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, *Santacruzodon 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.


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 brasilienis* 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,
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, *Pascalognathus* 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 *Masetognathus* 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, Pontificia 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  
OU/MNH  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 TRAVERSODONTIDA 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 cuspules as in ‘Scalenodon’ attridgei Crompton, 1972. As in many other cynodonts (e.g. Massetognathus, Exaeretodon), S. hopsoni features three labial cuspules 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 cuspules (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)

<table>
<thead>
<tr>
<th></th>
<th>MCN PV 2768 (Holotype)</th>
<th>MCN PV 2752</th>
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<tbody>
<tr>
<td>Rostrum</td>
<td>49.6</td>
<td>24.5</td>
</tr>
<tr>
<td>Orbital region</td>
<td>22.4</td>
<td>22.4</td>
</tr>
<tr>
<td>Orbital diameter</td>
<td>3.0</td>
<td>3.0</td>
</tr>
<tr>
<td>2nd upper incisor length</td>
<td>4.1</td>
<td>4.1</td>
</tr>
<tr>
<td>4th upper incisor length</td>
<td>3.6</td>
<td>3.6</td>
</tr>
<tr>
<td>Upper canine length</td>
<td>5.3</td>
<td>5.3</td>
</tr>
<tr>
<td>Upper postcanine length</td>
<td>29.2</td>
<td>29.2</td>
</tr>
<tr>
<td>1st upper postcanine length</td>
<td>2.1</td>
<td>2.1</td>
</tr>
<tr>
<td>1st upper postcanine width</td>
<td>2.2</td>
<td>2.2</td>
</tr>
<tr>
<td>Last upper postcanine length</td>
<td>3.9</td>
<td>3.9</td>
</tr>
<tr>
<td>Last upper postcanine width</td>
<td>5.4</td>
<td>5.4</td>
</tr>
<tr>
<td>Height of the preserved portion of the ascendant ramus of the mandible</td>
<td>28.2</td>
<td>32.1</td>
</tr>
<tr>
<td>Mandibular length (incomplete)</td>
<td>69.2</td>
<td>69.2</td>
</tr>
<tr>
<td>Length from the tip of the mandible to the angle</td>
<td>65.1</td>
<td>60.3</td>
</tr>
<tr>
<td>2nd lower incisor length</td>
<td>4</td>
<td>2.9</td>
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<tr>
<td>Lower canine length</td>
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<td>25.5</td>
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<tr>
<td>Last lower postcanine length</td>
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</tr>
<tr>
<td>Last lower postcanine width</td>
<td>4.0</td>
<td>3.8</td>
</tr>
</tbody>
</table>

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 cusp 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 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 cusp 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.

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); Scalenoodon (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, 1985, 1985; Abdala, Barberena & Dornelles, 2002); Gomphodontosuchus (Huene, 1928; 1936; Hopson, 1985); Traversodon (Huene, 1936; Barberena, 1974, 1981b); Andescynodon (Bonaparte, 1969; Goñi, 1986; Goñi & Goin, 1983); Pascaulgnathus (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 much of the information in Santacruzodon. Characters of postcanium 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
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, 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 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.

**PHYLGENETIC 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, Scalendonoides, 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, Scalendonoides, 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), Scalodon 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 traversodontids. Among the Ladinian/Carnian forms, Traversodon is the most basal member and Dadodon and Santacruzodon form a monophyletic group. Finally, a clade formed by Scalendonoides, 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, Scalendonoides, 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 shoudering 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 indication of which species of *Scalenodon* 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) *Pascualognathus* 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.

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 Exaretodon, 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 tripleteledontids, 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 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 ellipsoidal 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 Dadodon, 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-
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 cusps (see below). Its position on the upper postcanines, most traversodontids show three cusps (in 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 Scaleno-odontoides, Exaeretodon and Menadon.

Shouldering of the upper postcanines – the antero-labial 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 Scaleno-odontoides (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 shoul-dering, is present in the latter four genera, as well as ‘Scalenodon’ atttridgei, ‘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 Andescynodon sectorial crest is complicated by the presence of small accessory cuspules 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, Masseto- gnathus, Scaleno-odontoides 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 Scaleno-odontoides 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 Scaleno-odontosuchus and ‘Scalenodon’ hirschsoni, and, with a different morphology, also in Andescynodon; whereas a cingulum made up of small cuspules occurs in the same position in Luangwa. An external labial cingulum on the upper postcanine is recorded in Scaleno-odontosuchus, 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 Scaleno-odon 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. atttridgei 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 Scaleno-odontoides (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 Scaleno-odon was polyphyletic; Fig. 7D). Even in a different context, considering that they proposed a sister-group relationship of ‘S.’ hirschsoni with tritylodontids, our phylogeny con-irms the distant relationship between S. angustifrons and ‘S.’ hirschsoni. In addition, we agree with Hopson (1984) that the other two species included in Scaleno-odon should be placed in different genera, given the
remarkable differences in their postcanine morphology (although ‘S. attridgei’ 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. hirchsoni’ 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. hirchsoni’ 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 Rosiera 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 Luangvet, or Ladinian forms, such as Traversodon (Sues & Olsen, 1990; Sues et al., 1999). In addition, Plinthogomphodon features an anterolinal 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 Masseotongnathus (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 Rosiera 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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### 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, 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 canines**: 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 Postero-medial inclination of the last upper postcanines**: absent or small (0), oblique (1).
**10 Transverse crest of upper postcanines**: absent (0), small (1), present (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 Anterolinguinal 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**: absent (0), small (1), present (2).
**19 Number of cusps in the transverse crest of the lower postcanines**: two (0), three (1).
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

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<tr>
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<th>Diademodon</th>
<th>Trirachodon</th>
<th>Andescynodon</th>
<th>Massetognathus</th>
<th>Exaeretodon</th>
<th>Luangwa</th>
<th>Scalenodon angustifrons</th>
<th>Scalenodon hirschsoni</th>
<th>Traversodon</th>
<th>Gomphodontosuchus</th>
<th>Pascualgnathus</th>
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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.


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 ‘Scalenodon’ hirschsoni.
6 (1) Paracanine fossae medial to the upper canine.

Gomphodontosuchus + [Scalenodontoides, Exaeretodon, Menadon]

[Scalenodontoides, Exaeretodon, Menadon]
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.

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*.