynodon* (probably Late Scythian/Early Anisian) is the only traversodontid with the upper transverse crest located anteriorly (Fig. 9). Remaining traversodontids, ranging from the Anisian to the Carnian, show it in a posterior (or near-posterior) position as a synapomorphy (Fig. 9). In the upper postcanine, most traversodontids show three cusps (in all cases, the central cusp being closer to the lingual one). Two cusps, however, occur in *Pascualgnathus* and *Andescynodon* and in the clade composed of *Scalenodontoides*, *Exaeretodon* and *Menadon*.

Shouldering of the upper postcanines – the anterolabial border of the upper postcanine extending forward, and producing a ‘shoulder’-like process on the preceding tooth (see Romer, 1967) – appears in Ladinian forms such as *Massetognathus* (Fig. 10C) and is also present in *Dadadon* and *Santacruzodon*. It is, however, more extensively developed in *Exaeretodon* (as mentioned by Romer, 1967: 8; Fig. 10D), *Gomphodontosuchus*, *Menadon*, and *Scalenodontoides* (based on the similarity of isolated postcanines with those of *Exaeretodon*). The posteromedial inclination of the last postcanines in relation to the longitudinal axis of the skull, a feature presumably related to the shouldering, is present in the latter four genera, as well as ‘*Scalenodon*’ *atridgei*, ‘*S.*’ *charigi* (Crompton, 1972) and *Traversodon*.

A trend of increasing cusp number on the labial sectorial border seems to characterize upper traversodontid teeth. *S. angustifrons* is the only taxon to bear a single cusp. Two cusps are present in many Anisian/

Ladinian forms. Among these, the interpretation of the *Adescynodon* sectorial crest is complicated by the presence of small accessory cusps in addition to the two principal cusps (Goñi & Goin, 1987). Three cusps on the sectorial border are a shared feature of late traversodontids, including *Santacruzodon*, *Massetognathus*, *Scalenodontoides* and *Exaeretodon* (the condition is unknown in *Gomphodontosuchus*), but with both Madagascan taxa, *Menadon* and *Dadadon*, featuring two cusps. It is interesting to note that the extreme angulation of the upper postcanines in both *Exaeretodon* (Fig. 10D) and *Scalenodontoides* produces a remarkable separation between the sectorial border and the occlusal basin.

Two features of the cingulum, recorded mostly in African forms, are notable differences with other traversodontids. An isolated labial cusp, anterior to the transverse crest of the lower postcanine, occurs in *Scalenodon angustifrons* and ‘*Scalenodon*’ *hirschsoni*, and, with a different morphology, also in *Andescynodon*; whereas a cingulum made up of small cusps occurs in the same position in *Luangwa*. An external labial cingulum on the upper postcanine is recorded in *Scalenodon angustifrons*, *Luangwa* and *Dadadon*. In addition, *Traversodon* is the only post-Anisian traversodontid featuring a posterior cingulum in the upper postcanines.

SCALENODON MONOPHYLY AND THE MANDA BEDS

It is interesting to compare the different ‘species’ of *Scalenodon* from the Manda Formation in Tanzania. Crompton (1955) initially described *S. angustifrons* from material previously proposed as *Trirachodon angustifrons* by Parrington (1946). Crompton (1972) (Figs 7, 10A–C) recognized three additional species from the same beds: *S. hirschsoni*, *S. atridgei* and *S. charigi*. Considering the wide morphological variation between these taxa, Hopson (1984) suggested that they could be separated at the generic level, and later (Hopson, 1985) proposed a possible closer relationship between *S. charigi* with a clade comprising *Gomphodontosuchus*, *Exaeretodon*, and *Scalenodontoides* (Fig. 7A).

More recently, the phylogenetic proposal of Hopson & Kitching (2001, using a parsimony program) found that *S. angustifrons* and ‘*S.*’ *hirschsoni* were distant relatives (i.e. the genus *Scalenodon* was polyphyletic; Fig. 7D). Even in a different context, considering that they proposed a sister-group relationship of ‘*S.*’ *hirschsoni* with tritylodontids, our phylogeny confirms the distant relationship between *S. angustifrons* and ‘*S.*’ *hirschsoni*. In addition, we agree with Hopson (1984) that the other two species included in *Scalenodon* should be placed in different genera, given the

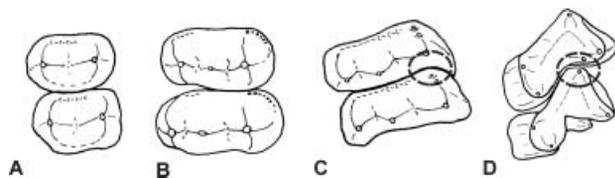


Figure 10. Upper postcanines of (A) *Pascualgnathus*, (B) *Scalenodon angustifrons*, (C) *Massetognathus* and (D) *Exaeretodon*. The circle shows ‘shouldering’ between the upper postcanines. Note the extreme development of this structure in *Exaeretodon*. (B) after Crompton (1972); (C) after Romer (1967) and Crompton (1972); (D) after Abdala *et al.*, (2002).

remarkable differences in their postcanine morphology (although '*S. atridgei*' and '*S. charigi*' may prove to be the same taxon).

The Manda fauna shows an unusual mixture of clearly plesiomorphic forms (e.g. *S. angustifrons*) and '*S. hirschsoni*' and '*S. charigi*', which share derived postcanine features with late Ladinian–Carnian forms (Hopson, 1984). This kind of assortment, unknown for traversodontid faunas until recently, was also reported from Madagascar (Flynn *et al.*, 1999, 2000) and Brazil (Abdala *et al.*, 2001). In both cases, taxa morphologically closer to Ladinian traversodontids, and others more closely related with typical Carnian ones, were found in association. The condition in the Manda Formation is more extreme because the fauna includes *Diademodon*-like forms and *Cricodon*, closely related to *Trirachodon*, suggesting a late Scythian/early Anisian age (Kitching, 1995; Hancox, 2000), whereas traversodontids like '*S. hirschsoni*' and '*S. charigi*' have features known otherwise in Ladinian and Carnian traversodontids. *S. angustifrons*, both for its morphological features, and by its direct association with the rhynchosaur *Stenaulorhynchus* and cynodont mandibles with diademodontid-like teeth (Crompton, 1955), seems to be older, whereas the other species of '*Scalenodon*' were seemingly isolated occurrences from different outcrops (Crompton, 1972). The extreme differentiation between these traversodontids suggests that, as proposed by Boonstra (1953) and, on the basis of more extensive evidence, by Charig (1963), more than one age could be represented in the fauna of the Manda Formation (see also Gay & Cruickshank, 1999: 199).

A WORD ABOUT LATE TRIASSIC LAURASIAN TRAVERSODONTIDS

A comparison between traversodontids of South America and Africa with those from North America (Hopson, 1984; Sues & Olsen, 1990; Sues *et al.*, 1992, 1994, 1999) and western Europe (Hahn *et al.*, 1988; Godefroit & Battail, 1997), which until recently have had a fragmentary record, highlights remarkable differences between Gondwanan and Laurasian traversodontids of the Late Triassic. Small individuals represent most Laurasian traversodontids. A bias of the record is the fact that *Boreogomphodon*, documented by various fragments, including three partial skulls, and a number of isolated dentaries and maxillae (Sues *et al.*, 1994), and the recently described *Plinthogomphodon* represented by a partial snout (Sues *et al.*, 1999), are known from small, juvenile individuals. In western Europe, the genera *Microscalenodon*, *Maubeugia* and *Rosieria* are represented by small isolated postcanines (Hahn *et al.*, 1988; Godefroit & Battail, 1997). In contrast, *Arctotraversodon*,

represented by two incomplete lower jaws lacking postcanines, one canine, and a single postcanine each from the upper and lower series, is the only large traversodontid from Laurasia (Hopson, 1984; Sues *et al.*, 1992).

The postcanine pattern of these Laurasian records does not match the morphology present in typical Gondwanan Late Triassic traversodontids. The upper postcanines in *Boreogomphodon* and *Plinthogomphodon* were found to be more similar with Anisian forms, such as *Luangwa*, or Ladinian forms, such as *Traversodon* (Sues & Olsen, 1990; Sues *et al.*, 1999). In addition, *Plinthogomphodon* features an anterolingual position of the paracanine fossa in relation to the upper canine, a clear plesiomorphy with respect to the Gondwanan Carnian forms. The same can be said for *Arctotraversodon*, which is most similar in the upper and lower postcanines to the Ladinian *Massetognathus* (Hopson, 1985; Sues *et al.*, 1992). In the case of the European traversodontids, the upper postcanines of *Maubeugia* seem to be more similar to those of *Boreogomphodon*, whereas *Rosieria* was found to share dental features with the Anisian *S. angustifrons* and the Ladinian *Traversodon* (Godefroit & Battail, 1997). Besides, three (rather than two) anterior cusps in the lower postcanines are known only in Laurasian forms (Sues *et al.*, 1992). These differences in the postcanine morphology indicate that Laurasian traversodontids with plesiomorphic dental features in their upper postcanines survived into the Carnian and even the Norian, denoting a slower rate of change in postcanine modification compared with Gondwanan traversodontids.

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REFERENCES

- Abdala F. 1996.** Los chiniquodontoideos (Synapsida, Cynodontia) sudamericanos. Unpublished Doctoral Thesis, Universidad Nacional de Tucumán.
- 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, Barberena MC, Dornelles J. 2002.** 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, Giannini NP. 2000.** Gomphodont cynodonts of the Chañares Formation: the analysis of an ontogenetic sequence. *Journal of Vertebrate Paleontology* **20**: 501–506.
- Abdala F, Giannini NP. 2002.** Chiniquodontid cynodonts: systematic and morphometric considerations. *Palaeontology* **45**: 1151–1170.
- Abdala F, Ribeiro AM, Schultz CL. 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.
- Barberena MC. 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.
- Barberena MC. 1981a.** Uma nova espécie de *Massetognathus* (*Massetognathus ochagaviae*, sp. nov.) da Formação Santa Maria, Triássico do Rio Grande do Sul. *Pesquisas* **14**: 181–195.
- Barberena MC. 1981b.** Novos materiais de *Traversodon stahleckeri* da Formação Santa Maria (Triássico do Rio Grande do Sul). *Pesquisas* **14**: 149–162.
- Battail B. 1991.** Les cynodontes (Reptilia, Therapsida): une phylogénie. *Bulletin du Muséum National d'Histoire Naturelle, 4^e Série* **13**: 17–105.
- Bonaparte JF. 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 JF. 1966.** Una nueva 'fauna' triásica de Argentina (Therapsida: Cynodontia Dicynodontia). Consideraciones filogenéticas y paleobiogeográficas. *Ameghiniana* **4**: 243–296.
- Bonaparte JF. 1969.** Dos nuevas 'faunas' de reptiles triásicos de Argentina. *Gondwana Stratigraphy, I.U.G.S. Symposium, Mar del Plata*, 283–306.
- Boonstra LD. 1953.** A report on a collection of fossil reptilian bones from Tanganyika Territory. *Annals of the South African Museum* **42**: 5–18.
- Bremer K. 1994.** Branch support and tree stability. *Cladistics* **10**: 295–304.
- Brink AS. 1955.** A study on the skeleton of *Diademodon*. *Palaeontologia Africana* **3**: 3–39.
- Brink AS. 1963.** Two cynodonts from the Ntawere Formation in the Luangwa valley of Northern Rhodesia. *Palaeontologia Africana* **8**: 77–96.
- Broili F, Schröder J. 1935a.** Beobachtungen and Wirbeltieren der Karrooformation. IX. Über den Schädel von *Gomphognathus* Seeley. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathemat.-Naturwissenschaftliche, Abteilung* **1935**: 115–182.
- Broili F, Schröder J. 1935b.** Beobachtungen and Wirbeltieren der Karrooformation. X. Über die Bezahnung von *Trirachodon* Seeley. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, Mathemat.-Naturwissenschaftliche, Abteilung* **1935**: 189–198.
- Broom R. 1919.** On the genus *Gomphognathus* and its allies. *Records of the Albany Museum* **111**: 223–232.
- Charig AJ. 1963.** Stratigraphical nomenclature in the Songea Series of Tanganyika. *Records of the Geological Survey of Tanganyika* **10**: 47–53.
- Chatterjee S. 1982.** A new cynodont reptile from the Triassic of India. *Journal of Paleontology* **56**: 203–214.
- Crompton AW. 1955.** On some Triassic cynodonts from Tanganyika. *Proceedings of the Zoological Society of London* **125**: 617–669.
- Crompton AW. 1972.** Postcanine occlusion in cynodonts and tritylodonts. *Bulletin of the British Museum (Natural History), Geology* **21**: 29–71.

- Crompton AW, 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.
- De Pinna MCC. 1991.** Concept and tests of homology in the cladistic paradigm. *Cladistics* **7**: 367–394.
- Flynn JJ, Parrish JM, Rakotosamimanana B, Ranivoharimanana L, Simpson WF, Wyss AR. 2000.** New traversodontids (Synapsida: Eucynodontia) from the Triassic of Madagascar. *Journal of Vertebrate Paleontology* **20**: 422–427.
- Flynn JJ, Parrish JM, Rakotosamimanana B, Simpson WF, Whateley RL, Wyss AR. 1999.** A Triassic fauna from Madagascar, including early dinosaurs. *Science* **286**: 763–765.
- Gay SA, Cruickshank ARI. 1999.** Biostratigraphy of the Permian tetrapod faunas from the Ruhuhu Valley, Tanzania. *Journal of African Earth Sciences* **29**: 195–210.
- Godefroit P, Battail B. 1997.** Late Triassic cynodonts from Saint-Nicolas-de-Port (north-eastern France). *Geodiversitas* **19**: 567–631.
- Goloboff PA. 1993a.** *NONA, ver 1.0. Pee-Wee (P)arsimony and (i)mplied weights, ver 2.0.* Program and documentation available from J. M. Carpenter, American Museum of Natural History, New York.
- Goloboff PA. 1993b.** Estimating character weights during tree search. *Cladistics* **9**: 83–91.
- Goñi RG. 1986.** Reemplazo de dientes postcaninos en *Andescynodon mendozensis* Bonaparte (Cynodontia, Traversodontidae). *Actas del IV Congreso Argentino de Paleontología y Bioestratigrafía* **2**: 7–14.
- Goñi RG, Goin FJ. 1987.** El origen de los postcaninos gonfodontes de *Andescynodon mendozensis* Bonaparte (Cynodontia, Traversodontidae). *Ameghiniana* **24**: 235–239.
- Goñi RG, Goin FJ. 1988.** Morfología dentaria y biomecánica masticatoria de los cinodontes (Reptilia-Therapsida) del Triásico argentino. I. *Andescynodon mendozensis* Bonaparte (Cynodontia, Traversodontidae). *Ameghiniana* **25**: 139–148.
- Gow CE, Hancox PJ. 1993.** First complete skull of the Late Triassic *Scalenodontoides* (Reptilia, Cynodontia) from southern Africa. In: Lucas SG, Morales M, eds. The nonmarine Triassic. *New Mexico Museum of Natural History & Science Bulletin* **3**: 161–168.
- Gradstein FM, Ogg J. 1996.** A Phanerozoic time scale. *Episodes* **19**: 3–5.
- Hahn G, Lepage J-C, Wouters G. 1988.** Traversodontiden-Zähne (Cynodontia) aus der Ober-Trias von Gaume (Süd-Belgien). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* **58**: 177–186.
- Hancox PJ. 2000.** The continental Triassic of South Africa. *Zentralblatt für Geologie und Paläontologie Teil I* (1998): 1285–1324.
- Hawkins JA. 2000.** A survey of primary homology assessment: different botanists perceive and define characters in different ways. In: Scotland R, Pennington RT, eds. *Homology and systematics: coding characters for phylogenetic analysis*. Oxford: The Systematic Association, Special Vol. 58, 22–53.
- Hopson JA. 1971.** Postcanine replacement in the gomphodont cynodont *Diademodon*. *Zoological Journal of the Linnean Society* **50**: 1–21.
- Hopson JA. 1984.** Late Triassic traversodont cynodonts from Nova Scotia and southern Africa. *Palaeontologia Africana* **25**: 181–201.
- Hopson JA. 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 JA. 1991.** Systematics of the nonmammalian Synapsida and implications for patterns of evolution in Synapsida. In: Schultze H-D, Trueb L, eds. *Origin of the higher groups of tetrapods, controversy and consensus*. Ithaca, NY: Comstock Publishing Associates, Cornell University Press, 635–693.
- Hopson JA. 1994.** Synapsid evolution and the radiation of non-eutherian mammals. In: Spencer RS, ed. *Major features of vertebrate evolution*. Knoxville, TN: The University of Tennessee, Knoxville, 190–219.
- Hopson JA, Barghusen HR. 1986.** An analysis of therapsid relationships. In: Hotton N III, Maclean PD, Roth JJ, Roth EC, eds. *The ecology and biology of mammal-like reptiles*. Washington: Smithsonian Institution Press, 83–106.
- Hopson JA, Kitching JW. 1972.** A revised classification of cynodonts (Reptilia, Therapsida). *Palaeontologia Africana* **14**: 71–85.
- Hopson JA, Kitching JW. 2001.** A probainognathian cynodont from South Africa and the phylogeny of nonmammalian cynodonts. *Bulletin of the Museum of Comparative Zoology* **156**: 5–35.
- von Huene F. 1928.** Ein Cynodontier aus des Trias Brasiliens. *Zentralblatt für Mineralogie, Geologie und Paläontologie* **1928** (B) : 251–270.
- von Huene F. 1936.** *Die fossilen Reptilien des südamerikanischen Gondwanalandes. Ergebnisse der Sauriergrabungen in Südbrasilien 1928–29. Lieferung 2.* Tübingen: Verlag Franz F. Heine, 93–159.
- Jenkins FA Jr. 1970.** The Chañares (Argentina) Triassic reptile fauna VII. The postcranial skeleton of the traversodontid *Massetognathus pascuali* (Therapsida, Cynodontia). *Breviora* **352**: 1–28.
- Kemp TS. 1980.** Aspects of the structure and functional anatomy of the Middle Triassic cynodont *Luangwa*. *Journal of Zoology* **191**: 193–239.
- Kemp TS. 1983.** The relationships of mammals. *Zoological Journal of the Linnean Society* **77**: 353–384.
- Kitching JW. 1995.** Biostratigraphy of the *Cynognathus* Assemblage Zone. In: Rubidge BS, ed. *Biostratigraphy of the Beaufort Group (Karoo Supergroup)*. Biostratigraphic Series no. 1. South African Committee for Stratigraphy, 40–45.
- Parrington FR. 1946.** On the cranial anatomy of cynodonts. *Proceedings of the Zoological Society of London* **116**: 181–197.
- Rogers RR, Arcucci AB, Abdala F, Sereno PC, Forster CA, May CL. 2001.** Paleoenvironment and taphonomy of the Chañares Formation tetrapod assemblage (Middle Triassic), northwestern Argentina: spectacular preservation in volcanogenic concretions. *Palaios* **16**: 461–481.
- Romer AS. 1967.** The Chañares (Argentina) Triassic reptile

- fauna. III. Two new gomphodonts, *Massetognathus pascuali* and *Massetognathus teruggii*. *Breviora* **264**: 1–25.
- Romer AS. 1972.** The Chañares (Argentina) Triassic reptile fauna. XVII. The Chañares gomphodonts. *Breviora* **396**: 1–9.
- Rowe T. 1986.** Osteological diagnosis of Mammalia, L. 1758, and its relationship to extinct Synapsida. PhD Dissertation. Berkeley: University of California.
- Rowe T. 1988.** Definition, diagnosis and origin of Mammalia. *Journal of Vertebrate Paleontology* **8**: 241–264.
- Rowe T. 1993.** Phylogenetic systematics and the early history of mammals. In: Szalay FS, Novacek MJ, McKenna MC, eds. *Mammal phylogeny. Mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials*. New York: Springer Verlag, 129–145.
- Seeley HG. 1894.** Researches on the structure, organization, and classification of the Fossil Reptilia. Part IX, Section 3. On *Diademodon*. *Philosophical Transactions of the Royal Society of London* **185**: 1029–1041.
- Seeley HG. 1895.** Researches on the structure, organization, and classification of the Fossil Reptilia. Part IX, Section 4. On the Gomphodontia. *Philosophical Transactions of the Royal Society of London* **186**: 1–57.
- Sues H-D. 1985.** The relationships of the Tritylodontidae (Synapsida). *Zoological Journal of the Linnean Society* **85**: 205–217.
- Sues H-D, Hopson JA, Shubin NH. 1992.** Affinities of ?*Scalenodontoides plemmyridon* Hopson, 1984 (Synapsida: Cynodontia) from the Upper Triassic of Nova Scotia. *Journal of Vertebrate Paleontology* **12**: 168–171.
- Sues H-D, Olsen PE. 1990.** Triassic vertebrates of Gondwanan aspect from the Richmond Basin of Virginia. *Science* **249**: 1020–1023.
- Sues H-D, Olsen PE, Carter JG. 1999.** A Late Triassic traversodontid cynodont from the Newark Supergroup of North Carolina. *Journal of Vertebrate Paleontology* **19**: 351–354.
- Sues H-D, Olsen PE, Kroehler PA. 1994.** Small tetrapods from the Upper Triassic of the Richmond basin (Newark Supergroup), Virginia. In: Fraser NC, Sues H-D, eds. *In the shadow of the dinosaurs. Early Mesozoic tetrapods*. Cambridge University Press, 161–170.
- Tatarinov LP. 1973.** Cynodonts of Gondwanan habit in the Middle Triassic of the USSR. *Paleontological Journal* **2**: 200–205.
- Wible JR. 1991.** Origin of Mammalia: the craniodental evidence reexamined. *Journal of Vertebrate Paleontology* **11**: 1–28.
- 111–64 A, 377–58 M; MCP 1522 PV; PVL 2473; PVSJ 157.
- Gomphodontosuchus*: GPIT without number.
- Luangwa*: BP/1/3731, OUMNH TSK 121.
- Massetognathus*: MCZ 3691, 3786, 3798, 3801, 3804, 3806, 3807, 4021, 4138, 4208, 4215, 4216, 4258, 4265, PULR 10, 11, 13, PVL 3901, 3902, 3904, 3906, 4726, 4727, 4728, 4729, 4613.
- Menadon*: UA-10601, FMNH PR 2104.
- Pascualgnathus*: MLP 65-VI-18–1, PVL 3466, 4416.
- Traversodon*: PV 0224T, GPIT 1045, 1063, 1069.
- Trirachodon*: BP/1/4256, 5362, SAM PK-K-11481.
- '*Scalenodon*' *attridgei*: BMNH R 8578.
- '*Scalenodon*' *hirschsoni*: BMNH R 8577.
- Scalenodontoides*: BP/1/5395.

APPENDIX 2

CHARACTER LIST

- 1 *Number of upper incisors*: four (0), three (1).
- 2 *Incisor size*: small (0), large (1).
- 3 *Diastema between upper incisors and canine*: present (0), absent (1).
- 4 *Upper canine size*: large (0), reduced (1).
- 5 *Lower canine size*: large (0), reduced (1).
- 6 *Position of paracanine fossae in relation to the upper canine*: antero-medial (0), medial (1), postero-medial (2).
- 7 *Overall morphology of the upper postcanines*: ovoid-ellipsoid (0), rectangular-trapezoidal (1).
- 8 *Shouldering in upper postcanines*: absent (0), present (1).
- 9 *Posteromedial inclination of the last upper postcanines*: absent or small (0), oblique (1).
- 10 *Transverse crest of upper postcanines*: central (0), anterior (1), posterior (2).
- 11 *Number of cusps in the transverse crest of the upper postcanines*: two (0), three (1).
- 12 *Central cusp of upper transverse crest*: midway between buccal and lingual cusps (0), closer to the lingual cusp (1).
- 13 *Posterior cingulum in upper postcanines*: present (0), absent (1).
- 14 *External cingulum in the anterior portion of the upper postcanines*: absent (0), present (1).
- 15 *Anterolingual cusp in upper postcanines*: absent (0), present (1).
- 16 *Number of cusps in the sectorial border of the upper postcanines*: three (0), one (1), two (2).
- 17 *Overall morphology of the lower postcanines*: ovoid-ellipsoid (0), quadrangular (1).
- 18 *Transverse crest in lower postcanines*: central (0), anterior (1).
- 19 *Number of cusps in the transverse crest of the lower postcanines*: two (0), three (1).

APPENDIX 1

MATERIAL CONSULTED

- Andescynodon*: PVL 3833, 3836, 3894–1, 3894–2, 3899, 4390.
- Dadadon*: UA-10606.
- Diademodon*: BP/1/3754, 3769, 4669, BS1934VIII₁₄, VIII₁₅, VIII₁₆, VIII₁₇, VIII₁₉, HMN R1004, SAM PK-K5223, K5716.
- Exaeretodon*: MACN 18114, 18125; MCZ 3779, 4493,

- 20** *Size of the anterior cusps in the lower postcanines:* labial lower than lingual (0), labial higher than lingual (1).
- 21** *Cingulum in front of the transverse crest in the lower postcanines:* absent (0), present (1).
- 22** *Internarial bar:* present (0), absent (1).
- 23** *Maxillary labial platform:* absent (0), present (1).
- 24** *Parietal foramen in adults:* present (0), absent (1).
- 25** *Zygomatic process of the jugal:* conspicuously projected (0), little projected (1), a ball-like process (2), absent (3).
- 26** *Posterior extension of the jugal above the squamosal in the zygoma:* absent or with a small extension (0), well developed (1).
- 27** *Coronoid process of the mandible:* cover the last postcanine (0), does not cover (1).
- 28** *Dentary angle:* not or weakly projected posteriorly (0), well projected posteriorly (1).

APPENDIX 3

DATA MATRIX

	12345	67891 0	11111 12345	11112 67890	22222 12345	222 678
<i>Diademodon</i>	00000	00000	000??	0000?	?0000	000
<i>Trirachodon</i>	00000	00000	100??	1001?	?0100	010
<i>Andescynodon</i>	00000	01001	0?001	11101	10113	0?0
<i>Massetognathus</i>	00111	11112	11100	01100	00111	000
<i>Exaeretodon</i>	11101	21112	0?101	01101	01110	101
<i>Luangwa</i>	00000	01002	11011	21100	10101	000
<i>Scalenodon angustifrons</i>	00000	01000	11010	11100	1010?	?0?
<i>Scalenodon hirschsoni</i>	1111?	010?2	11001	21100	101??	???
<i>Traversodon</i>	00000	01012	11000	01100	00101	?0?
<i>Gomphodontosuchus</i>	01111	11112	??10?	?1101	001??	?0?
<i>Pascualgnathus</i>	10000	01000	0?0?1	111??	??111	000
<i>Scalenodontoides</i>	111??	211?2	0?10?	01101	0111?	101
<i>Menadon</i>	11111	?1112	0?101	2? ???	?11?3	101
<i>Dadadon</i>	000??	01112	11111	2? ???	?01?2	???
<i>Santacruzodon</i>	000??	01112	11101	01101	001?2	?00

APPENDIX 4

SYNAPOMORPHIES OF THE MONOPHYLETIC GROUPS
DEFINED IN THE MOST PARSIMONIOUS TREE*Traversodontidae*

- 7 (1) Upper postcanine morphology rectangular-trapezoidal.
- 12 (1) Central cusp of the upper transverse crest closer to the lingual cusp. Non-applicable in traversodontids with two cusps in the upper transverse crest.
- 17 (1) Lower postcanine morphology quadrangular.
- 18 (1) Transverse crest in lower postcanines anterior.
- 25 (1) Zygomatic process of the jugal little projected. Reversion in *Exaeretodon*.

Andescynodon (Pascualgnathus)

- 11 (0) Two cusps in the upper transverse crest. Convergence in [*Scalenodontoides*, *Exaeretodon*, *Menadon*].

- 24 (1) Absence of the parietal foramen in adults. Convergence in *Massetognathus*, *Exaeretodon* and *Scalenodontoides*.

Clade a

- 10 (2) Posterior or near posterior position of the transverse crest in upper postcanines.

Luangwa ('Scalenodon' hirschsoni)

- 16 (2) Two cusps in the sectorial border of the upper postcanines. Convergence in *Dadadon* and *Menadon*.

Clade b

- 9 (1) Last upper postcanines of the series oblique.
- 16 (0) Three cusps in the sectorial portion of the upper postcanines. Reversion in *Dadadon* and *Menadon*.
- 21 (1) Absence of the cingulum in front of the transverse crest in lower postcanine.

Clade c

- 8 (1) Presence of the shouldering in the upper postcanines.
 13 (1) Absence of the posterior cingulum in the upper postcanines.

Dadadon + Santacruzodon

- 25 (2) A ball-like zygomatic process of the jugal.

Massetognathus + [Gomphodontosuchus

[*Scalenodontoides, Exaeretodon, Menadon*]

- 3 (1) Absence of the diastema between upper incisors and canine. Convergence in '*S. hirschsoni*'.
 6 (1) Paracanine fossae medial to the upper canine.

Gomphodontosuchus + [Scalenodontoides, Exaeretodon, Menadon]

- 2 (1) Large-sized incisor. Convergence in '*S. hirschsoni*'.

- 5 (1) Lower canine reduced. Potential synapomorphy, unknown condition in *Dadadon*, *Santacruzodon* and *Menadon*.
 20 (1) Labial anterior cusp higher than lingual in the lower postcanines. Convergence in *Andescynodon* and *Santacruzodon*.

[*Scalenodontoides, Exaeretodon, Menadon*]

- 1 (1) Three upper incisors. Convergence in '*S. hirschsoni*' and *Pascualgnathus*.
 6 (2) Paracanine fossae posterior to the upper canine.
 11 (0) Two cusps in the transverse crest of the upper postcanines. Convergence in [*Andescynodon, Pascualgnathus*].
 22 (1) Absence of the internarial bar.
 26 (1) Well developed posterior extension of the jugal above of the squamosal in the zygoma. Potential synapomorphy, condition unknown in *Gomphodontosuchus*.
 28 (1) Angle of the dentary well projected posteriorly. Potential synapomorphy, condition unknown in *Gomphodontosuchus*.