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A new trirachodontid cynodont from the lower levels of the Burgersdorp Formation (Lower Triassic) of the Beaufort Group, South Africa and the cladistic relationships of Gondwanan gomphodonts

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We describe a new trirachodontid cynodont from the base of the Burgersdorp Formation (Subzone A fauna of the *Cynognathus* Assemblage Zone), of the South African Karoo Basin. ***Langbergia modisei*** **gen. et sp. nov.** is characterized by circular to ovoid in outline upper postcanines and the absence of a maxillary platform lateral to the postcanine series. Apart from the new taxon, we recognize two other species of this family in the *Cynognathus* Assemblage Zone: *Trirachodon berryi* and *Cricodon metabolus*, the latter also represented in the Tanzanian Manda Formation. A phylogenetic analysis of gomphodont cynodonts was conducted using a data matrix of 43 craniodental characters and 18 terminals. Trirachodontidae appears as a monophyletic assemblage, with *Langbergia* appearing as the sister taxon of *Cricodon*. The monophyly of trirachodontids is weakly supported, however, with one extra step breaking it. Traversodontid cynodont relationships were also inspected and compared with a recent phylogeny proposed for this group. Considering the resulting phylogeny and the sudden appearance and diversification of Cynognathia representatives, the origin of basal Cynognathia (i.e. *Cynognathus*, *Diademodon*, and trirachodontids) is suggested to predate their first appearance in the fossil record. © 2006 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2006, **147**, 383–413.

ADDITIONAL KEYWORDS: Early/Middle Triassic – Gondwana – phylogeny – Trirachodontidae.

INTRODUCTION

Since the discovery of vertebrate fossils in the Beaufort Group, this unit has been the subject of successive biozonation schemes, most of them based on the record of key taxa (or index fossils) and their associated fauna (Seeley, 1892; Broom, 1907; Watson, 1914; Kitching, 1977; Keyser & Smith, 1977–78; Rubidge *et al*., 1995). Eight successive assemblage zones (AZ), ranging from the Late Permian to the Middle Triassic, are currently recognized (Rubidge *et al*., 1995; Hancox, 2000). The youngest of these, the *Cynognathus* AZ, has been intensively researched over the last 10 years and its biostratigraphy substantially refined. Thus, three informal subzones (A, B, and C) have been proposed for the *Cynognathus* AZ, based mainly on the distribution of key temnospondyl amphibian taxa (Hancox *et al*., 1995; Shishkin, Rubidge & Hancox, 1995) and corroborated by dicynodonts and cynodonts (Hancox & Rubidge, 1994, 1996; Abdala, Hancox & Neveling, 2005). Based on the recorded faunas, an age ranging from Late Olenekian to Late Anisian was proposed for this AZ (Hancox, 2000; Hancox & Rubidge, 2001; Damiani & Hancox, 2003; Abdala *et al*., 2005). The oldest Subzone A of the *Cynognathus* AZ can be characterized as depauperate in its content of tetrapod fossils, with most of the material being fragmentary or poorly preserved (Neveling, 2002, 2004). Temnospondyl amphibians, represented by at least three different families (Damiani, 2004), dominate this fossil fauna, which also includes remains of an

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*Corresponding author. E-mail: abdalaf@geosciences.wits.ac.za undescribed archosaur, probably congeneric with the Russian *Garjainia* (Hancox, 2000) and cynodonts (Neveling, Rubidge & Hancox, 1999; Neveling, 2004).

Cynodonts are well represented in the South African Karoo where as many as 18 different taxa have been recognized, most of them collected from the Beaufort Group. The *Cynognathus* AZ contains the most diverse cynodont fauna of the Beaufort Group, with six taxa recognized thus far (Abdala *et al*., 2005), including *Diademodon*, *Cynognathus*, *Lumkuia*, *Trirachodon*, *Bolotridon* and *Cricodon*. An important component of this fauna is the herbivorous/omnivorous gomphodont cynodonts. Gomphodontia was originally proposed to include animals in which the 'molar teeth are expanded transversely, and have more or less tuberculate crowns, of the type shown in *Diademodon*' (Seeley, 1895a, 1908). This term was informally used to include cynodonts such as diademodontids, trirachodontids and traversodontids, with a buccolingually expanded crown showing a sort of rudimentary occlusion (e.g. Crompton, 1955, 1972a; Bonaparte, 1963; Romer, 1967; Battail, 1991). Hopson & Barghusen (1986: 102) also included among gomphodonts the tritylodontid cynodonts, whereas Hopson & Kitching (2001: fig. 7) defined Gomphodontia in a phylogenetic context as a monophyletic group including diademodontids, trirachodontids, traversodontids and tritylodontids. Abdala & Ribeiro (2003: 535) consider gomphodonts to be a monophyletic assemblage composed of diademodontids, trirachodontids and traversodontids (identical to the informal grouping of previous authors), whereas tritylodontids are closely related to Mammaliaformes (Kemp, 1982, 1983; Rowe, 1988, 1993; Wible, 1991) instead of to traversodontids, as proposed by Battail (1991: fig. 8) and Hopson & Kitching (2001). Our use of gomphodonts in this contribution follows the meaning of Abdala & Ribeiro (2003).

The oldest known gomphodonts are from Subzone A of the *Cynognathus* AZ, although the traversodontids from the Puesto Viejo Formation of Argentina (Bonaparte, 1966; Kokogian *et al*., 1999) may be of similar age. Diademodontid and trirachodontid gomphodonts are abundant in some classical localities of the *Cynognathus* AZ of Kitching (1977, 1995; = Subzone B), whereas trirachodontids are the dominant tetrapods of Subzone C (Abdala *et al*., 2005).

The most remarkable feature of trirachodontids is the shape of their postcanines, which consist of transversely widened teeth with three main cusps disposed in a transverse row across the centre of the tooth, and a small cingulum of cusps formed on the rim. Until recently, all the known trirachodontids from the Karoo Basin were collected in the Eastern Cape and southern Free State. It was only when Welman, Groenewald & Kitching (1991) drew attention to the occurrence of *Cynognathus* AZ fossils in the northern Free State that the geographical range of this group was extended. Subsequent work has shown that this new fossil fauna from the northern Free State Province predates the classic *Cynognathus* AZ fauna of the Eastern Cape and southern Free State (Hancox *et al*., 1995). Trirachodontid material from Subzone A, which was also found associated with burrow complexes (Groenewald, Welman & MacEachern, 2001), has been assigned to *Trirachodon kannemeyeri* in earlier biostratigraphic works (e.g. Hancox, 2000: fig. 4). However, a suite of diagnostic features allows for the recognition of a new taxon, described here as *Langbergia modisei*.

LIST OF INSTITUTIONAL ABBREVIATIONS

AM, Albany Museum, Grahamstown, South Africa; AMNH, American Museum of Natural History, New York, USA; BMNH, Natural History Museum, London, UK; BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, South Africa; BSP, Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany; CGP, Council for Geosciences, Pretoria, South Africa; FMNH, Field Museum of Natural History, Chicago, USA; GPIT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Germany; GSN, Geological Survey, Windhoek, Namibia; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MB, Humboldt Museum für Naturkunde, Berlin, Germany; MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCP, 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, USA; MLP, Museo de La Plata, Buenos Aires, Argentina; NMQR, National Museum, Bloemfontein, South Africa; OUMNH, Oxford University Museum of Natural History, Oxford, UK; PULR, Museo de Antropología, Universidad Nacional de La Rioja, Argentina; 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, South Africa; UA, University of Antananarivo, Madagascar; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; UMZC, University Museum of Zoology, Cambridge, UK.

SUMMARY OF TRIRACHODONTID TAXONOMY

The first quotation of *Trirachodon* in the literature is contained in the description of *Diademodon browni* by

Seeley (1894), who mentions that the postcanine teeth of that species are 'somewhat intermediate between types like *Diademodon* and *Trirachodon*' (Seeley, 1894: 1039). He also provides an illustration of *T. berryi*, 'figured for comparison with *Tritylodon*', based on a partial skull represented by the snout and orbital region (Seeley, 1894: plate 89, fig. 16). In a second contribution, Seeley (1895a) erected two species: *T. kannemeyeri*, based on three specimens (AM 461, BMNH 3306 and 3307; Seeley, 1895a: 48; plate 2, figs 1–8) and *T. berryi*, based on the partial skull (BMNH R3579; Seeley, 1895a: 53; plate 2, fig. 9) already illustrated in his previous report. The differences between the purported species were the more expanded form of the snout and the transversely narrower and more numerous postcanine teeth of *T. berryi* (Seeley, 1895a: 53).

Much of the ulterior descriptive work on *Trirachodon* can be attributed to Robert Broom, who made some insightful contributions (e.g. Broom, 1903, 1911) as well as very short accounts of new taxa, supported by either poor or no illustrations (e.g. Broom, 1905a, 1915a). Broom (1903, 1904) described and figured the proatlas, atlas and axis of the holotype of *T. kannemeyeri* and referred three new specimens from the Albany Museum to this species. Broom added two more species to the genus: *T. minor*, based on a deformed and badly weathered snout (SAM-PK-5873; Broom, 1905a) and *T. browni*, represented by a small skull with only the snout and orbital region preserved [BMNH R3721; mistakenly quoted as BMNH R3307 by Broom (1915a)]. Broom did not specify the diagnostic features for *T. minor* and he expressed some doubts about its assignation to *Trirachodon* (Broom, 1905a: 272). The only trait that he (Broom, 1915a: 173) provided as distinctive for the different trirachodontid species was the anteroposterior length of the 'seven largest molars', being 21–22 mm in *T. kannemeyeri*, 18.5 mm in *T. minor* and 14 mm in *T. browni*. In a comparative account of the principal cynodont morphotypes, Broom (1911) presented a description of the skull of *Trirachodon*, and later (Broom, 1915b) included a specimen from the American Museum collection in *T. kannemeyeri*. In his synthesis on the mammal-like reptiles of South Africa, Broom (1932) recognized four species: *T. kannemeyeri*, *T. minor*, *T. browni* and *Trirachodontoides berryi*, but provided poor diagnoses for the putative species. He also considered the possibility that the type of *T. minor* could represent a juvenile of *T. kannemeyeri*, whereas the only trait that seems to have distinguished *T. browni* was its small size. Finally, he transferred *Trirachodon berryi* Seeley to *Trirachodontoides berryi* and used the same characters proposed by Seeley (1895a) for *T. berryi* as diagnostic.

Broili & Schröder (1935a) described two maxillae from Lady Frere, one of them with nearly all the postcanines in good condition, which they assigned to *T. kannemeyeri* (BSP 1934VIII 21 and 22). Parrington (1946) assigned fragmentary cynodont remains from the Ruhuhu Valley in Tanzania to *Trirachodon* based on the general shape of the skull and crown pattern of the first, weathered postcanines in one of the specimens. Based on the comparatively narrow skull and the great anterior extension of the frontal, this material was allocated to a new species, *T. angustifrons* (Parrington, 1946). Subsequent studies by Crompton (1955, 1972a) demonstrated this taxon to be a traversodontid cynodont and the species was transferred to *Scalenodon angustifrons*. Among the new material coming from the same locality, Crompton (1955) established the new species *Cricodon metabolus*, whose postcanine morphology is very similar to that of *Trirachodon*. Brink & Kitching (1953) erected the species *Inusitatodon smithi*, represented by the snout, orbits, and lower jaw (BP/1/1194) of a small gomphodont cynodont collected at Lady Frere (Subzone B of the *Cynognathus* AZ). The new taxon was considered allied to *Trirachodon*, but distinct from the latter by virtue of its dental formula, the shape of the coronoid process, and the putative short temporal area (actually not preserved; Brink & Kitching, 1953: 46).

In their revision of cynodont taxonomy, Hopson & Kitching (1972) synonymized *T. kannemeyeri*, *T. minor*, *Trirachodontoides berryi* and *Inusitatodon smithi* with *Trirachodon berryi*, the only species recognized for the genus. In addition, Hopson & Kitching (1972) reassigned *T. browni* to *Diademodon tetragonus*. In his monumental work on the distribution of Karoo vertebrates, Kitching (1977) made taxonomical statements about trirachodontids, but did not discuss the characters on which his decisions were based. He proposed to revalidate *T. kannemeyeri* based in his restudy of the holotype and a new specimen discovered from Winnaarsbaken (Kitching, 1977: 101, 106). In addition, he considered a specimen (BP/1/995) assigned to the primitive cynodont *Silphedocynodon gymnotemporalis* by Brink (1951) to be a juvenile of *T. berryi*. However, the holotype of the species erected by Brink (1951) was discovered in the *Dicynodon* AZ, whereas the specimen reassigned to *T. berryi* by Kitching (1977) came from the *Cynognathus* AZ. The new identity for this specimen was based on both morphological features, including tooth pattern, and its stratigraphic placement (Kitching, 1977: 106).

Hopson & Kitching (1972) included two other species in their Trirachodontinae apart from *T. berryi*, namely *C. metabolus* and *Sinognathus gracilis*, the latter being a cynodont from China, originally reported as a galesaurid (= Cynosauridae; Young, 1959). Skulls of trirachodontids have subsequently been recovered from the Omingonde Formation of Namibia (Keyser, 1973; Smith & Swart, 2002), whereas isolated teeth are known from the Yerrapali Formation of India (Bandyopadhyay & Sengupta, 1999). Three isolated teeth assigned to Trirachodontidae were also reported from the Redonda Formation in the USA (Lucas *et al*., 1999). A lower jaw from the Donguz Formation in Russia, previously considered to be a traversodontid, was redescribed as *Neotrirachodon expectatus* (Tatarinov, 2002). Finally, Abdala *et al*. (2005) reported remains of *C. metabolus* as the most abundant cynodont of the Subzone C fauna of the *Cynognathus* AZ of the Karoo Basin.

From the above summary, it is apparent that detailed descriptive work on African trirachodontids has been largely neglected, with the contributions of Seeley (1895a), Broom (1911), and Crompton (1955) being the wealthier in anatomical information on trirachodontids. Together with the description of the new species *L. modisei* we will provide a synthesis of anatomical data on trirachodontid species (particularly those from the other subzones of the *Cynognathus* AZ). This will allow us to discuss the taxonomy of this successful Early to Middle Triassic group. We also performed a cladistic analysis of gomphodont cynodonts to determine the phylogenetic placement of the new species described. For such purpose, we updated a data matrix recently used for a phylogenetic analysis of traversodontid cynodonts by Abdala & Ribeiro (2003).

MATERIALS

Specimens of trirachodontids coming from the base of the Burgersdorp Formation (Subzone A of the *Cynognathus* AZ) are listed in Table 1 (see also Fig. 1). In addition, the following material of trirachodontids coming from Subzones B and C of the *Cynognathus* AZ of the Karoo Basin, the Omingonde Formation (Namibia) and the Manda Formation (Tanzania) was also studied: *Trirachodon berryi*: AM 434, 461 (holotype of *Trirachodon kannemeyeri*); BMNH R3306, R3307, R3350, R3579 (holotype of *Trirachodon berryi*), R3721 (holotype of *Trirachodon browni*), R3722; BP/1/3511, 3775, 4258, 4658, 4661, 5050; BSP 1934VIII 21, 1934VIII 22, 1934VIII 23; GSN R327; NMQR 122, 1399, 3279; SAM-PK-4801, 5873 (holotype of *Trirachodon minor*), 5881, 7888, K171. *Cricodon metabolus*: UMCZ T.905 (holotype of *Cricodon metabolus*); BP/1/5538, 5540, 5835, 6102, 6159.

SYSTEMATIC PALAEONTOLOGY

THERAPSIDA
EUCYNODONTIA
GOMPHODONTIA
TRIRACHODONTIDAE***LANGBERGIA MODISEI* GEN. ET SP. NOV.**

Holotype: NMQR 3255. A complete skull without a lower jaw (Figs 2–6).

Locality: Langberg 556 (S28°13′48′–E27°57′57′), Paul Roux District, Free State Province, South Africa (Fig. 1).

Referred material*:* NMQR 3251 (Figs 7, 8B), 3256 (Fig. 9), 3268, 3280, 3281; BP/1/5362, 5363, 5400, 5401, 5404; CGP/1/33 120; SAM PK 11481 (see Table 1).

Table 1. *Lanbergia modisei* material from Subzone A of the *Cynognathus* Assemblage Zone

Number	Description	District	Farm
NMQR 3268	Partial snout	Paul Roux (FSP)	Rexford Store 433
NMQR 3280	Small skull and lower jaw	Kestell (FSP)	Eerste Geluk 131
NMQR 3281	Burrow cast including three skulls and part of the postcranium	Kestell (FSP)	Eerste Geluk 131
NMQR 3251	Snout and anterior part of lower jaw	Marquard (FSP)	Goedgedacht 15
NMQR 3255	Skull and lower jaw	Paul Roux (FSP)	Langberg 556
NMQR 3256	Skull and lower jaw	Paul Roux (FSP)	Langberg 556
BP/1/5362	Skull and lower jaw	Paul Roux (FSP)	Langberg 556
BP/1/5363	Snout and orbits and anterior part of lower jaw	Bethlehem (FSP)	Rexford Store 433
BP/1/5400	Partial skull and postcranial material	Senekal (FSP)	Bosrand 12
BP/1/5404	Partial skull and postcranial material	Senekal (FSP)	Bosrand 12
BP/1/5666	Two upper postcanines	Paul Roux (FSP)	Driefontein
SAM PK-K11481	Small skull and lower jaw	Rouxville (FSP)	Kaaimansgat 146
CGP 1/33	Skull and lower jaw	Rouxville (FSP)	Moerbeidal 648
CGP 1/120	Skull and lower jaw and part of postcranium	Tarkastad (ECP)	Palmiet Fontein 94

ECP, Eastern Cape Province; FSP, Free State Province.

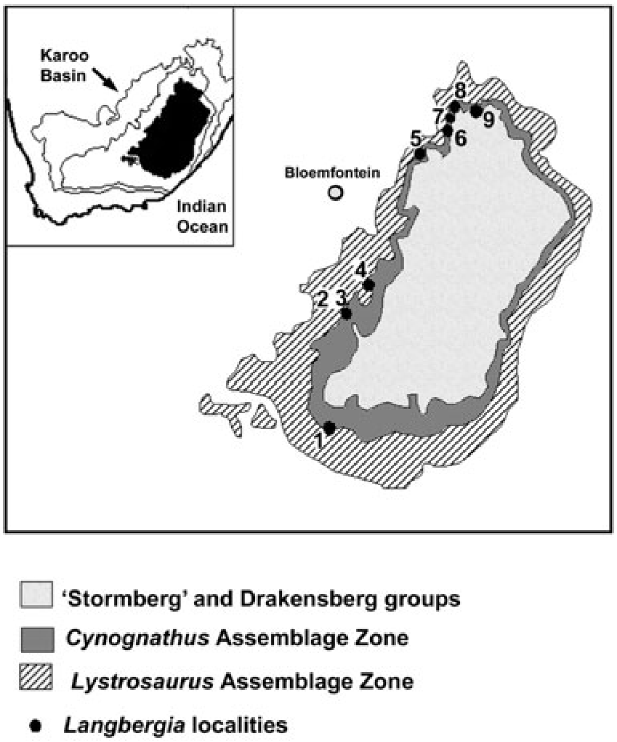

Figure 1. Map with the location of the outcrops with remains of *Langbergia modisei*. The dark area in the inset map is enlarged to show the localities. 1, Palmiet Fontein 94, Tarkastad. 2, Moerbeidal 648, Rouxville. 3, Kaaimansgat 146, Rouxville. 4, Hugo's Kop 620, Rouxville. 5, Goedgedacht 15, Marquard. 6, Bosrand 12, Senekal. 7, Rexford Store 433, Bethlehem. 8, Langberg 556, Bethlehem. 9, Eerste Geluk 131, Bethlehem.

Horizon: Lower horizons of the Burgersdorp Formation, Beaufort Group, Karoo Supergroup, South Africa. The new species is known from numerous localities throughout the Free State and the Eastern Cape (Welman *et al*., 1991; Hancox *et al*., 1995; Neveling, 2002, 2004; see Fig. 1 and Table 1). The southernmost specimen (CGP/1/120) was collected in the Tarkastad District, Eastern Cape Province.

Age: Late Olenekian (Hancox *et al*., 1995; Hancox, 2000).

Etymology: Named after the farm Langberg 566, where the holotype was found. The species' name is in honour of the late Gert Modise, a brilliant preparator of the Bernard Price Institute, University of the Witwatersrand, who dedicated his life to palaeontology and who prepared part of the material studied here.

Diagnosis: A small gomphodont cynodont with a skull size similar to that of *T. berryi*. Seven to eight upper postcanines in adults. The upper gomphodont postcanines are circular to oval in occlusal view with the width only slightly longer than the anterior–posterior length. A high central cusp is located in the middle of the crown and, as is common in trirachodontids, there is a transverse ridge along the midline of the tooth connecting the central cusp with the lingual and labial cusps. The lower gomphodont postcanines are less expanded buccolingually than the upper, and orientated obliquely or parallel to the long axis of the lower jaw. They feature the same basic morphology with large central, labial and lingual cusps, the last two somewhat displaced (anteriorly and posteriorly, respectively) from the extremes of the crown. Large cuspules on the tooth margin form the cingulum around the central cusps, generally eight in number. The maxilla lacks the platform lateral to the dental series. The ventral margin of the dentary displays a slight curvature.

Comments: In only two of the specimens listed in Table 1 is it possible to examine the shape of the postcanines in crown view. The diagnosis for *L. modisei* is thus based on the upper gomphodont teeth observed in NMQR 3255 and NMQR 3251 and the lower gomphodont teeth examined in the latter specimen. All of the remaining individuals are assigned to the new species based on the absence of the platform of the maxilla lateral to the teeth series, and the curvature in the ventral margin of the dentary. The last trait is not entirely reliable, as in some specimens (e.g. BP/1/5362, 5363) the ventral margin of the dentary is straight.

DESCRIPTION

SKULL ROOF

The largest skull of *L. modisei* has a basal length of 113 mm (see Table 2 for measurements in most complete specimens of *L. modisei*), somewhat larger than the largest representative of *T. berryi*. However, most of the specimens of these species show a comparable skull size (see Tables 3 and 4), well below the 160–200 mm found in *C. metabolus*. As in *T. berryi*, the snout is subequal in length to the temporal region, whereas the zygomatic arch extends almost parallel to the skull, forming a more or less rectangular temporal opening (Fig. 2).

The premaxilla has a well-developed internasal process that outlines the external naris, and is clasped deeply between the anterior portions of the nasals. Only the posterodorsal process of the septomaxilla is preserved in NMQR 3255, which is embraced in the anterodorsal margin of the maxilla (Fig. 3). There is a small septomaxillary foramen between the posterodorsal process of the septomaxilla and the maxilla. The maxilla in *L. modisei* curves gently at its ventral margin, reaching the row of postcanines. In contrast,

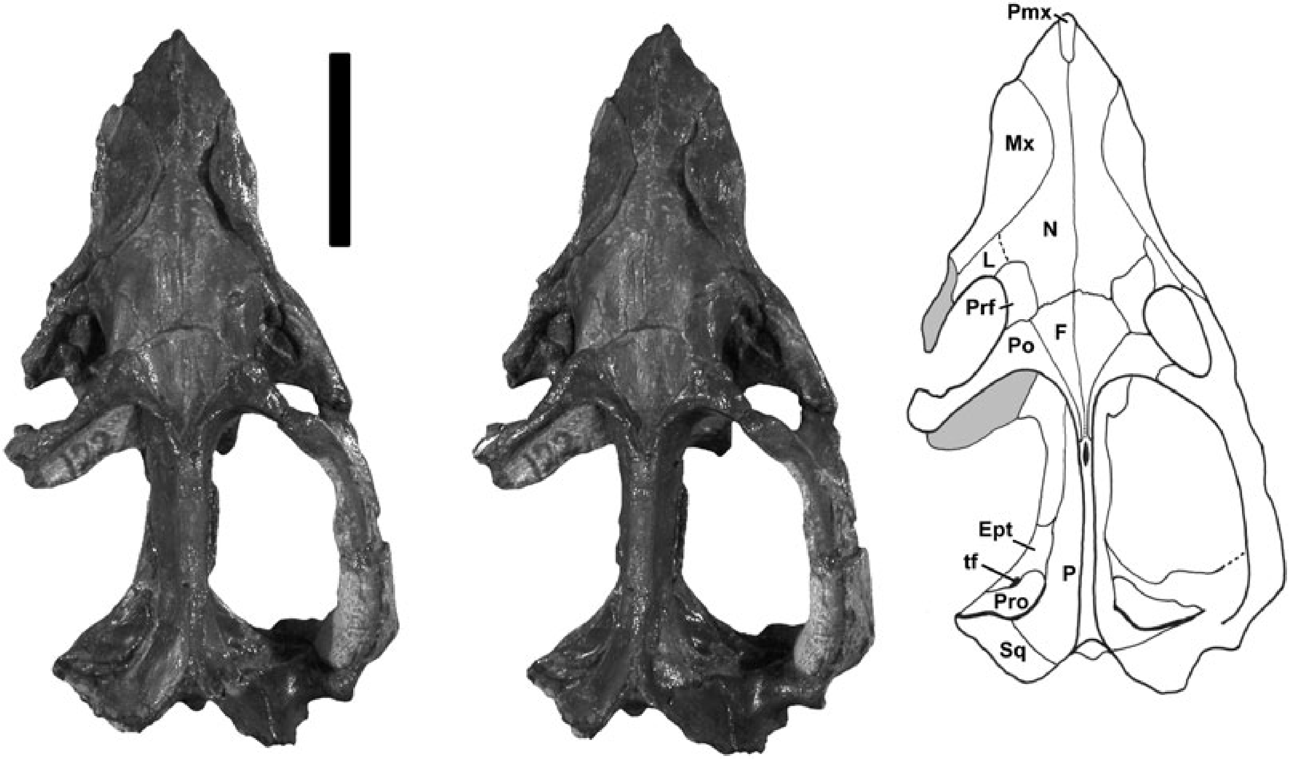

Figure 2. Stereopair and interpretative drawing of NMQR 3255, holotype of *Langbergia modisei*, in dorsal view. Ept, epipterygoid; L, lacrimal; Mx, maxilla; N, nasal; F, frontal; P, parietal; Pmx, premaxilla; Po, postorbital; Prf, prefrontal; Pro, prootic; Sq, squamosal; tf, trigeminal foramen (for maxillary and mandibular divisions of the trigeminal nerve). Note that bones in the facial region (maxillae, nasals, lacrimals, and prefrontals) are not in their original position. Shading indicates a broken portion (in the jugal) and sediment posteriorly of the postorbital bar. Scale bar = 3 cm.

Table 2. Cranial measurements of *Langbergia modisei* (in mm)

	BP/1/5362	NMQR 3255	NMQR 3251	NMQR 3256	CGP 1/33
Total length of the skull	113	99		82	90*
Muzzle length	49	43	40	35	40*
Orbital length	18	16		11	11
Temporal region length	48	40		25	30
Interorbital distance	23	22		19	20
Transverse process width		25	21		
Palate length	46	39	34		32
Upper dental series length	57	52	49*	42	45
Maximum skull width	72	68		54	66
Mandibular length	99			73	
Length from the tip to the angle of the mandible	79			61	63
Lower dental series length			46		

*Estimated.

Measurements are defined in Abdala & Giannini (2000: fig. 2) except for the upper dental series length, the length from the tip to the angle of the mandible, and the lower dental series length.

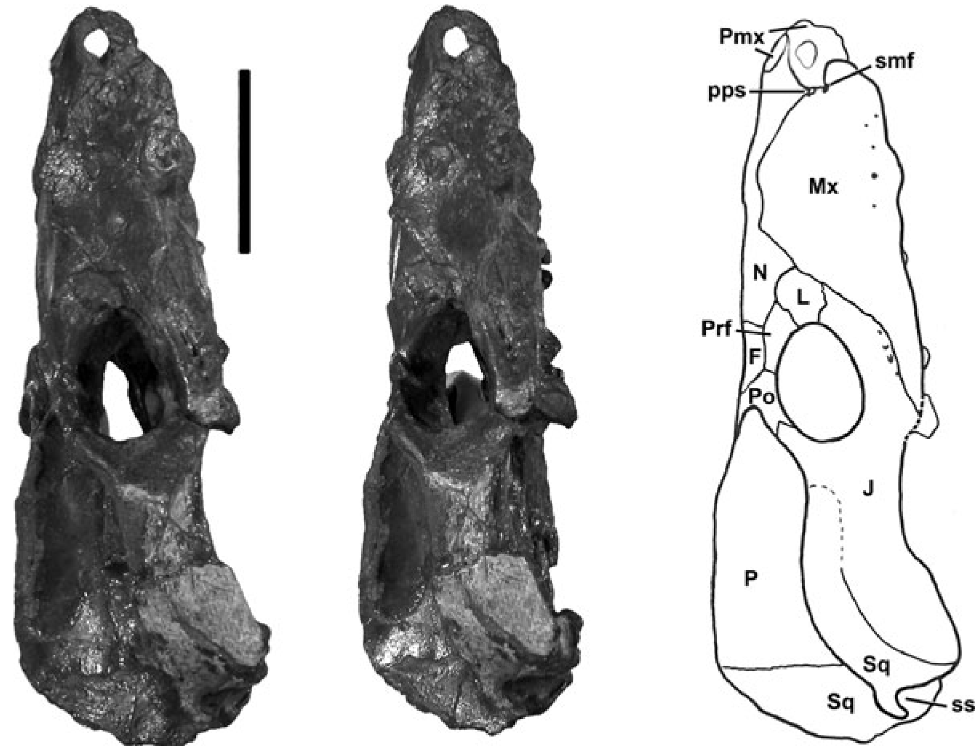

Figure 3. Stereopair and interpretative drawing of NMQR 3255, holotype of *Langbergia modisei*, in right lateral view. J, jugal; L, lacrimal; Mx, maxilla; N, nasal; F, frontal; P, parietal; Pmx, premaxilla; Po, postorbital; Prf, prefrontal; pps, posterodorsal process of the septomaxilla; smf, septomaxillary foramen; Sq, squamosal; ss, squamosal sulcus. Note that bones in the facial region (maxillae, nasals, lacrimals, and prefrontals) are not in their original position. Scale bar = 3 cm.

Table 3. Relationships between the basal skull length (BSL), postcanine number, diastema between the canine and first postcanine, and the number of sectorial posterior postcanines in *Langbergia modisei*. The presence or absence of a diastema refers only to upper dentition; in the lower dentition there is always a diastema between the canine and first postcanine

Number	BSL	Postcanine number	Diastema	Sectorial teeth number
BP/1/5362	113	7?	?	2?
NMQR 3255	99	7	Absent	3
NMQR 3268	90*	8	Absent	2?
CGP 1/33	90*	7/8?	Absent	3
NMQR 3256	82	6–7?	Present?	?
NMQR 3251	80*	9/8	Absent	3/3
BP/1/5363	80*	8	Absent	2
NMQR 3281	70	9–10?	Absent	1?
NMQR 3280	67	9/6–7?	Absent	3
SAM-PK-11481	66	9	Absent	2?

*Partial skull. The measurement is an estimation of the skull length.
The postcanine and sectorial teeth numbers refer to upper dentition only, except when the number is to the right of the slash, indicating lower postcanines.

the maxilla in *T. berryi* and *C. metabolus* curves sharply inward to form a platform lateral to the postcanine teeth. A shallow depression is present on the highest portion of the maxilla, close to its suture with the nasal in NMQR 3268 and BP/1/5363. This depression is also present in long-snouted cynodonts such as *Cynognathus*, *Diademodon* and some traversodontids. Many small nutritive foramina are visible in the

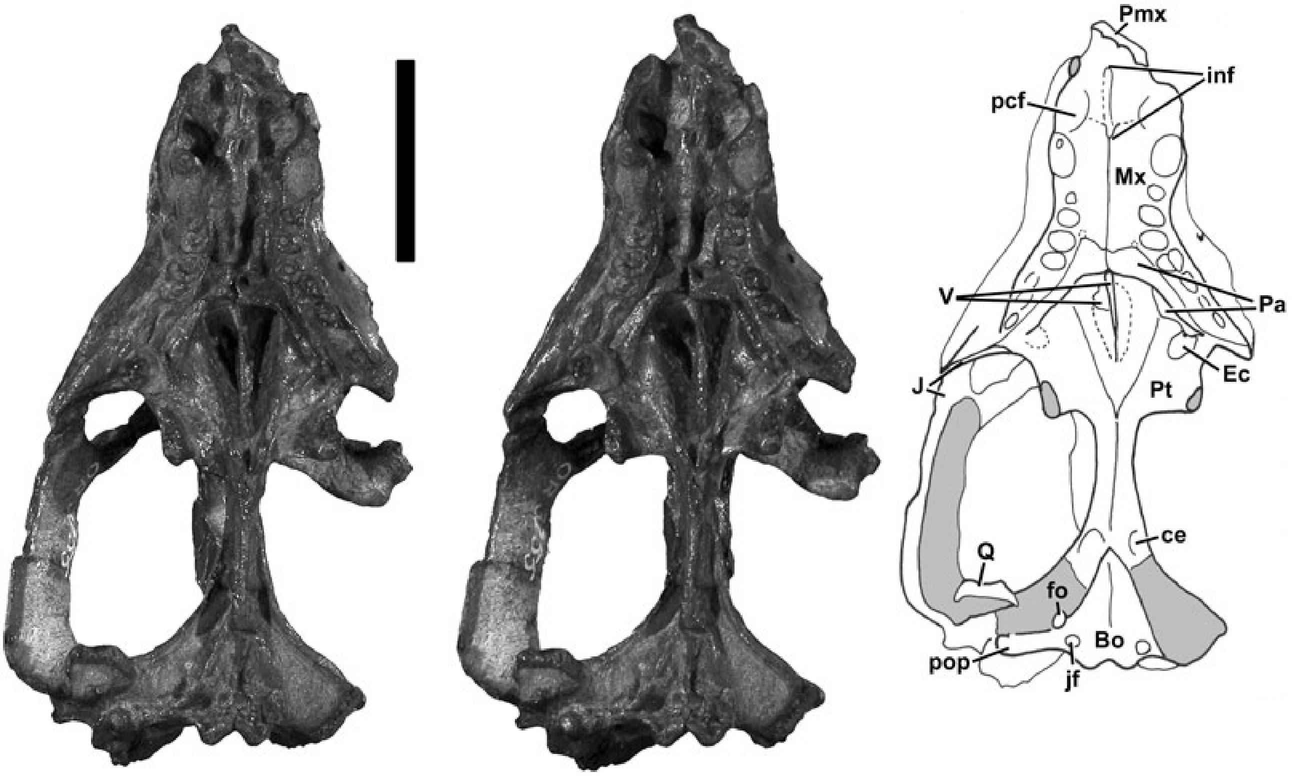

Figure 4. Stereopair and interpretative drawing of NMQR 3255, holotype of *Langbergia modisei*, in ventral view. Bo, basioccipital; ce, cavum epiptericum; Ec, ectopterygoid; fo, fenestra ovalis; inf, incisive foramen; jf, jugular foramen; J, jugal; Mx, maxilla; Pa, palatine; pcf, paracanine fossa; Pmx, premaxilla; pop, paroccipital process; Pt, pterygoid; Q, quadrate; V, vomer. Shading indicates a broken portion (in the pterygoid flanges) and sediment covering part of the basicranium and zygoma. Scale bar = 3 cm.

Figure 5. Stereopair and interpretative drawing of the lateral wall of the braincase in NMQR 3255, holotype of *Langbergia modisei*. Ept, epipterygoid; otg, external orbitotemporal groove; pao, pila antotica of the prootic; P, parietal; Pro, prootic; Sq, squamosal; tf, trigeminal foramen. The dashed lines indicate broken and displaced surfaces of the epipterygoid. Shading indicates the broken surface of the prootic. Scale bar = 1 cm.

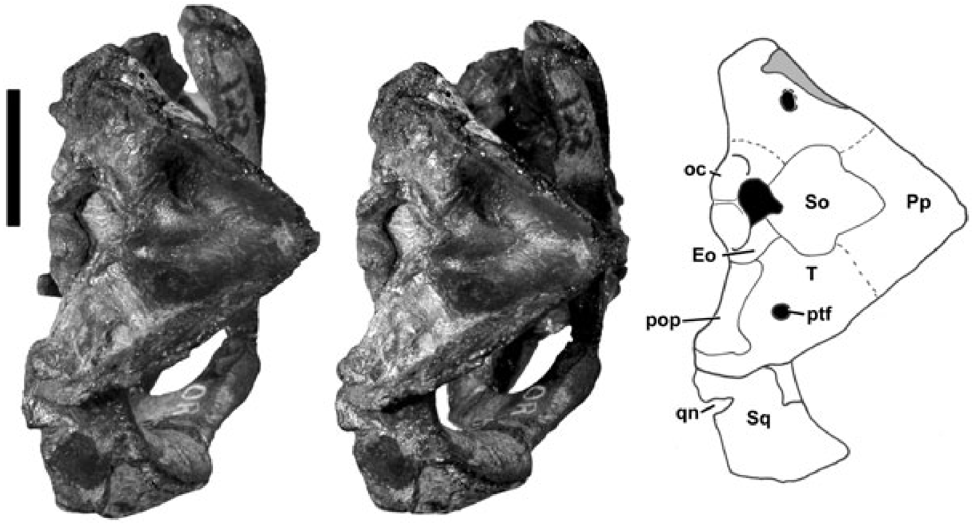

Figure 6. Stereopair and interpretative drawing of NMQR 3255, holotype of *Langbergia modisei*, in occipital view. Eo, exoccipital; pop, paroccipital process of the opistotic; oc, occipital condyle; Pp, postparietal; ptf, post-temporal foramen; qn, quadrate notch of the squamosal; So, supraoccipital; T, tabular; Sq, squamosal. Shading indicates the broken surface of the bone. Scale bar = 2 cm.

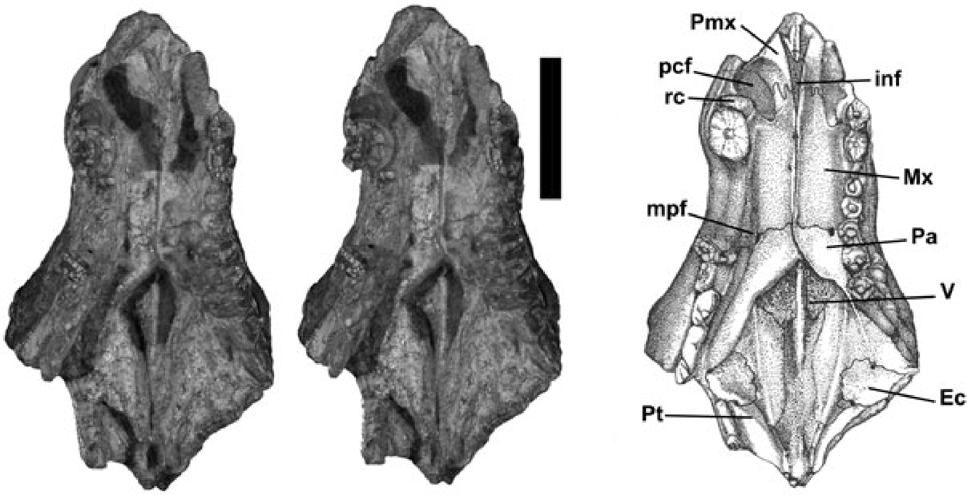

Figure 7. Stereopair and interpretative drawing of the palate of NMQR 3251. Ec, ectopterygoid; inf, incisive foramen; mpf, major palatine foramen; Mx, maxilla; Pa, palatine; pcf, paracanine fossa; Pmx, premaxilla; Pt, pterygoid; rc, replacement canine; V, vomer. Scale bar = 2 cm.

maxilla of NMQR 3255, at the level of the canine (Fig. 3). The maxilla in this specimen also shows an infraorbital foramen anteroventrally orientated, located slightly forward to the orbit, at the level of the third postcanine. This foramen is remarkably more developed in the left side of the specimen (see Fig. 4). The infraorbital foramen in the maxilla of *T. berryi* specimens is larger than in NMQR 3255 and in many cases (BP/1/4258, SAM PK K7888, NMQR 1342, see also Broom, 1911: 906) double, with the anterior one usually more developed and orientated anteriorly.

The frontals are located slightly below the level of the postorbital bones. The latter converge posteriorly, contributing to a long temporal crest formed mostly by the parietals (Fig. 2). A small parietal foramen opens in the anterior half of the crest in CGP 1/33 and NMQR 3280. The foramen is a long cleft in the holotype NMQR 3255, whereas in the largest skull (BP/1/5362) an elongated space is present between the parietals, behind the posterior processes of the postorbitals. This space is interpreted as a remnant of the parietal foramen. The

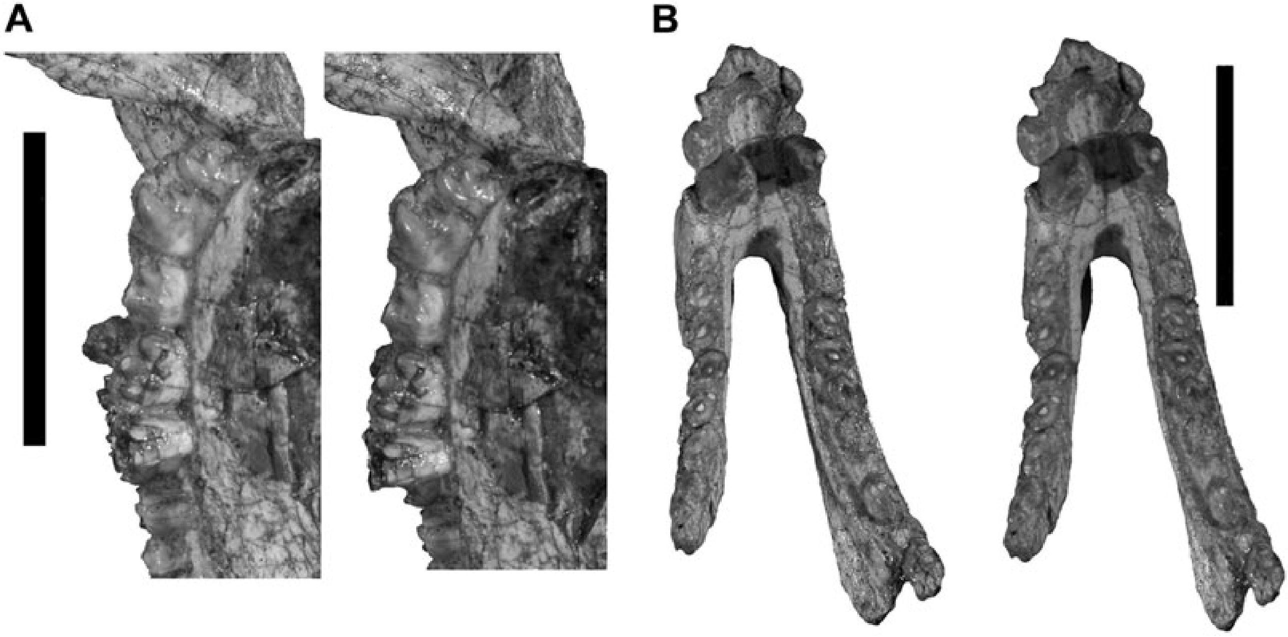

Figure 8. Stereopair of NMQR 3251. A, last left postcanines in lateral view (anterior, bottom). B, lower jaw in occlusal view. Note the replacement of the canine in the left ramus of the lower jaw. Scale bars = 2 cm.

Table 4. Relationships between the basal skull length (BSL), postcanine number, diastema between the canine and first postcanine, and the number of sectorial posterior postcanines in *Trirachodon berryi*. The presence or absence of a diastema refers only to upper dentition

Number	BSL	Postcanine number	Diastema	Sectorial teeth number
BM R3579	100*	11	Present	0
NMQR 1399	100*	?	?	1
AM 461	97*	9	Absent	1
BP/1/4658	96	8/9	Present	1/2
BP/1/3775	96*	8–9?	Absent?	?
SAM-PK-K7888	90*	10/9	Present	0/0
BSP 1934 VIII 21	90*	12	Absent	0/0
BM R 3306	87*	7–8?	Absent	?
CGP/1/79	87	8	Present	1?
BP/1/4661	86*	7/6?	Absent	1?
BM R3307	77*	7	Absent	0
BP/1/4258	75*	6?	Present	?
BP/1/3511	52	6	Present	2
SAM-PK-K171	?	8/8	Absent	1?/1

*Partial skull. The measurement is an estimation of the skull length.
The postcanine and sectorial teeth numbers refer to upper dentition only, except when the number is to the right of the slash, indicating lower postcanines.

relative position of the parietal foramen shows variation in relation to the skull size. In the small individual NMQR 3280, it is located in the anterior portion of the sagittal crest, whereas in the larger NMQR 3255, the foramen is more posteriorly located. The parietal foramen shows some variation in *T. berryi*: in the well-preserved skull AM 461 the foramen is absent, whereas a tiny opening can be observed in AM 434 (with a skull size approximately similar to AM 461) and BMNH 3307.

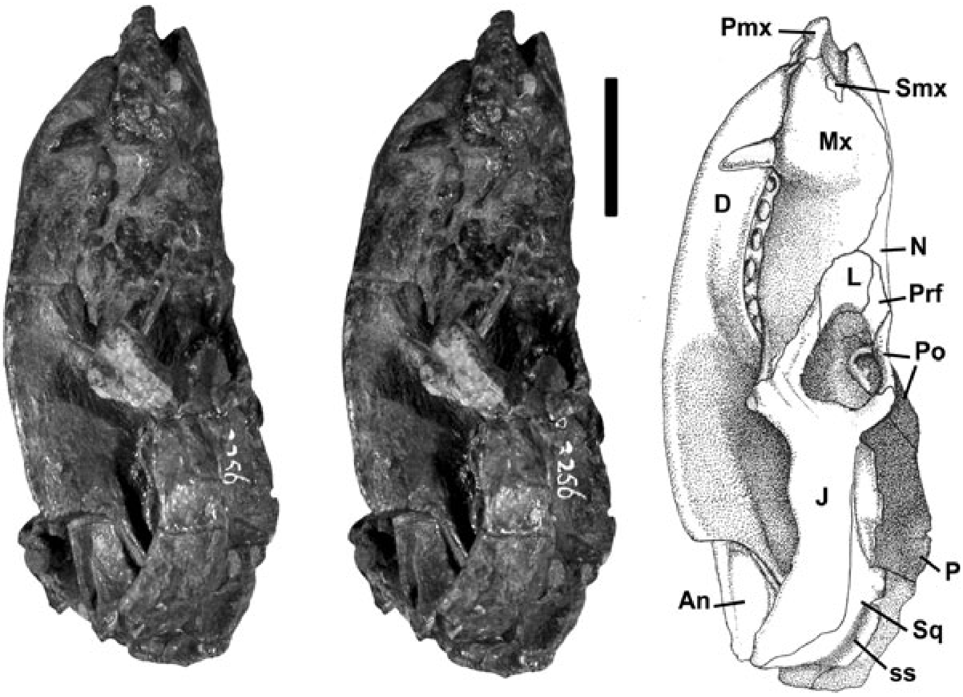

Figure 9. Stereopair and interpretative drawing of NMQR 3256, in left lateral view. An, angular; D, dentary; J, jugal; L, lacrimal; Mx, maxilla; N, nasal; P, parietal; Pmx, premaxilla; Po, postorbital; Prf, prefrontal; Smx, septomaxilla; Sq, squamosal; ss, squamosal sulcus. Scale bar = 2 cm.

PALATE

The palate extension represents 36–39% of the basal length in the new species, values quite close to the 41% documented in *T. berryi*. The palate either extends up to the level of the fourth postcanine (NMQR 3255, NMQR 3268) or between the fifth and sixth postcanines (NMQR 3251). Most of the margins of the incisive foramen are formed by the premaxilla, but the posterior border is delimited by the maxilla (Fig. 4). This is also the condition observed in *T. berryi* (BP/1/4658). A deep paracanine fossa is located anteromedially to the large upper canine. In *Langbergia* and *Trirachodon*, the lateral margin of the fossa is formed by the maxilla, whereas the premaxilla and maxilla contribute to its medial margin. The contribution of the palatine to the osseous secondary palate is remarkably short (Fig. 4).

The long, vertical plate of the vomer is extended behind the choana as a ventral keel, almost reaching the level of the base of the pterygoid processes. The latter are robust and directed ventrally and slightly posteriorly. The high lateral pterygoid crests are directed posteromedially and they meet in the anterior portion of the thin basicranial girder. The ectopterygoid in NMQR 3251 appears as a quadrangular in outline bone at the base of the lateral margin of the pterygoid process. An ectopterygoid foramen is present. This bone is also visible in the left side of NMQR 3255 where it appears to be dislocated from its original position (Fig. 4). A facet on the pterygoid for the unpreserved ectopterygoid was also observed in *T. berryi* (BP/1/4658).

As in *Trirachodon*, a thin basicranial girder is formed by a median rostrum of the parasphenoid, covered laterally by the posterior projections of the pterygoid. The basioccipital and basisphenoid–parasphenoid form a triangular plate in ventral view, with a thin, low central crest all along its extension. The paroccipital process is well developed, with its distal margin slightly projected ventrally.

ZYGOMA AND TEMPORAL REGION

A series of small foramina opens on the suture between the maxilla and the jugal in NMQR 3255 (Fig. 3), whereas only one seems to be present in CGP 1/33. In *Trirachodon* (SAM PK K171, BP/1/4661) there are one to three foramina on the suture between the jugal and the maxilla or in the anterior margin of the jugal, close to the aforementioned suture. The lacrimal in NMQR 3268 shows a large ventral and tiny dorsal foramina disposed internally to the orbits. A very small foramen is also present in the facial exposure of the lacrimal in front of the orbit. The descending process of the jugal is a small convex projection at the level of the posterior border of the orbit (see Fig. 9). In BP/1/5363, the process is smaller than in other specimens, but more ventrally projected.

The temporal opening shows the same width throughout the entire temporal region. The zygoma is robust and high, with the tall posterior portion of the jugal reaching the posterior end of the zygomatic arch (Figs 3, 9). The zygomatic portion of the squamosal projects anteriorly and dorsally as a small wedge that extends close to the base of the postorbital bar. The squamosal sulcus is an incipient projection on the lateral surface of the zygoma and notably more developed on the posterior face of the squamosal (Fig. 3), where the sulcus is directed medially and then ventrally.

The quadrate is preserved in NMQR 3255 (Fig. 4), whereas the quadrate/quadratojugal complex is preserved in CGP 1/33 and in the juvenile SAM-PK-K11481. The general morphology of this bone complex is similar to that of *Trirachodon* (Crompton, 1972b: plate 2). The dorsal plate of the quadrate is directed dorsally, and the trochlea is cylindrical without the ventrally projected lateral condyle that externally limits the trochlear trough observed in *Cynognathus* and some traversodontids (Luo & Crompton, 1994; Abdala & Teixeira, 2004). The quadrate and quadratojugal are clearly separated in the juvenile, although their condition is not clear in adults (in CGP 1/33 there is an indication of a possible suture between these bones). Medially, the quadrate is in contact with the quadrate ramus of the epipterygoid and the squamosal, the latter interposed between the paroccipital process and the quadrate. CGP 1/33 shows a poorly preserved right stapes. As in *Thrinaxodon*, the anterior crus of this bone seems to be more developed than the posterior crus (Fourie, 1974: fig. 25B).

BRAINCASE

The external orbitotemporal groove, running between the parietal/squamosal dorsally and posteriorly and the epipterygoid/prootic ventrally and anteriorly, is well developed, with a large vascular foramen in the anterior portion of the prootic. The lateral wall of the braincase is preserved in NMQR 3255, 3256, and 3280. The epipterygoid shows an ascending lamina with practically the same extension anteroposteriorly as the anterior lamina of the prootic (Fig. 5). A similar condition is also present in *Trirachodon* (BP/1/4658; see also Gow, 1986: fig. 3A). In NMQR 3255, the anterior lamina of the prootic is notably concave outwards, whereas the epipterygoid is broken and somewhat displaced from its natural location (Fig. 5). Only one opening for the exit of the trigeminal nerve is observed between the alisphenoid and prootic in NMQR 3255, but the damaged condition of the epipterygoid in this specimen hampers confidence in the definitive number of openings. Two openings are present in the small NMQR 3280, the ventral one being more developed. A similar condition is also known in *Trirachodon* (Gow, 1986: fig. 3A).

OCCIPUT

In occipital view (Fig. 6), the skull is triangular, showing a well-developed V-shaped notch developed between the lambdoidal crest and the zygomatic arch. The exoccipitals form the occipital condyles, which are connected at their bases by a neck formed by the basioccipital. The exoccipitals have a swelling on the rim of the foramen magnum, next to the dorsal border, for articulation with the proatlas. These structures are incipient in NMQR 3255, but well developed in NMQR 3256.

The supraoccipital forms the dorsal margin of the foramen magnum and extends above the latter for practically one-third of the height of the occipital plate (Fig. 6). The uppermost dorsal extension of the supraoccipital forms a wide median ridge, which borders the rounded parasagittal fossae formed at the suture between supraoccipital and postparietal. The circular post-temporal foramen is completely encircled by the tabular.

LOWER JAW

The dentaries are fused at the symphysis. In many specimens (e.g. NMQR 3256, NMQR 3280) the ventral edge of the dentary is notably convex (Fig. 9). Variation exists in the pattern of the angle of the dentary: in CGP 1/33, NMQR 3256 and BP/1/5362 the angle is almost 90°, whereas in NMQR 3280 it is slightly wider (*c*. 110°). The masseteric fossa extends up to the level of the sixth and seventh postcanines (the first and second sectorial teeth, respectively) in NMQR 3251. The dorsal limit of the fossa is prominent, particularly in CGP 1/33, because of the presence of a sharp ridge in the dorsal margin of the dentary at the beginning of the coronoid process.

The postdentary bones are preserved in NMQR 3256 (Fig. 9) and BP/1/5362. The anterior portion of the splenial is a lamina extended towards the symphysal region, whereas posteriorly it is a more robust bone extending close to the angle of the dentary. This bone is covered laterally and ventrally by the dentary.

In lateral view the postorbital rod is formed by the angular and surangular in a similar way to that in *Trirachodon* sp. (see Crompton, 1963: fig. 10). The angular is widely exposed posterolaterally, being somewhat concave externally and covered dorsally by the lateral ridge of the dentary. In its posterior extension, the angular is covered dorsally and posteriorly by a strip of bone formed by the surangular. The reflected lamina of the angular is preserved on the left side of BP/1/5362, being a thin projection somewhat expanded distally. The lamina is similar, although comparatively longer, to that illustrated by Crompton (1963: fig. 10) in *Trirachodon*. Somewhat anterior to the craniomandibular joint, the surangular shows a slight projection laterally (articular boss), that contacts the descending flange of the squamosal. As in *Trirachodon* (Crompton, 1972b: plate 2), a prominent retroarticular process of the articular orientated ventrally is observed in BP/1/5362.

DENTITION

As is common in most of the basal eucynodonts, four upper and three lower peg-like incisors are present. The upper incisors point downwards, whereas the lower ones are directed anterodorsally. They are slightly recurved and circular in cross-section, with no ridges or serrated edges. The upper and lower canines are well developed with serrations along the anterior and posterior margins. In NMQR 3251 and 3268, the upper canines are being replaced, with the new teeth emerging anteriorly to the older ones (Fig. 7). In NMQR 3251, the lower canines are being replaced, with the new ones emerging posterior to the older ones (Fig. 8B). Most of the specimens do not exhibit a diastema between the upper canine and the first postcanine (see Table 3), but a diastema is present and mostly well developed behind the canine in the lower jaw.

Between seven and eight postcanines are normally borne by the maxilla (Table 3). The first tooth is generally simple, whereas the number of posterior sectorials varies between two and three in specimens where it is possible to observe these elements with certainty (Table 3). The holotype of *L. modisei* (NMQR 3255) shows seven upper postcanines: a poorly developed simple anterior tooth, three buccolingually expanded gomphodont teeth and three sectorial teeth (Fig. 4). In addition, this specimen shows the replacement of the anterior-most sectorial by a gomphodont (Figs 4, 10A), a condition also observed in *C. metabolus* (Crompton, 1955).

The description of the upper postcanines of *L. modisei* is based on specimens NMQR 3251 and 3255. The postcanines increase in size posteriorly up to the fourth or fifth tooth before decreasing in size again. The first tooth is remarkably small, compared with the remaining postcanines, and features a single blade-like cusp. In occlusal view, the gomphodont teeth are circular to ovoid, with the long axis of the postcanine orientated at right angles to the long axis of the skull and its width only slightly larger than its anterior–posterior length (Figs 7, 10A). It is dominated by a large central cusp, with smaller labial and lingual cusps on the extremities. A transverse ridge connects the labial and lingual cusps with the central cusp. A crenulated ridge, consisting of small accessory cusps, borders the anterior and posterior rims of the postcanine (Fig. 10A). In both upper and lower gomphodont postcanines, the size of the accessory cusps decreases anteriorly and posteriorly so that the postcanines appear tricuspid in lateral view. Shallow fossae are formed between the crenulated and transverse ridges.

The lower postcanines, only visible in occlusal view in NMQR 3251, are slightly smaller than the upper postcanines and their transverse axes orientated at approximately 45° relative to the long axis of the lower jaw (Fig. 10B). The first tooth is simple, featuring a sectorial margin formed by a main cusp, an anterior accessory cusp, and an incipient posterior accessory cusp. In addition, it carries a cingulum lingually expressed as a faint ridge. The morphology of this tooth is notably similar to the P-type postcanines of *Procynosuchus* (Kemp, 1979), although no cuspules are discernible in the lingual cingulum. Gomphodont lower postcanines also show three main cusps with a large, central cusp located in the middle of the crown. The labial and lingual cusps differ, however, in that they are located slightly in front of and behind the transverse ridge, respectively (Fig. 10B). Development of the crenulated ridge is also asymmetrical, so that the cusps immediately behind the lingual cusp and immediately in front of the labial cusp are larger than the rest of the ridge. Consequently, the crenulated ridge is highest at the anteriolingual and posterolabial margins.

Upper and lower sectorial postcanines show many similarities with the postcanine teeth of *Thrinaxodon*. In NMQR 3251, the sectorial postcanines are oval in occlusal view, with the long axis orientated anteroposteriorly. The upper postcanines show a main cusp curved backwards, one large anterior accessory cusp, and two posterior accessory cusps, the second one being tiny (Fig. 10C). Four sectorial cusps are also observed in NMQR 3255, as well as a lingual cingulum composed of four to five cuspules (Fig. 10D). The largest cuspule of the cingulum is located at the level of the main cusp and anterior accessory cusp, followed by an isolated tiny cuspule located in the middle of the cingulum (Fig. 10D). Two posterior cuspules and a short crest form the posterior portion of the lingual cingulum. The lower sectorial postcanines in NMQR 3251 are similar to the uppers, except that

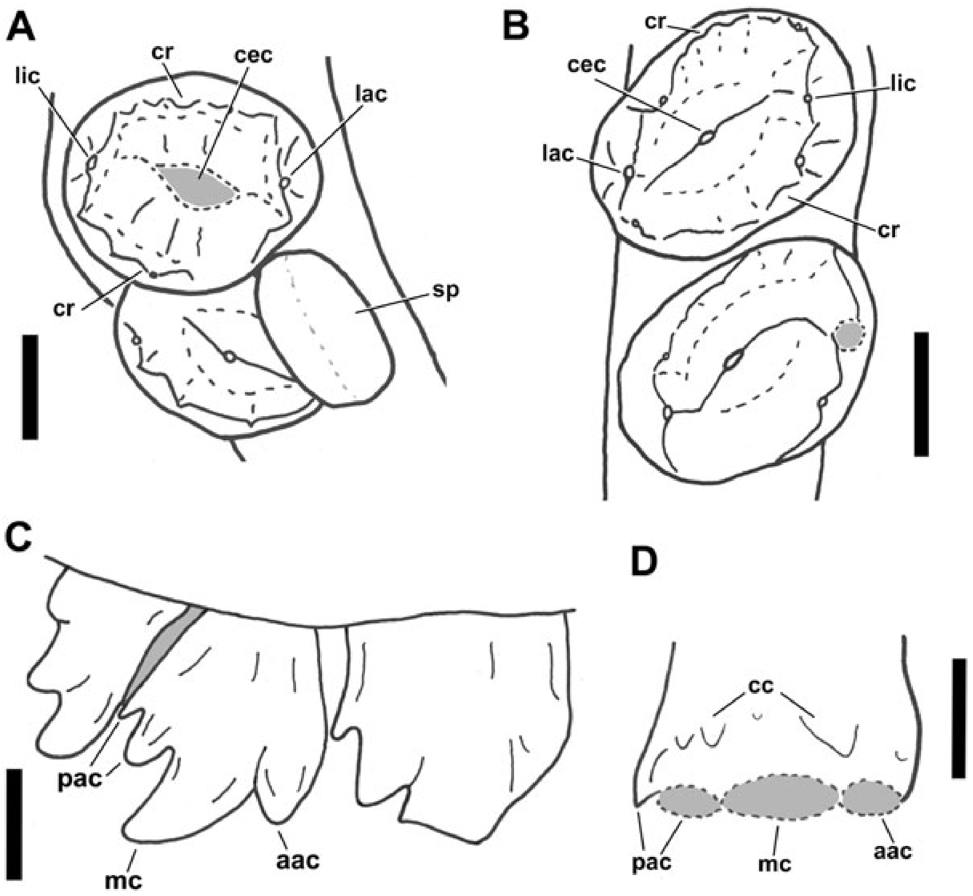

Figure 10. Postcanine teeth of *Langbergia modisei*. A, third and fourth upper left postcanines of the holotype NMQR 3255 in occlusal view. Note the replacement of the sectorial teeth by a gomphodont. B, third and fourth lower left postcanines of NMQR 3256 in occlusal view. C, last three right sectorial upper postcanines of NMQR 3256 in labial view (see also Fig. 8A). D, left sectorial upper postcanine of NMQR 3255 in lingual view. aac, anterior accessory cusp; cc, cingular cusps; cec, central cusp; cr, crenulated ridge; lac, labial cusp; lic, lingual cusp; mc, main cusp; pac, posterior accessory cusp; sp., sectorial postcanine. Scale bars = 2 mm.

the lingual cingulum is less prominent. The latter is formed by an anterior cuspule followed by a ridge and a series of tiny cuspules along the posterior portion of the crown.

DISCUSSION

SOUTH AFRICAN TRIRACHODONTIDS

After examination of all the relevant material of South African trirachodontids, we believe that there is no clear morphological differentiation between *T. berryi* and *T. kannemeyeri* from Subzone B of the *Cynognathus* AZ. Accordingly, we consider the latter species a junior synonym of *T. berryi* following Hopson & Kitching (1972). The skull morphology of *L. modisei* appears remarkably similar to that of *T. berryi*, whereas its comparison with *C. metabolus* is hampered by a lack of well-preserved and complete specimens of the latter (see Abdala *et al*., 2005). The most notable cranial difference between the new species and the other trirachodontids is the absence of the maxillary platform lateral to the postcanine series in *L. modisei*, a condition only known in *Diademodon* among gomphodont cynodonts (Abdala & Ribeiro, 2003). Other diagnostic features of the new species are based on the shape of the postcanine teeth. The upper postcanine in the new species is circular to slightly ovoid in outline, and the central cusp of the transverse ridge is located in the middle of the crown. The morphology of the upper postcanines in *T. berryi* is clearly more ellipsoid, with the buccolingual extension significantly broader than the anteroposterior length and the central cusp of the transverse ridge frequently positioned closer towards the lingual cusp. The latter condition is also present in *C. metabolus*, which differs from *T. berryi* only in that the gomphodont upper teeth are more ovoid in outline (Fig. 11).

Skull sizes seem to be quite similar in *L. modisei* and *T. berryi*, with larger skulls ranging from 100 to 113 mm in length (see Tables 3 and 4). *Cricodon*, on the other hand, is significantly larger, with skull lengths ranging from 160 to 200 mm or even more (Abdala *et al*., 2005). Most of the specimens of *L. modisei* do not show a diastema between the upper canine and the first postcanine. As a general trend, the number of upper postcanines of *L. modisei* decreases from nine in smaller specimens to seven in larger ones, whereas the sectorial postcanine number oscillates between one and three, apparently being independent of the size of the specimen (Table 3). The condition of the postcanine series is particularly remarkable in the holotype of *L. modisei*, showing practically the same number of gomphodont and sectorial teeth. Thus, three gomphodont teeth are followed by three sectorial ones, with the first of the sectorial elements on the left side in the process of replacement by a gomphodont tooth (see Fig. 10A). The postcanine series in the larger sample of *T. berryi* appears to be more variable than in *L. modisei*. The presence or absence of a diastema between the upper canine and the first postcanine has a random distribution in *T. berryi* and appears to be independent of the size or number of postcanines present in the specimen. The number of upper postcanines in *T. berryi* varies between six and 12, whereas sectorial teeth reach a maximum of two and are absent in some specimens (Table 4). It is not possible to recognize a clear ontogenetic trend in the number of postcanines of this species, but it is interesting to note that there are no sectorial teeth at the back of the postcanine row in the three specimens with the greatest number of postcanines (BM R3579; BSP 1934 VIII 21; SAM-PK-K-7888; see Table 4).

Examination of BP/1/995 (formerly assigned to *Silphedocynodon gymnotemporalis*) from the *Cynognathus* AZ does not support the trirachodontid relocation proposed by Kitching (1977). The specimen, indeed a juvenile, is poorly preserved. The postcanine morphology cannot be asserted with certainty, but it seems to be more plausible that it corresponds to a sectorial cynodont. We consider BP/1/995 as Cynodontia *incertae sedis*.

The distribution of trirachodontid species in the Karoo seems to have a fairly direct correlation with different biostratigraphic horizons. Thus, *L. modisei* is restricted to the older Subzone A of the *Cynognathus* AZ, *T. berryi* appears in outcrops of the classical [i.e. *Cynognathus* AZ of Kitching (1977, 1995)] Subzone B, and *Cricodon* is found in the younger Subzone C in the main Karoo Basin, as well as in the Manda Formation of Tanzania. We should mention, however, that specimen SAM-PK-5881 collected from the farm Erf 1, Aliwal North, corresponding to Subzone B, shows large, ovoid in outline, upper postcanines resembling the pattern of *Cricodon*. In addition, the large skull BP/1/5362 from the farm Langberg (Table 3) shows seven upper postcanines and a curved lower margin of the mandible, but a platform seems to be present lateral to the postcanine series. However, the snout is distorted, with the maxilla on both sides broken, and postmortem deformation could thus be responsible for the presence of the lateral platform. We tentatively include the specimen in *L. modisei*, but an alternative identity as *T. berryi* cannot be completely ruled out. Finally, the skull NMQR 3279 from the locality of Kestell has a maxillary platform lateral to the postcanines, indicating the presence of *T. berryi* in Subzone A.

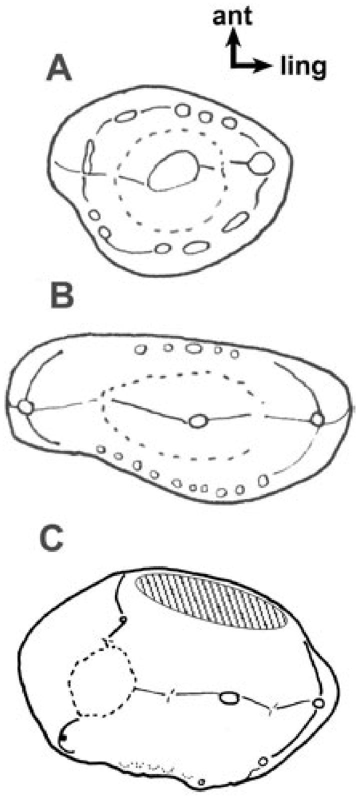

Figure 11. Upper postcanine morphology of the three South African trirachodontids. A, *Langbergia*. B, *Trirachodon*. C, *Cricodon*. The hatched pattern indicates wear. Modified from Abdala *et al*. (2005).

NON-SOUTH AFRICAN TRIRACHODONTIDS

Other known species of trirachodontids include *Sinognathus gracilis* from the Upper Ermaying Formation, China (Sun, 1988) and the recently reassigned *Neotr-*

irachodon expectatus from the Donguz Formation, Russia (Tatarinov, 2002). The first species, represented by a single skull with an occluded lower jaw, was originally considered a member of the family Cynosuchidae and closely related to *Thrinaxodon* (Young, 1959). Subsequent preparation of this material revealed trirachodontid-like postcanines (Sun, 1988). The poorly preserved upper postcanines have an ellipsoid morphology that resembles that of *T. berryi*, but no cingular cusps are preserved on the anterior and posterior margins of the teeth (Sun, 1988: fig. 4). In cranial morphology, the Chinese species is notably distinct, because of its extremely short snout and extraordinarily expanded temporal opening. The latter trait makes this species one of the cynodonts with the widest temporal region in the skull. In addition, the zygoma attains its wide expansion in the middle of the temporal region and the suborbital process of the jugal seems to be absent.

A left dentary with postcanines was recently reassigned to the new Russian species *Neotrirachodon expectatus* (Tatarinov, 2002). This specimen was originally identified as the traversodontid *Antecosuchus ochevi* (Tatarinov, 1973, 1988), whereas Battail & Surkov (2000) considered it as a bauriid therocephalian closely related to the Chinese bauriid *Traversdontoides wangwuensis*. Reassignment of the material to Trirachodontidae, as proposed by Tatarinov (2002), is based on skull size (approximately 12 cm) and the shape of the postcanines. In the best-preserved and newly erupted postcanine 7, the overall morphology is reminiscent of the trirachodontid pattern, with the presence of a transverse crest and cingular cusps on the margin. Unlike trirachodontids, however, the transverse crest in *Neotrirachodon* is displaced towards the anterior portion of the teeth (without reaching the margin) and is formed by two cusps, the lingual one removed from the margin of the teeth. In addition, numerous cingular cusps are located on the labial and lingual margins of the teeth. These pronounced differences hamper a reliable assignation of *Neotrirachodon expectatus* to Trirachodontidae and we consider this Russian taxon as a Gomphodontia *incertae sedis*. It should be mentioned, however, that two cusps forming the transverse crest and the anterior location of the latter are traits typical of traversodontids (Abdala & Ribeiro, 2003). The lower postcanines of *Neotrirachodon* appear to represent some kind of transitional stage between the trirachodontid and traversodontid condition in gomphodont teeth. New material of this enigmatic taxon is needed to provide a more precise taxonomic placement.

The remaining record of trirachodontids consists of isolated teeth from the Yerrapali Formation, India (Bandyopadhyay & Sengupta, 1999) and from the Redonda Formation, USA (Lucas *et al*., 1999), as well as a series of skulls from the Omingonde Formation, Namibia (Keyser, 1973; Smith & Swart, 2002). The teeth from the Yerrapali Formation remain undescribed and have only been reported in faunal and taphonomic studies (e.g. Bandyopadhyay & Sengupta, 1999). The three teeth from the Redonda Formation should be considered with caution, because the shape of the crowns does not closely match the trirachodontid pattern (i.e. two of them lack cingular cusps on one of the buccolingually expanded margins). Furthermore, the strongest evidence presented by Lucas *et al*. (1999) to demonstrate the cynodont affinity of these teeth is the presence of columnar enamel. However, enamel with columns [or columnar units in prismless enamel in von Koenigswald & Sander's (1997) terminology] has been demonstrated to be widely distributed in many amniotes (Sander, 1999) and even in some sarcopterygian fish (Smith, 1989).

Trirachodontids from the Omingonde Formation have been described by Keyser (1973) and quoted as a faunal component in the taphonomic study by Smith & Swart (2002). The specimen described by Keyser (1973) as *Trirachodon* sp. (GSN R327) shows a skull size of 107 mm, comparable with that of *T. berryi* and *L. modisei*, and exhibits a lateral platform of the maxilla, a feature that suggests its affiliation to the first species. However, postcranial material associated with the skull (e.g. a distal portion of humerus with a width of 55 mm) indicates larger sizes than that represented by the skull and thus the presence of *Cricodon*, instead of *T. berryi*, cannot be entirely ruled out. Specimens identified as *Trirachodon* in a taphonomic study by Smith & Swart (2002) are, in fact, representatives of the traversodontid *Luangwa* and the probainognathian *Aleodon* (F. Abdala, pers. observ.). Cynodonts represent an extremely diverse Middle Triassic fauna in the Omingonde Formation and will be the subject of a forthcoming contribution.

CLADISTIC ANALYSIS

A data matrix with 43 craniodental characters and 18 taxa was assembled, using as the starting point the data matrix of Abdala & Ribeiro (2003) (28 craniodental characters and 15 terminals). Most of the characters were examined first hand on material from different collections (see Appendix 1 for the list of the material and the literature relevant for each taxon included in the data matrix, Appendix 2 for a character list, and Appendix 3 for the data matrix). Following an unpublished cladistic analysis of nonmammaliaform cynodonts by Abdala (see Abdala & Ribeiro, 2003), gomphodont cynodonts are considered a monophyletic group that do not include tritylodontids. The results of the same analysis support the carnivorous *Cynognathus* as the basal taxon closely related to gomphodont cynodonts [i.e. the monophyly of Cynognathia, a hypothesis supported by Broom (1905b) and, in a cladistic context, by Hopson (1991) and Hopson & Kitching (2001)] and accordingly, we used *Cynognathus* to root our cladograms. As discussed by Abdala & Ribeiro (2003), gomphodont postcanines are interpreted to have originated from the expansion of the lingual margin of the teeth and the homologies are recognized accordingly with this scheme.

The main objective of this analysis was to identify the phylogenetic placement of *L. modisei*. In addition, the resulting hypothesis represents a test for the recently proposed phylogeny of Traversodontidae advanced by Abdala & Ribeiro (2003), in light of the increased number of taxa and craniodental characters.

The cladistic analysis was performed with the program TNT (Goloboff, Farris & Nixon, 2003), with all characters having equal weights. A traditional search was implemented, with 50 random addition sequences (50 Wagner trees randomizing the order of the terminals) and tree-bisection-reconnection swapping, storing ten trees per replication. The run was performed with collapsing rule 1, which collapses branches with ambiguous support (see Coddington & Scharff, 1994). Thirty-eight most-parsimonious trees (MPTs) were recovered with this routine, but an increase to 100 random addition sequences recovered two additional MPTs. A second analysis was performed with similar settings but using implied weights (Goloboff, 1993), with the constant of concavity set at 3.

Forty MPTs of length 103, a consistency index for informative characters of 0.55, and a retention index of 0.71 resulted from the cladistic analysis with characters having equal weights. The majority-rule consensus tree resulting from this analysis is shown in Figure 12A (see Appendix 4 for unambiguous synapomorphies of monophyletic groups present in the majority-rule consensus tree). Bremer support values were low, with most of the monophyletic groups not being recovered in the consensus of suboptimal trees of one extra step. The exceptions were [Trirachodontidae, Traversodontidae], which appeared in the consensus of suboptimal trees with two extra steps, and Traversodontidae and the clade [*Scalenodontoides* [*Exaeretodon*, *Menadon*]] with three extra steps.

Trirachodontidae appears as a monophyletic group and among them *Cricodon* and *Langbergia* as more closely related taxa, both relationships being weakly supported, as is apparent from the values of the Bremer support. The weak support of trirachodontid monophyly is unexpected, considering that it is easy to recognize members of this family as different from other gomphodonts because of their postcanine morphology. Most postcanine characters (particularly those referring to the cingular cusps in the anterior and posterior margins of the teeth) included in the data matrix, however, are not exclusive to the group. The only dental feature synapomorphic for trirachodontids is the presence of three cusps in the transverse crest of the lower postcanines. A second synapomorphy is the pattern of occlusion of the postcanines, as recognized by Crompton (1972a). Thus, trirachodontids lack shearing planes between the outer surface of the main cusp of the lower and the inner surfaces of the main cusps of the upper postcanines.

Regarding traversodontids, the strict consensus tree shows a dense polytomy at the base of this group, followed by the clade [*Gomphodontosuchus* [*Scalenodontoides* [*Exaeretodon*, *Menadon*]]]. In the majority-rule consensus (Fig. 12A), *Luangwa* and *Scalenodon angustifrons* form a polytomy at the base of traversodontids, followed by a second polytomy including ‘*Scalenodon*’ *hirschsoni*, *Pascualgnathus*, and *Traversodon*. *Andescynodon* follows this second polytomy and thereafter a clade including Ladinian–Norian traversodontids. The latter clade comprises [*Dadadon* [*Santacruzodon* [*Massetognathus* [*Gomphodontosuchus* [*Scalenodontoides* [*Menadon*, *Exaeretodon*]]]]]].

Four MPTs with a total fit of 36.36 and an adjusted homoplasy of 8.64 resulted from the analysis using implied weights. The main differences when comparing the majority-rule consensus tree obtained in this analysis with the one obtained with characters having equal weights (cf. Fig. 12A and B) are: (a) *Traversodon* and *Andescynodon* swap positions, and (b) *Pascualgnathus* appears basal to *Andescynodon* and ‘*Scalenodon*’ *hirschsoni*. Obviously, the location of *Traversodon* as the most basal Ladinian traversodontid, with a similar placement as in Abdala & Ribeiro’s (2003) MPT, is poorly supported, not being recovered in the consensus of suboptimal trees of 0.15 fit of difference. The placement of *Traversodon* is possibly a result of the good fit of characters 8 (inclination of the last upper postcanines) and 20 (anterior cingulum in the lower postcanines). The more basal placement of *Pascualgnathus* relative to *Andescynodon* and ‘*Scalenodon*’ *hirschsoni* probably results from the fit of character 6 (overall morphology of the upper postcanines in occlusal view).

Comparing these results with the MPT presented by Abdala & Ribeiro (2003), it is evident that basal traversodontid relationships (including taxa from the Olenekian to the Anisian) show the major variation between these hypotheses. Only *Scalenodon angustifrons* remains among the most basal traversodontids in both hypotheses. However, *Luangwa* appears as the other basal traversodontid in the hypotheses presented here, whereas the clade [*Pascualgnathus*, *Andescynodon*] was part of the basal polytomy of traversodontids in Abdala & Ribeiro’s (2003) MPT. In both cladistic analyses, the Brazilian *Traversodon* appears as the most basal Ladinian traversodontid, forming the base of the Ladinian (and younger traversodontids) in Abdala & Ribeiro's (2003) MPT. This taxon has a similar placement in the four MPTs resulting from the analysis using implied weights, but it is located in a polytomy with Olenekian–Anisian traversodontids, followed by *Andescynodon* in the majority-rule consensus of the analysis with characters having equal weights (see above). The disparity in the placement of *Traversodon* and *Andescynodon* in the cladistic analyses suggests that these two taxa may represent a link between the Olenekian–Anisian and Ladinian–Norian traversodontids. Most Ladinian and younger traversodontids have a similar placement in the hypotheses presented here and in the MPT of Abdala & Ribeiro (2003), but two major differences should be noted: (a) *Dadadon* and *Santacruzodon* do not form a monophyletic group and (b) *Menadon* is the sister taxon of *Exaeretodon*. The latter relationship contrasts with that obtained by Flynn *et al*. (2000), in which *Exaeretodon* was the sister taxon of *Scalenodontoides*, and *Menadon* was its successive outgroup.

CONCLUDING REMARKS

There was a burst of cynodont diversification, particularly of gomphodonts, during the Olenekian–Anisian interval. Considering the cynodonts represented in this phylogeny, two different morphotypes appear simultaneously in the Upper Olenekian Subzone A of the *Cynognathus* AZ: cynognathids and trirachodontids, the latter represented by two taxa (Fig. 13). This explosion of diversity and the phylogenetic placement of these taxa are suggestive that some of them should be found earlier in the fossil record than is currently known (perhaps in the Lower Olenekian or even the Induan).

Concerning trirachodontids of the Karoo Basin, it is clear that *Langbergia* is dominant in the Late Olenekian, *Trirachodon* in the Early Anisian (plus a single record from the Late Olenekian), and *Cricodon* in the Late Anisian (and a possible single record in the Early Anisian). The close relationships between the youngest *Cricodon* with the oldest *Langbergia* and the most

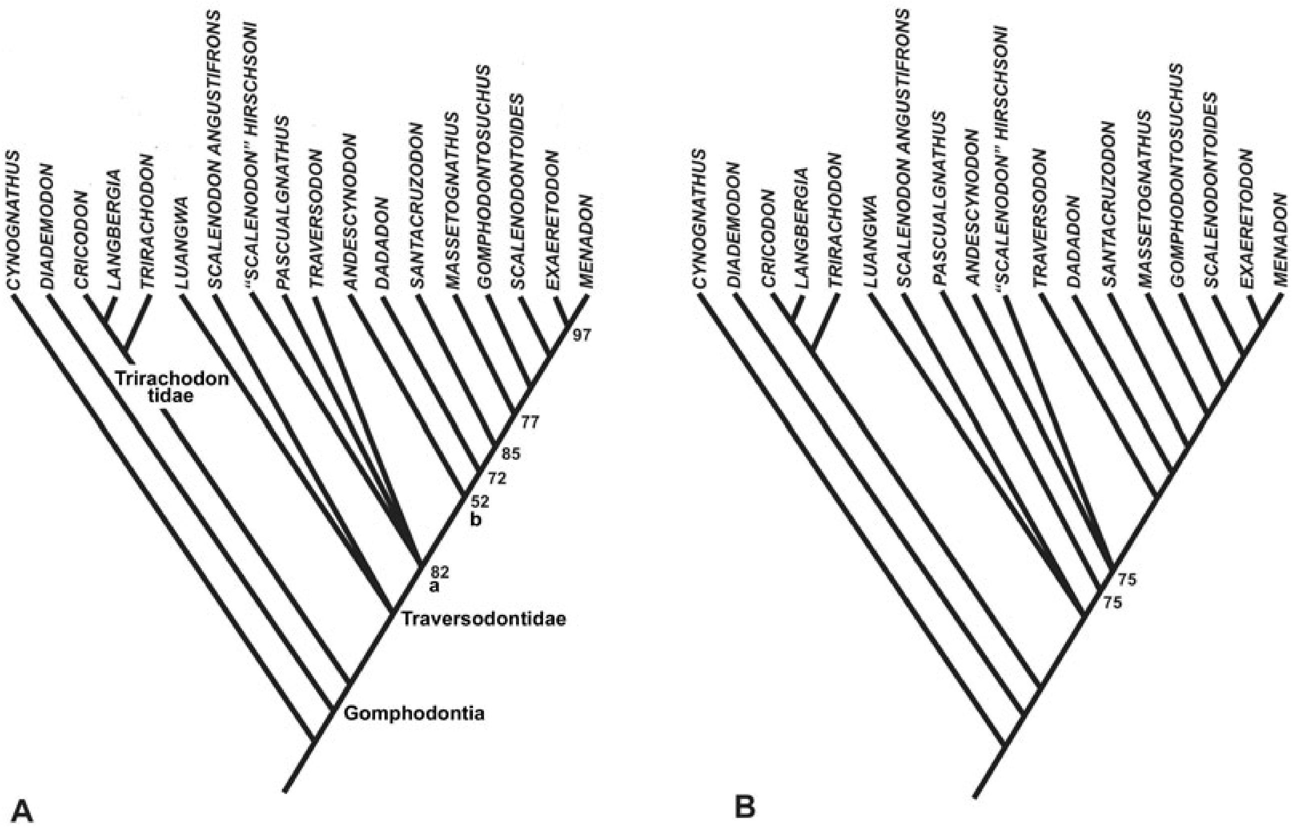

Figure 12. Majority-rule consensus tree of: A, 40 most-parsimonious trees obtained from the analysis with characters having equal weights (length = 103, consistency index for informative characters = 0.55, retention index = 0.71); B, four most-parsimonious trees obtained from the analysis using implied weights (total fit = 36.36; adjusted homoplasy = 8.64). The numbers indicate the frequency of clades in the fundamental trees. The nodes without a number indicate that the clades are present in all of the most-parsimonious trees of the analysis. The letters (a, b) are used to name the clades (see Appendix 4).

basal location of the temporally intermediate *Trirachodon* are unexpected results in a temporal framework (Fig. 13). These relationships contradict the interpretation of Karoo trirachodontid taxa as a morphological succession throughout the stratigraphic range as advanced by Rubidge & Sidor (2001).

Basal traversodontids are first known from East African and South American faunas. In the Anisian, this group is already well diversified with five species in east Africa and three to four in South America. We should mention, however, that more than one age – upper Anisian and younger – can be represented in the east African Manda Formation, which includes four different species of traversodontids (Abdala & Ribeiro, 2003). Only one traversodontid species is represented in both the upper Ntawere and Puesto Viejo formations from east Africa and Argentina, respectively (see Appendix 1). The only putative early fauna in which two traversodontid taxa (*Andescynodon* and *Rusconiodon*) are known to coexist is the Cerro de las Cabras Formation (= Rio Mendoza Formation; Bonaparte, 1969a) from Argentina. There are disagreements how-

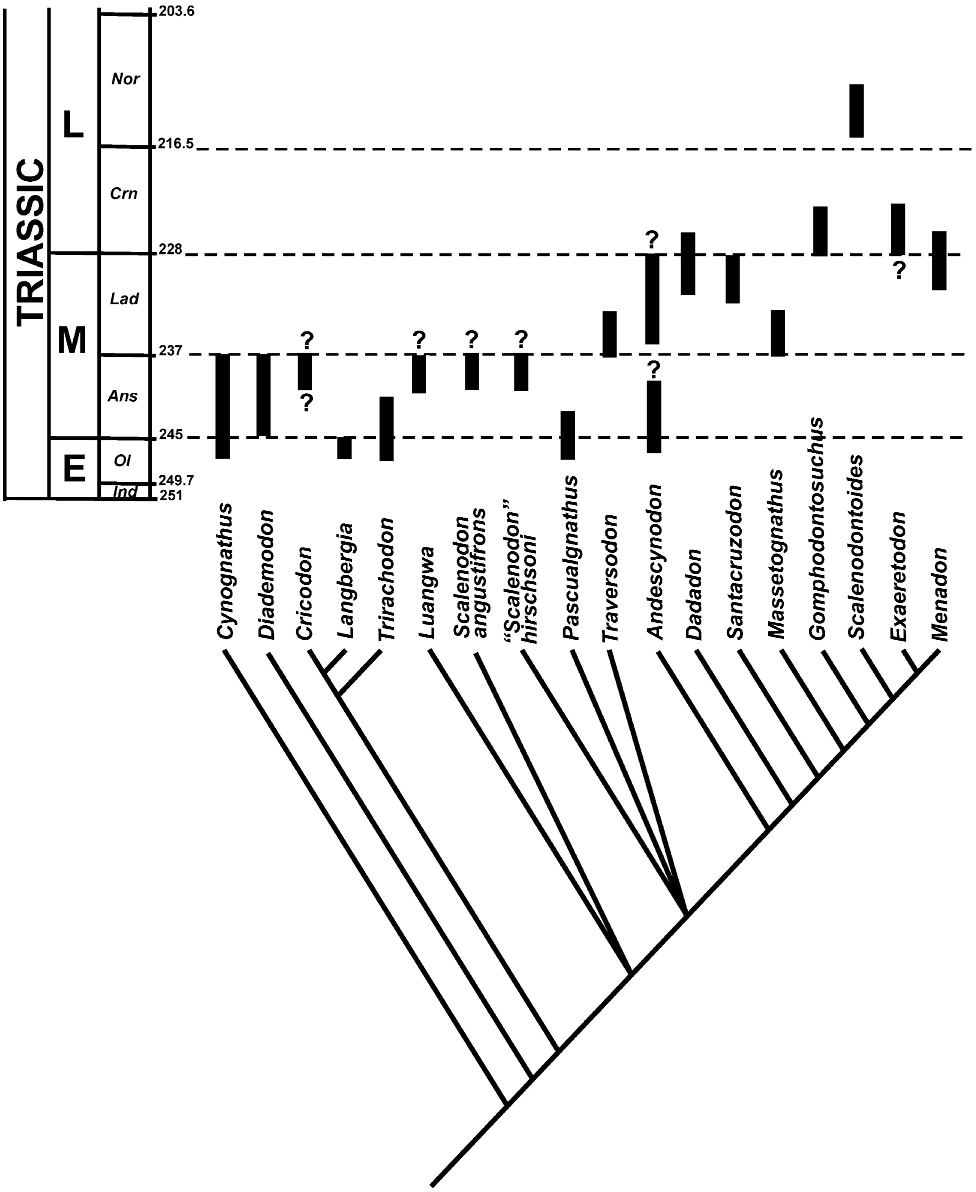

Figure 13. Majority-rule consensus tree of the analysis with characters having equal weights plotted against the geological time scale to indicate temporal distribution of the taxa included in the analysis (see Appendix 1). The geological time scale is based on Gradstein & Ogg (2004). Ans, Anisian; Crn, Carnian; E, Early; Ind, Induan; L, Late; Lad, Ladinian; M, Middle; Nor, Norian; Ol, Olenekian.

ever, about the age of this unit, with fossil plants indicating the Early Triassic to early Middle Triassic (Morel, Artabe & Spalleti, 2003) and palynology suggesting the late Middle Triassic (Zavattieri & Arcucci, 2003). The location of *Andescynodon* in our cladograms is supportive of a Late Anisian or Early Ladinian age for this taxon, and thus more in accordance with palynomorph dates. In conclusion, traversodontids also seem highly diversified by the time of their first appearance in the fossil record, but difficulties and disagreements on the dates of key faunas, including the earliest traversodontids, imply that no confident statements can be made about a possible older origin for this group.

Finally, this study confirms a Ladinian–Norian monophyletic clade of Gondwanan traversodontids (clade b in Fig. 12A) whose basal form could be *Andescynodon* or *Traversodon* (cf. Fig. 12A and B).

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REFERENCES

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, Hancox PJ, Neveling J. 2005. Cynodonts from the uppermost Burgersdorp Formation, South Africa, and their bearing on the biostratigraphy and correlation of the Triassic *Cynognathus* Assemblage Zone. *Journal of Vertebrate Paleontology* **25:** 192–199.

Abdala F, Ribeiro AM. 2003. A new traversodontid cynodont from the Santa Maria Formation (Ladinian–Carnian) of southern Brazil, with a phylogenetic analysis of Gondwanan traversodontids. *Zoological Journal of the Linnean Society* **139:** 529–545.

Abdala F, 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.

Abdala F, Teixeira AMS. 2004. A traversodontid cynodont of African affinity in the South American Triassic. *Palaeontologia Africana* **40:** 11–22.

Bandyopadhyay S, Sengupta DP. 1999. Middle Triassic vertebrates of India. *Journal of African Earth Sciences* **29:** 233–241.

Barberena MC. 1974. *Contribuição ao conhecimento dos cinodontes gonfodontes (Cynodontia, Tritylodontoidea) do Brasil.* Tese para obtenção do título de Livre Docente inédita. Rio Grande do Sul: Ministério de Educação e Cultura, Universidade Federal do Rio Grande do Sul.

Barberena MC. 1981. Novos materiais de *Traversodon stahleckeri* da Formação Santa Maria (Triássico do Rio Grande do Sul). *Pesquisas* **14:** 149–162.

Battail B. 1983. La phylogénie des cynodonts gomphodontes. *Acta Palaeontologica Polonica* **28:** 19–30.

Battail B. 1991. Les cynodontes (Reptilia, Therapsida): une phylogénie. *Bulletin du Muséum National d'Histore Naturelle de Paris* **13:** 17–105.

Battail B. 2004. New data on *Scalenodontoides macrodontes* (Cynodontia: Traversodontidae). In: Ashwal LD, ed. *Geosciences Africa 2004, Abstracts*. Johannesburg: University of the Witwatersrand, 49–50.

Battail B, Surkov MV. 2000. Mammal-like reptiles from Russia. In: Benton MJ, Shishkin MA, Unwin DM, Kurochkin EN, eds. *The age of dinosaurs in Russia and Mongolia*. Cambridge: Cambridge University Press, 86–119.

Bonaparte JF. 1962. Descripción del cráneo y mandíbula de *Exaeretodon frenguellii,* 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. 1963. La Familia Traversodontidae (Terapsida-Cynodontia). *Acta Geologica Lilloana* **4:** 163–194.

Bonaparte JF. 1966. Una nueva 'fauna' triásica de Argentina (Therapsida: Cynodontia Dicynodontia). Consideraciones filogenéticas y paleobiogeográficas. *Ameghiniana* **4:** 243–296.

Bonaparte JF. 1969a. Dos nuevas 'faunas' de reptiles triásicos de Argentina. *Gondwana stratigraphy.* Mar del Plata: IUGS, 283–306.

Bonaparte JF. 1969b. *Cynognathus minor* n. sp. (Therapsida-Cynodontia). Nueva evidencia de vinculación faunística afrosudamericana a principios del Triásico. *Gondwana stratigraphy*. Mar del Plata: IUGS, 273–281.

Bonaparte JF, Martinelli AG, Schultz CL, Rubert R. 2003. The sister group of mammals: small cynodonts from the Late Triassic of southern Brazil. *Revista Brasileira de Paleontologia* **5:** 5–27.

Brink AS. 1951. Some small cynodonts. *South African Journal of Science* **47:** 338–342.

Brink AS. 1955a. On the Cynognathidae. *Palaeontologia Africana* **3:** 47–55.

Brink AS. 1955b. 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.

Brink AS, Kitching JW. 1953. On some new *Cynognathus* Zone specimens. *Palaeontologia Africana* **1:** 29–48.

Broili F, Schröder J. 1934. Zur Osteologie des Kopfes von *Cynognathus*. *Sitzungsberichte der Bayerischen Akademie der Wissenchaften, Mathematisch-Naturwissenschaftliche, Abteilung* **1934:** 95–128.

Broili F, Schröder J. 1935a. Beobachtungen an Wirbeltieren der Karrooformation. X. Über die Bezahnung von *Trirachodon* Seeley. *Sitzungsberichte der Bayerischen Akademie der Wissenchaften, Mathematisch-Naturwissenschaftliche, Abteilung* **1935:** 189–198.

Broili F, Schröder J. 1935b. Beobachtungen an Wirbeltieren der Karrooformation. XI. Über den Schädel von *Cynidiognathus* Haughton. *Sitzungsberichte der Bayerischen Akademie der Wissenchaften, Mathematisch-Naturwissenschaftliche, Abteilung* **1935:** 199–222.

Broili F, Schröder J. 1935c. Beobachtungen an Wirbeltieren der Karrooformation. IX Über den Schädel von *Gomphognathus* Seeley. *Sitzungsberichte der bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche, Abteilung* **1935:** 115–182.

Broom R. 1903. On the axis, atlas, and proatlas in the higher theriodonts. *Proceedings of the Zoological Society of London b* **1903:** 177–180.

Broom R. 1904. On the theriodonts in the Albany Museum. *Records of the Albany Museum* **1:** 82–87.

Broom R. 1905a. Preliminary notice of some new fossil reptiles collected by Mr. Alfred Brown at Aliwal North, S. Africa. *Records of the Albany Museum* **1:** 269–275.

Broom R. 1905b. On some points in the anatomy of the theriodont reptile *Diademodon*. *Proceedings of the Zoological Society of London b* **1905:** 96–102.

Broom R. 1907. On the geological horizons of the vertebrate genera of the Karroo Formation. *Records of the Albany Museum* **2:** 156–163.

Broom R. 1911. On the structure of the skull in cynodont reptiles. *Proceedings of the Zoological Society of London b* **1911:** 893–925.

Broom R. 1915a. On some new carnivorous therapsids in the collection of the *British Museum*. *Proceedings of the Zoological Society of London b* **1915:** 163–173.

Broom R. 1915b. Catalogue of types and figures specimens of fossil vertebrates in the American Museum of Natural History. II. Permian, Triassic and Jurassic reptiles of South Africa. *Bulletin of the American Museum of Natural History* **25:** 105–164.

Broom R. 1919. On the genus *Gomphognathus* and its allies. *Records of the Albany Museum* **3:** 223–232.

Broom R. 1932. *The mammal-like reptiles of South Africa and the origin of mammals*. London: H. F. & G. Witherby.

Chatterjee S. 1982. A new cynodont reptile from the Triassic of India. *Journal of Paleontology* **56:** 203–214.

Coddington J, Scharff N. 1994. Problems with zero-length branches. *Cladistics* **10:** 415–423.

Crompton AW. 1955. On some Triassic cynodonts from Tanganyika. *Proceedings of the Zoological Society of London* **125:** 617–669.

Crompton AW. 1963. On the lower jaw of *Diarthrognathus* and the origin of the mammalian lower jaw. *Proceedings of the Zoological Society of London* **140:** 697–749.

Crompton AW. 1972a. Postcanine occlusion in Cynodonts and Tritylodontids. *Bulletin of the British Museum of Natural History, Geology* **21:** 27–71.

Crompton AW. 1972b. The evolution of the jaw articulation in cynodonts. In: Joysey KA, Kemp TS, eds. *Studies in vertebrate evolution*. Edinburgh: Oliver & Boyd, 231–251.

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.

Damiani R. 2004. Temnospondyls from the Beaufort Group (Karoo Basin) of South Africa and their biostratigraphy. *Gondwana Research* **7:** 165–173.

Damiani R, Hancox PJ. 2003. New mastodonsaurid temnospondyls from the *Cynognathus* Assemblage Zone (Upper Beaufort Group; Karoo Basin) of South Africa. *Journal of Vertebrate Palaeontology* **23:** 54–66.

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, Whatley RL, Wyss AR. 1999. A Triassic fauna from Madagascar, including early dinosaurs. *Science* **286:** 763–765.

Fourie S. 1974. The cranial morphology of *Thrinaxodon liorhinus* Seeley. *Annals of the South African Museum* **65:** 337–400.

Goloboff PA. 1993. Estimating character weights during tree search. *Cladistics* **9:** 83–91.

Goloboff PA, Farris JS, Nixon KC. 2003. T.N.T. tree analysis using new technology. http://www.zmuc.dk/public/phylogeny.

Goñi RG. 1986. Reemplazo de dientes postcaninos en *Andescynodon mendozensis* Bonaparte (Cynodontia, Traversodontidae). *Actas del IV Congreso Argentino de Paleontología y Bioestratigrafia* **2:** 7–14.

Goñi RG, Goin FJ. 1988. Morfología dentaria y biomecánica maticatoria de los cinodontes (Reptilia-Therapsida) del Triásico argentino. I. *Andescynodon mendozensis* Bonaparte (Cynodontia, Traversodontidae). *Ameghiniana* **25:** 139–148.

Gow CE. 1986. The side wall of the braincase in cynodont therapsids, and a note on the homology of the mammalian promontorium. *South African Journal of Zoology* **21:** 136–148.

Gow CE, Hancox PJ. 1993. First complete skull of the Late Triassic *Scalenodontoides* (Reptilia, Cynodontia) from southern Africa. *New Mexico Museum of Natural History & Science Bulletin* **3:** 161–168.

Gradstein FM, Ogg JG. 2004. Geologic time scale 2004 – why, how, and where next! *Lethaia* **37:** 175–181.

Grine FE. 1977. Postcanine tooth function and jaw movements in the gomphodont cynodont *Diademodon* (Reptilia; Therapsida). *Palaeontologia Africana* **20:** 123–135.

Groenewald GH, Welman J, MacEachern JA. 2001. Vertebrate burrow complexes from the Early Triassic *Cynognathus* Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa. *Palaios* **16:** 148–160.

Hammer WR. 1995. New therapsids from the Upper Fremouw Formation (Triassic) of Antarctica. *Journal of Vertebrate Paleontology* **15:** 105–112.

Hancox PJ. 2000. The Continental Triassic of South Africa. *Zentralblatt für Geologie und Paläontologie, Teil I, Heft 11–12* **1998:** 1285–1324.

Hancox PJ, Rubidge BS. 1994. A new dicynodont therapsid from South Africa: implications for the biostratigraphy of the Upper Beaufort (*Cynognathus* Assemblage Zone). *South African Journal of Science* **90:** 98–99.

Hancox PJ, Rubidge BS. 1996. The first specimen of the Mid-Triassic dicynodont *Angonisaurus* from the Karoo of South Africa: implications for the dating and biostratigraphy of the Upper Beaufort Group. *South African Journal of Science* **92:** 391–392.

Hancox PJ, Rubidge BS. 2001. Breakthroughs in the biodiversity, biogeography, biostratigraphy and basin analysis of the Beaufort Group. *Journal of African Earth Sciences* **33:** 563–577.

Hancox PJ, Shishkin MA, Rubidge BS, Kitching JW. 1995. A threefold subdivision of the *Cynognathus* Assemblage Zone (Beaufort Group, South Africa) and its palaeogeographic implications. *South African Journal of Science* **91:** 143–144.

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 synapsids. In: Schultze H-D, Trueb L, eds. *Origin of the higher groups of tetrapods: controversy and consensus*. Ithaca: Comstock Publishing Associates, Cornell University Press, 635–693.

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. *Centralblatt für Mineralogie, Geologie und Paläontologie* **1928B:** 251–270.

von Huene F. 1936. Die fossilen Reptilien der südamerikanischen Gondwanalandes. *Ergebnisse der Sauriergrabungen in Südbrasilien 1928–29. Lieferung 2.* Tübingen: Verlag Franz F. Heine, 93–159.

Kemp TS. 1979. The primitive cynodont *Procynosuchus*: functional anatomy of the skull and relationships. *Philosophical Transactions of the Royal Society of London B* **285:** 73–122.

Kemp TS. 1980. Aspects of the structure and functional anatomy of the Middle Triassic cynodont *Luangwa*. *Journal of Zoology* **191:** 193–239.

Kemp TS. 1982. *Mammal-like reptiles and the origin of mammals*. London: Academic Press.

Kemp TS. 1983. The relationships of mammals. *Zoological Journal of the Linnean Society* **77:** 353–384.

Keyser AW. 1973. A new vertebrate fauna from South West Africa. *Palaeontologia Africana* **16:** 1–15.

Keyser AW, Smith RMH. 1977–78. Vertebrate biozonation of the Beaufort Group with special reference to the western Karoo Basin. *Annals of the Geological Survey* **12:** 1–35.

Kitching JW. 1977. *The distribution of the Karoo vertebrate fauna.* Memoir 1. Johannesburg: Bernard Price Institute for Palaeontological Research, University of the Witwatersrand.

Kitching JW. 1995. Biostratigraphy of the *Cynognathus* Assemblage Zone. In: Rubidge B, ed. *Biostratigraphy of the Beaufort Group (Karoo Supergroup).* Biostratigraphic Series 1. Pretoria: South African Committee for Stratigraphy, 40–45.

von Koenigswald W, Sander PM. 1997. Glossary of terms used for enamel microstructures. In: von Koenigswald W, Sander PM, eds. *Tooth enamel microstructure*. Rotterdam: Balkema, 267–280.

Kokogian DA, Spalletti L, Morel E, Artabe A, Martínez RN, Alcober OA, Milana JP, Zavattieri AM, Papú OH. 1999. Los depósitos continentales Triásicos. Geología Argentina. *Anales del Instituto de Geología y Recursos Minerales* **29:** 377–398.

Lucas SG, Estep JW, Heckert AB, Hunt AP. 1999. Cynodont teeth from the Upper Triassic of New Mexico, USA. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **1999:** 331–344.

Lucas SG, Hancox PJ. 2001. Tetrapod-based correlation of the nonmarine Upper Triassic of Southern Africa. *Albertiana* **25:** 5–9.

Lucas SG, Luo Z. 1993. *Adelobasileus* from the Upper Triassic of west Texas: the oldest mammal. *Journal of Vertebrate Paleontology* **13:** 309–334.

Luo Z. 1994. Sister-group relationships of mammals and transformations of diagnostic mammalian characters. In: Fraser NC, Sues H-D, eds. *The shadow of the dinosaurs – early Mesozoic tetrapods*. Cambridge: Cambridge University Press, 98–128.

Luo Z, Crompton AW. 1994. Transformation of the quadrate (incus) through the transition from non-mammalian cynodonts to mammals. *Journal of Vertebrate Paleontology* **14:** 341–374.

Martínez RN, May CL, Forster CA. 1996. A new carnivorous cynodont from the Ischigualasto Formation (Late Triassic, Argentina), with comments on eucynodont phylogeny. *Journal of Vertebrate Paleontology* **16:** 271–284.

Morel EM, Artabe AE, Spalletti LA. 2003. Triassic floras of Argentina: biostratigraphy, floristic events and comparison with other areas of Gondwana and Laurasia. *Alcheringa* **27:** 231–243.

Neveling J. 2002. Biostratigraphic and sedimentological investigation of the contact between the Lystrosaurus and Cynognathus Assemblage Zones (Beaufort Group: Karoo Supergroup). PhD Thesis, University of the Witwatersrand, Johannesburg.

Neveling J. 2004. Stratigraphic and sedimentological investigation of the contact between the Lystrosaurus and Cynognathus Assemblage Zones (Beaufort Group: Karoo Supergroup). *Bulletin of the Council for Geosciences, South Africa*, **137:** 1–165.

Neveling J, Rubidge BS, Hancox PJ. 1999. A lower *Cynognathus* Assemblage Zone fossil from the Katberg Formation (Beaufort Group, South Africa). *South African Journal of Science* **95:** 555–556.

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), north-western Argentina: spectacular preservation in volcanogenic concretions. *Palaios* **16:** 461–481.

Rogers RR, Swisher CC III, Sereno PC, Monetta AM, Forster CA, Martínez RN. 1993. The Ischigualasto tetrapod assemblage (Late Triassic, Argentina) and ^{40}Ar/^{39}Ar dating of dinosaurs origins. *Science* **260:** 794–797.

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.

Rougier GW, Wible JR, Hopson JA. 1992. Reconstruction of the cranial vessels in the Early Cretaceous mammal *Vincelestes neuquenianus*: implications for the evolution of the mammalian cranial vascular system. *Journal of Vertebrate Paleontology* **12:** 188–216.

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, 129–145.

Rubidge BS, Johnson MR, Kitching JW, Smith RMH, Keyser AW, Groenewald GH. 1995. An introduction to the biozonation of the Beaufort Group. In: Rubidge B, ed. *Biostratigraphy of the Beaufort Group (Karoo Supergroup).* Biostratigraphic Series 1. Pretoria: South African Committee for Stratigraphy, 1–2.

Rubidge BS, Sidor CA. 2001. Evolutionary patterns among Permo-Triassic therapsids. *Annual Review of Ecology and Systematics* **32:** 449–480.

Sander PM. 1999. The microstructure of reptilian tooth enamel: terminology, function and phylogeny. *Münchner Geowissenschaftliche Abhandlungen* **38:** 1–102.

Seeley HG. 1892. Researches on the structure, organization, and classification of the Fossil Reptilia. VII. Further observations on *Pareiasaurus*. *Philosophical Transactions of the Royal Society of London* **183:** 311–370.

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. 1895a. 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.

Seeley HG. 1895b. Researches on the structure, organization, and classification of the Fossil Reptilia. Part IX, Section 5. On the skeleton in new Cynodontia from the Karroo rocks. *Philosophical Transactions of the Royal Society of London* **186:** 59–148.

Seeley HG. 1908. Additional evidence as to the dentition and structure of the skull in the South African fossil reptile genus *Diademodon*. *Proceedings of the Zoological Society of London b* **1908:** 611–617.

Shishkin MA, Rubidge BS, Hancox PJ. 1995. Vertebrate biozonation of the Upper Beaufort Series of South Africa – A new look on correlation of the Triassic biotic events in Euramerica and southern Gondwana. In: Sun A, Wang Y, eds. *Sixth symposium on Mesozoic terrestrial ecosystems and biota, short papers*. Beijing: China Ocean Press, 39–41.

Sidor CA, Smith RMH. 2004. A new galesaurid (Therapsida: Cynodontia) from the Lower Triassic of South Africa. *Palaeontology* **47:** 535–556.

Smith MM. 1989. Distribution and variation in enamel structure in the oral teeth of sarcopterygians: its significance for the evolution of a protoprismatic enamel. *Historical Biology* **3:** 97–126.

Smith RMH, Swart R. 2002. Changing fluvial environments and vertebrate taphonomy in response to climatic drying in a Mid-Triassic rift valley fill: the Omingonde Formation (Karoo Supergroup) of central Namibia. *Palaios* **17:** 249–267.

Sues H-D. 1985. First record of the tritylodontid *Oligokyphus* (Synapsida) from the Lower Jurassic of western North America. *Journal of Vertebrate Paleontology* **5:** 328–335.

Sues H-D. 1986. The skull and dentition of two tritylodontid synapsids from the Lower Jurassic of western North America. *Bulletin of the Museum of Comparative Zoology* **151:** 217–268.

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.

Sun A. 1984. Skull morphology of the tritylodont genus *Bienotheroides* of Sichuan. *Scientia Sinica* **27:** 970–984.

Sun A. 1988. Additional study on *Sinognathus gracilis* (Cynodontia; Reptilia). *Vertebrata Palasiatica* **26:** 173–180.

Tatarinov LP. 1973. Cynodonts of Gondwanan habit in the Middle Triassic of the USSR. *Paleontological Journal* **1973:** 200–205.

Tatarinov LP. 1988. On the morphology and systematic position of the gomphodont cynodont *Antecosuchus ochevi*. *Paleontological Journal* **1988:** 82–90.

Tatarinov LP. 2002. Gomphodont cynodonts (Reptilia, Theriodontia) from the Middle Triassic of the Orenburg Region. *Paleontological Journal* **36:** 176–179.

Watson DMS. 1911. The skull of *Diademodon*, with notes on those of some other cynodonts. *Annals and Magazine of Natural History* **8:** 293–330.

Watson DMS. 1914. The zones of the Beaufort beds of the Karroo System in South Africa. *Geological Magazine, New Series* **6:** 203–208.

Welman J, Groenewald GH, Kitching JW. 1991. Confirmation of the occurrence of *Cynognathus* Zone (*Kannemeyeria*-*Diademodon* Assemblage-zone) deposits (uppermost Beaufort Group) in the northeastern Orange Free State, South Africa. *South African Journal of Geology* **94:** 245–248.

Wible JR. 1991. Origin of Mammalia: the craniodental evidence reexamined. *Journal of Vertebrate Paleontology* **11:** 1–28.

Young C-C. 1959. Note on the first cynodont from the *Sinokannemeyeria* faunas in Shansi, China. *Vertebrata Palasiatica* **3:** 124–131.

Zavattieri AM, Arcucci AB. 2003. Edad y posición estratigráfica de los tetrápodos de la localidad Cerro Bayo de Potrerillos (Triásico), Mendoza, Argentina. *Ameghiniana* **40:** 75R.

APPENDIX 1

LIST OF MATERIAL, LITERATURE CONSULTED, GEOLOGICAL AND BIOSTRATIGRAPHICAL LOCATION, AND AGE FOR TAXA INCLUDED IN THE PHYLOGENETIC ANALYSIS

Andescynodon: PVL 3833, 3836, 3894-1, 3894-2, 3899, 4390; (Bonaparte, 1969a; Goñi, 1986; Goñi & Goin, 1988). This taxon is traditionally considered as coming from the Rio Mendoza Formation, Mendoza Province, Argentina (Bonaparte, 1969a; Goñi & Goin, 1988; Abdala & Ribeiro, 2003). Recent works, however, indicate that the fauna including *Andescynodon* comes from the Cerro de las Cabras Formation (Zavattieri & Arcucci, 2003); Early Triassic–Late Ladinian (Morel *et al.*, 2003; Zavattieri & Arcucci, 2003).

Cricodon: see Materials; (Crompton, 1955; Abdala *et al.*, 2005). Burgersdorp Formation, Karoo Basin, South Africa, Subzone C of the *Cynognathus* Assemblage Zone (AZ); Manda Formation, Tanzania. SAM-PK-5881 from Subzone B of the *Cynognathus* AZ shows upper postcanines resembling *Cricodon* (see Discussion); Late Anisian–?earlier (Abdala & Ribeiro, 2003; Abdala *et al.*, 2005).

Cynognathus: AM 460, 2190, 3587, 4202, 5800; AMNH 5641; BMNH R2571 R3580; BP/1/1181, 2095, 3755, 4664; BS1934 VIII 1, VIII 2, VIII 3, VIII 4, VIII 6; NMQR 1444; PVL 3859; SAM-PK-6224, 6235, 11264, 11484; (Seeley, 1895b; Broili & Schröder, 1934, 1935b; Brink, 1955a). Burgersdorp Formation, Karoo Basin, South Africa, Subzones A–C of the *Cynognathus* AZ (Hancox, 2000); Omingonde Formation, Namibia (Smith & Swart, 2002); Puesto Viejo Formation, Argentina (Bonaparte, 1969b); Fremouw Formation, Antarctica (Hammer, 1995); Late Olenekian–Late Anisian (Hancox, 2000).

Dadadon: UA-10606; (Flynn *et al.*, 2000). 'Isalo II', Morondava Basin, Madagascar; undifferentiated Middle or Late Triassic (Flynn *et al.*, 1999, 2000).

Diademodon: AM 3753; BMNH R2578, 3304, 3587, 3588, 3765, BP/1/3754, 3769, 4669; BS1934 VIII 14, VIII 15, VIII 16, VIII 17, VIII 19; MB R1004; SAM PK-K5223, K5716; (Seeley, 1894, 1895a; Watson, 1911; Broili & Schröder, 1935c; Brink, 1955b; Hopson, 1971). Burgersdorp Formation, Karoo Basin, South Africa, Subzones B–C of the *Cynognathus* AZ (Neveling, 2004); Omingonde Formation, Namibia (Keyser, 1973); Early to Late Anisian (Hancox, 2000; Neveling, 2004).

Exaeretodon: MACN 18114, 18125; MCZ 3779, 4493, 111–64A, 377–58M; MCP 1522 PV; PVL 2473; PVSJ 157; (Bonaparte, 1962; Chatterjee, 1982; Hopson, 1984, 1985; Abdala, Barberena & Dornelles, 2002). Ischigualasto Formation, Ischigualasto–Villa Union Basin, Argentina; Santa Maria Formation, Paraná Basin, Brazil, *Dinodontosaurus* (*Exaeretodon major*) and *Rhynchosaur* Biozones (*Exaeretodon riograndensis*); Maleri Formation, India; the presence of *Exaeretodon* in the Ladinian of Brazil should be considered with caution, because the taxonomical identity of *Exaeretodon major* is tentative (see Abdala *et al.*, 2002);?Ladinian–Carnian (Rogers *et al.*, 1993; Abdala, Ribeiro & Schultz, 2001).

Gomphodontosuchus: GPIT without number (von Huene, 1928, 1936; Hopson, 1985). Santa Maria Formation, Paraná Basin, Brazil, *Rhynchosaur* Biozone; Carnian (Abdala *et al.*, 2001).

Luangwa: BP/1/3731, OUMNH TSK 121 (Brink, 1963; Kemp, 1980; Abdala & Teixeira, 2004). Upper Ntawere Formation, Zambia; Santa Maria Formation, Brazil; Anisian–?Ladinian (Abdala & Teixeira, 2004).

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 (Romer, 1967, 1972; Crompton, 1972a; Abdala & Giannini, 2000). Chañares Formation, Ischigualasto–Villa Union Basin, Argentina; Santa Maria Formation, Paraná Basin, Brazil, *Dinodontosaurus* Biozone; Early Ladinian (Rogers *et al.*, 2001; Abdala *et al.*, 2001).

Menadon: UA-10601, FMNH PR 2104 (Flynn *et al.*, 2000). 'Isalo II', Morondava Basin, Madagascar; undifferentiated Middle or Late Triassic (Flynn *et al.*, 1999, 2000).

Pascualgnathus: MLP 65-VI-18-1, PVL 3466, 4416 (Bonaparte, 1966). Puesto Viejo Formation, Argentina; Late Olenekian–Early Anisian (Kokogian *et al.*, 1999).

Santacruzodon: MCN PV 2751, 2752, 2768, 2770; MCP PV 4034, 4044 (Abdala & Ribeiro, 2003). Santa Maria Formation, Paraná Basin, Brazil, Traversodontid Biozone; Late Ladinian (Abdala *et al.*, 2001).

Scalenodon angustifrons: UMZC T.907, T.908, T.909, T.910, T.911, T.912, T.913, T.914, T.915, T.916, T.917, T.918 (Parrington, 1946; Crompton, 1955, 1972a). Manda Formation, Tanzania; Late Anisian–?earlier (Abdala & Ribeiro, 2003).

'*Scalenodon*' *hirschsoni*: BMNH R 8577 (Crompton, 1972a). Manda Formation, Tanzania; Late Anisian–?earlier (Abdala & Ribeiro, 2003).

Scalenodontoides: BP/1/5395 (Crompton & Ellenberger, 1957; Hopson, 1984; Gow & Hancox, 1993; Battail, 2004). Lower Elliot Formation, Karoo Basin, South Africa; Early Norian (Lucas & Hancox, 2001).

Traversodon: UFRGS PV 0224T, GPIT 1045, 1063, 1069 (von Huene, 1936; Barberena, 1974, 1981). Santa Maria Formation, Paraná Basin, Brazil, *Dinodontosaurus* Biozone; Early Ladinian (Abdala *et al.*, 2001).

Trirachodon: see Materials. Burgersdorp Formation, Karoo Basin, South Africa, Subzone B of the *Cynognathus* AZ; Omingonde Formation, Namibia (Keyser, 1973). NMQR 3279 has a maxillary platform lateral to the postcanines, indicating the presence of *T. berryi* in Subzone A (see Discussion); Late Olenekian–Early Anisian (Hancox, 2000).

APPENDIX 2

CHARACTER LIST

Characters 0–27 are from Abdala & Ribeiro (2003), with the states of characters 20 and 24 having been modified. Three multistate characters (5, 15, and 36) were treated as additive. The abbreviation after the character states indicates authors that previously used the character in data matrices including non-mammaliaform cynodonts, and the corresponding number of the character: R, Rowe (1988); W, Wible (1991); LL, Lucas & Luo (1993); L, Luo (1994); M, Martínez, May & Forster (1996); F, Flynn *et al*. (2000); HK, Hopson & Kitching (2001); B, Bonaparte *et al*. (2003); SS, Sidor & Smith (2004). Asterisks following the author abbreviation indicate that the definition of the character or the character states is not the same as provided here. Most characters are discussed and rationale for scoring made explicit. The score for *Traversodon* upper postcanines is based on a right maxilla (GPIT 1069) showing a well-preserved last postcanine in eruption. von Huene (1936: table 15, fig. 5) described this material, but the preparation was incomplete at that time and the last postcanine was apparently not exposed.

0. Number of upper incisors: (0) four; (1) three. R81, W63, M1, F4, HK53, B3, SS45. Three upper incisors are present in *Pascualgnathus* (Bonaparte, 1966: fig.

4; F. Abdala, pers. observ., contra Hopson & Kitching, 2001: character 53), *Exaeretodon* (Bonaparte, 1962: fig. 4; Abdala *et al*., 2002: fig. 2B), '*Scalenodon*' *hirschsoni* (Hopson & Kitching, 2001), *Scalenodontoides* (Hopson, 1984: fig. 2a; Gow & Hancox, 1993: fig. 4), and *Menadon* (Flynn *et al*., 2000: character 4). See also Abdala & Ribeiro (2003: fig. 8).

1. Incisor size: (0) small; (1) large. F3, HK56, B5, 6. The size of the incisors seems to have some relationship with the number of upper incisors. Forms with three upper incisors, such as *Exaeretodon* (Abdala *et al*., 2002: fig. 2B), *Scalenodontoides* (Hopson, 1984: fig. 2A), '*Scalenodon*' *hirschsoni*, and *Menadon* (Flynn *et al*., 2000), show large incisors when compared with remaining gomphodont cynodonts. *Cricodon* also shows large incisors, remarkably higher than the postcanine crown (Abdala *et al*., 2005). The lower incisors of *Exaeretodon*, *Menadon*, and *Scalenodontoides* are, in addition, directed anteriorly (procumbent). Small incisor size is scored in *Gomphodontosuchus*, following reconstruction by Hopson (1985: fig. 2), contra Abdala & Ribeiro (2003: character 2).

2. Diastema between upper incisors and canine: (0) present; (1) absent. The absence of a diastema between the last upper incisor and the canine is scored in *Massetognathus* (Romer, 1967: fig. 2), '*Scalenodon*' *hirschsoni* (F. Abdala, pers. observ.), *Gomphodontosuchus* (Hopson, 1985: fig. 3), *Exaeretodon* (Bonaparte, 1962: fig. 4; Abdala *et al*., 2002: fig. 2B), *Menadon* (Flynn *et al*., 2000: fig. 2B), and *Scalenodontoides* (Hopson, 1984: fig. 2a). See also Abdala & Ribeiro (2003: fig. 8).

3. Upper canine size: (0) large; (1) reduced. L6* (referred by L as canine size), HK57. Upper and lower canines in *Massetognathus* are slightly larger than the incisors (Romer, 1967: fig. 2). These teeth are not completely preserved in *Gomphodontosuchus*, but following reconstruction by Hopson (1985: fig. 2) they are scored as reduced.

4. Lower canine size: (0) large; (1) reduced. L6* (referred by L as canine size), HK58. *Exaeretodon* represents the only taxon in which the upper canine is large but the lower is remarkably reduced (Bonaparte, 1962: figs 2, 9; Chatterjee, 1982: text-fig. 5). Scoring in other taxa is discussed under character 3.

5. Position of paracanine fossae in relation to the upper canine: (0) anteromedial; (1) medial; (2) posteromedial. This character was considered after Hopson (1985: 289), who described the fossa in *Gomphodontosuchus* as being medial to the upper canines 'as in other advanced traversodonts, rather than anteromedial to them as in primitive gomphodonts and carnivorous cynodonts'. The fossa is also medial in *Massetognathus* (Romer, 1967: fig. 2), and posteromedial in *Exaeretodon* (Bonaparte, 1962: fig. 4) and *Scalenodontoides* (Hopson, 1984: fig. 2a). See also Abdala & Ribeiro (2003: fig. 8).

6. Overall morphology of the upper postcanines in occlusal view: (0) sectorial; (1) ovoid–ellipsoid; (2) rectangular–trapezoidal. (Only gomphodont teeth are referred in states 1 and 2). HK62*, M5* (referred by M as postcanine shape), L13*. This character may allow for further subdivision, but the boundaries between different states would then become diffuse. Ovoid–ellipsoid tooth morphology is scored for diademodontids, trirachodontids, and some traversodontids (e.g. *Pascualgnathus*, *Scalenodon angustifrons*, and *Luangwa*). These traversodontids were previously scored as rectangular–trapezoidal (Abdala & Ribeiro, 2003), but their outline is clearly more similar to the ovoid shape of *Diademodon* and *Cricodon*.

7. Shouldering in upper postcanines: (0) absent; (1) present. F2*. Shouldering can be defined as the extension of the anterolabial margin of the upper postcanine forward, producing a 'shoulder-like' process over the preceding teeth. Romer (1967) first defined this feature for *Massetognathus* postcanines, in which the shouldering pattern is incipient (contra Flynn *et al*., 2000: character 2). This definition differs from the 'shouldering' of Hopson (1984), which refers to the lateral extension of the outer surface of the external main cusp in the upper postcanines. 'Shouldering' in our data matrix refers to Romer's (1967) definition. This feature is extremely accentuated in *Exaeretodon*, where the shouldering practically separates the sectorial margin (lateral lobe) of the postcanine from the long medial lobe that includes the occlusal basin. The same pattern appears to be in *Gomphodontosuchus*, although there is no separation between the sectorial and the medial lobes of the tooth (Hopson, 1985: fig. 4).

8. Inclination of the last upper postcanines in relation to the axis of the skull: (0) absent or small; (1) oblique. F9*, HK72*. The small inclination included in the plesiomorphic state refers to angles up to 20°. This inclination is observed in the last postcanines of *Scalenodon angustifrons* (Crompton, 1955: figs 8, 9) and *Luangwa* (Kemp, 1980: fig. 1). Both states are present in the large sample of *Massetognathus*: PVL 3901 (basal skull length of 124 mm) shows the last postcanines oblique (see also Romer, 1967: fig. 9), whereas in PVL 3902 (basal skull length 127 mm) they show low inclination.

9. Location of the transverse crest of upper postcanines: (0) central; (1) anterior; (2) posterior. HK64*. This trait was scored as polymorphic (i.e. located central and posteriorly) for *Trirachodon* and *Scalenodon angustifrons*. The location of the crest in the first taxon is clearly central in many specimens (e.g. BP/1/4661, SAM-PK-K-171), but is quite close to the posterior margin in some postcanines of BSP 1934 VIII 21 (see Broili & Schröder, 1935a: fig. 3). In UMCZ T. 910 (the best-preserved series of postcanines in *Scalenodon angustifrons*), the upper postcanines of the middle

of the series show the crest close to the middle of the crown, whereas in the posterior teeth the crest is closer to the posterior margin.

10. Number of cusps in the transverse crest of the upper postcanines: (0) two; (1) three or more. F8*, HK63. Four cusps in the transverse crest of the upper postcanines are only known in *Luangwa*, in which there is a tiny cusp located between the central and the lateral cusps (Kemp, 1980: fig. 3B).

11. Central cusp of upper transverse crest: (0) midway between buccal and lingual cusps; (1) closer to lingual cusp. HK65. *Langbergia* is the only taxon showing the central cusp located midway between the buccal and lingual cusps. The score of this character for *Diademodon* in Abdala & Ribeiro (2003: character 12) is a *lapsus calami*, considering that this taxon was scored as having only two cusps in the transverse crest of the upper postcanines (Abdala & Ribeiro, 2003: character 11). Extensive studies on *Trirachodon* material indicate that the central cusp is closer to the lingual in this taxon (contra Abdala & Ribeiro, 2003: character 12), but a midway location between the buccal and lingual cusp is observed in BMNH 3307. This character is coded as polymorphic for *Trirachodon*.

12. Posterior cingulum on upper postcanines: (0) present; (1) absent. F7. Characters 12, 20, 39, and 40 refer to cingula on upper and lower postcanine crowns. The presence of a cingulum bordering the entire anterior and posterior margins on both the upper and lower postcanines is among the features that allows a quick identification of Trirachodontidae teeth among gomphodonts. However, none of the four characters is synapomorphic for the group. Although less extended, a cingulum on the posterior margin of the upper postcanines is known in *Diademodon* (Crompton, 1972a; Grine, 1977). Some traversodontids show a well-developed posterior cingulum on practically the entire margin of the upper postcanines (e.g. *Traversodon*, *Luangwa*).

13. External cingulum on the anterior portion of the upper postcanines: (0) absent; (1) present. HK61. A cingulum formed by one or more cuspules is located externally to the anterior portion of the upper postcanines of *Luangwa* (Kemp, 1980: 195), *Scalenodon angustifrons* (Crompton, 1972a: figs 4C, D), and *Dadadon* (Flynn *et al*., 2000: 425). A tiny cingular cusp with the same placement is present in *Traversodon*.

14. Anterolingual cusp in upper postcanines: (0) absent; (1) present. HK69. This character refers to the presence of a distinctive cusp observed in traversodontids where the transverse crest of the tooth is located in the middle or posterior portion of the crown. In *Andescynodon*, the crest is anterior and for that reason we considered the character as inapplicable for this genus. In taxa with a series of cingular cusps in the anterolingual portion of the postcanine, but without a larger dominant one (e.g. *Santacruzodon*), this character was scored as absent.

15. Number of cusps in the sectorial border (i.e. labial margin) of the upper postcanines: (0) more than two; (1) two; (2) one. The number of sectorial cusps in the upper postcanines of *Diademodon* is three, based on the well-preserved teeth in MB R1004, BMNH R3765, and BS1934 VIII 14. In trirachodontids, this character is particularly problematic. We scored three sectorial cusps in both *Langbergia* and *Cricodon*, because in lateral view it is possible to observe them (see Abdala *et al*., 2005: fig. 6). The anterior and posterior cingular labial cusps, however, are also part of the anterior and posterior cingula of the postcanine. This obviously allows for an alternative way of scoring, considering the presence of only one cusp in the sectorial border of all trirachodontids. This character was scored as polymorphic for *Luangwa* because OUMNH TSK 121 shows two labial cusps, whereas in BP/1/3731 there are one large and three tiny accessory cusps in addition to the main one (Abdala & Teixeira, 2004).

16. Overall morphology of lower postcanines in occlusal view: (0) sectorial; (1) circular; (2) ovoid–ellipsoid; (3) quadrangular. (Only gomphodont teeth are referred in states 1, 2, and 3. HK62*, M5* (referred by M as postcanine shape). *Diademodon* shows circular in outline lower postcanines (Crompton, 1972a: fig. 3A, B), whereas in trirachodontids they vary between ovoid and ellipsoid (Crompton, 1972a: fig. 3E; Abdala *et al*., 2005). Traversodontid lower postcanines are quadrangular in outline (Crompton, 1972a: fig. 13B, E, H; Hopson, 1984: fig. 3). The lower postcanine morphology in the Madagascan traversodontids *Menadon* and *Dadadon* is not known.

17. Position of the transverse crest in lower postcanines: (0) central; (1) anterior. All traversodontids show the transverse crest of the lower postcanine located anteriorly (Battail, 1983), whereas in diademodontids and trirachodontids the transverse crest is central (Crompton, 1972a: fig. 3; Grine, 1977).

18. Number of cusps in the transverse crest of the lower postcanines: (0) two; (1) three. HK73. All the traversodontids included in this analysis have two cusps in the transverse crest, but some Late Triassic representatives of this group from Laurasia show three cusps (Sues, Hopson & Shubin, 1992).

19. Size of the anterior cusps in the lower postcanines: (0) labial lower than lingual; (1) labial higher than lingual. F11, HK76. Lower postcanines with the labial cusp lower than the lingual are scored in *Massetognathus* following Crompton (1972a: plate 7A) and Hopson (1985), contra Romer (1967: 10).

20. Anterior cingulum in the lower postcanines: (0) cuspules disposed on the entire margin; (1) one or more cuspules located anterolabially; (2) absent. HK74*. This is the only character referring to the

postcanine anterior (= mesial) and posterior (= distal) cingula (12, 20, 39, and 40), which is not coded as a nominal variable (= presence/absence). The restricted anterolabial location of this character in traversodontids with an anterior cingulum in the lower postcanines allows for the recognition of an additional state. In this state are included forms with the cingulum formed by an isolated cusp, as in *Scalenodon angustifrons*, '*Scalenodon*' *hirschsoni* (Crompton, 1972a), and *Andescynodon* (Goñi, 1986; Goñi & Goin, 1988), or by a series of tiny cuspules, as in *Luangwa drysdalli* (Abdala & Teixeira, 2004).

21. Internarial bar: (0) present; (1) absent. F5. The only nonmammaliaform cynodonts lacking an internarial bar are *Exaeretodon* (Chatterjee, 1982; Abdala *et al*., 2002), *Scalenodontoides* (Hopson, 1984: fig. 2a), and *Menadon* (Flynn *et al*., 2000: fig. 2A).

22. Maxillary labial platform lateral to the postcanine series: (0) absent; (1) present. HK77. The plesiomorphic condition is known in the carnivorous *Cynognathus*, and the gomphodonts *Diademodon* and *Langbergia*. Remaining taxa included in the analysis have a maxillary labial platform that could be poorly developed (e.g. *Menadon*, Flynn *et al*., 2000: fig. 2B; *Andescynodon*, Bonaparte, 1969a: fig. 1A) or extensive (e.g. *Luangwa*, Brink, 1963: fig. 15B; *Massetognathus*, Romer, 1967: fig. 9). In many instances it is difficult to be certain of the boundary between the poorly developed/extensive labial platforms, and thus we opted to score this character as a nominal variable (presence/absence).

23. Parietal foramen in adults: (0) present; (1) absent. R8, W12, LL34, L64, M31, F6, HK7, B24. The parietal foramen is scored as absent in *Massetognathus*. The foramen is present in individuals of small to medium size, but large specimens interpreted to be adults lack it (Abdala & Giannini, 2000). The foramen is also absent in *Pascualgnathus* (Bonaparte, 1966: fig. 1, contra Hopson & Kitching, 2001: character 7) and *Andescynodon*. An examination of *Scalenodontoides* (BP/1/5395) indicates that the parietal foramen is absent (contra Gow & Hancox, 1993: fig. 2). This character is coded as polymorphic in *Trirachodon*, because it is absent in the well-preserved specimen AM 461, whereas a small foramen is observed in AM 434 and BMNH 3307, both skulls comparable in size with AM 461.

24. Zygomatic process of the jugal: (0) slightly projected; (1) conspicuously projected; (2) absent; (3) a ball-like process. F16*, HK21*. The polarity and scoring of this character have changed in relation to Abdala & Ribeiro (2003). The plesiomorphic condition now, process slightly projected, is scored in *Cynognathus* and, among gomphodonts, only *Pascualgnathus* (Bonaparte, 1966: fig. 1). The zygomatic process of the jugal is remarkably large in *Diademodon*, whereas the processes of *Exaeretodon* (Chatterjee, 1982: text-fig. 5), *Trirachodon* (BP/1/5362), *Luangwa* (Kemp, 1980: fig. 6A), *Langbergia*, and *Traversodon* are conspicuously smaller than that of *Diademodon*. Both conditions, however, are included in the same state (process conspicuously projected). In the only specimen of *Scalenodon angustifrons* with the zygoma adequately preserved (UMCZ T.907), the process is absent (contra Hopson & Kitching, 2001: character 21). *Massetognathus* lacks a suborbital process (Romer, 1967), but was scored as having a process by Flynn *et al*. (2000: character 16) and having a small projected process by Abdala & Ribeiro (2003: character 25). In *Gomphodontosuchus*, the zygoma is not preserved (contra Flynn *et al*., 2000), whereas in *Scalenododontoides* (BP/1/5395) the arch is too poorly preserved to determine the presence of a process with any certainty (contra Gow & Hancox, 1993). We score the absence of the process in *Menadon* following Flynn *et al*. (2000: character 16, fig. 2A), but contra Flynn *et al*. (2000: 422), who quote the presence of the suborbital process in the diagnosis of *Menadon*. The score of this character for *Traversodon* is based on a fragment consisting of the posterior portion of the orbit and anteriormost end of the zygomatic arch, which preserves the process (GPIT 1069). This material was previously considered to be a partial rib (von Huene, 1936), but has subsequently been recognized as part of the zygoma by Hopson in a label left with the specimen at the Tübingen collection.

25. Posterior extension of the jugal above the squamosal in the zygoma: (0) absent or with a small extension; (1) well developed. F15. This feature refers to the posterior projection of the jugal above the squamosal immediately behind the postorbital bar. This projection is particularly long in *Exaeretodon* (Hopson, 1984: fig. 2) and *Scalenodontoides* (Gow & Hancox, 1993: fig. 1), and although somewhat less developed, also long in *Menadon* (Flynn *et al*., 2000: fig. 2A).

26. Coronoid process of the mandible: (0) covers the last postcanine in lateral view; (1) does not cover. *Diademodon* is scored as polymorphic because the dental series may finish just anterior to the coronoid process (e.g. SAM-PK-4002) or the last postcanine may appear partially covered by the rising process (e.g. SAM-PK-K5877). A score of (1) in *Cricodon* is following the reconstruction by Crompton (1955: fig. 3). The only evidence of this character in *Langbergia* is based on NMQR 3251, in which the last lower postcanines are implanted along the ascending margin of the coronoid process (i.e. are not covered in lateral view).

27. Dentary angle: (0) not projected posteriorly; (1) weakly projected; (2) well projected posteriorly. Most cynodonts show the ventral and posterior margins of the dentary (= angle of the dentary) meeting in a right or quite obtuse angle not projected posteriorly. In

Luangwa, the angle of the dentary is projected slightly backwards (Kemp, 1980: fig. 6), whereas it is well projected in *Exaeretodon* (Bonaparte, 1962: fig. 8) and *Menadon* (Flynn *et al*., 2000: fig. 2A). The angle of the dentary scored as well projected for *Scalenodontoides* is based on BP/1/5395. A fragment of the dentary of this specimen, including the angle and coronoid process, was found between miscellaneous fragments after the publication of Gow & Hancox (1993), and remains unpublished. Some tritylodontids, such as *Bienotheroides* (Sun, 1984: figs 7, 8) and juvenile specimens from the Kayenta Formation, including one individual assigned to *Kayentatherium* (Sues, 1985: fig. 5A; Sues, 1986: fig. 13), also present a posteriorly projected angle of the dentary.

28. Snout: (0) longer than temporal region; (1) subequal. The temporal region length is measured from the confluence of the postorbital bars to the end of the sagittal crest (see Abdala & Giannini, 2000: fig. 2A).

29. Incisive foramen: (0) posteriorly closed by maxilla; (1) completely enclosed by premaxilla. M19, HK1*, B21*. An incisive foramen enclosed by the premaxilla is only present in *Massetognathus* (F. Abdala, pers. observ.; Hopson & Kitching, 2001: character 1; contra Romer, 1967: fig. 9 and Martínez *et al*., 1996: character 19) and *Exaeretodon* (Abdala *et al*., 2002: fig. 2B). In nine taxa of the data matrix, the condition of this character is unknown.

30. Ectopterygoid: (0) present, (1) absent. HK9*, SS15*. This bone is absent in *Exaeretodon* (Abdala *et al*., 2002) and in the large sample of *Massetognathus* (Barberena, 1974; F. Abdala, pers. observ.). Hopson & Kitching (2001: character 9) also endorsed this coding, but they extended the absence of the bone to other gomphodonts (e.g. *Pascualgnathus*, *Scalenodon angustifrons*, *Luangwa*) in which the material is scarce or the preservation is not good enough to be certain about the condition of this character. In 12 taxa of our data matrix, this character is scored as unknown.

31. Maxilla in the margin of the subtemporal fenestra: (0) excluded; (1) included. R15, W14, L62, M16. This character was first proposed by Barberena (1974: fig. 13; see also Barberena, 1981), who recognized that the jugal and pterygoid contact excluded the maxilla from the margin of the subtemporal fenestra in *Diademodon* and some traversodontids (e.g. *Traversodon* and *Massetognathus*). The maxilla is clearly excluded from the subtemporal fenestra in *Trirachodon* (BP/1/4658) and *Langbergia* (NMQR 3255).

32. Epipterygoid–quadrate contact: (0) present; (1) squamosal interposed. M53*. The squamosal is interposed between the epipterygoid and quadrate in *Massetognathus* (Rougier, Wible & Hopson, 1992: fig. 7D) and *Exaeretodon* (Abdala *et al*., 2002: fig. 6). The condition of this character is unknown in 12 of the taxa included in the analysis.

33. Temporal fenestra: (0) widest posteriorly; (1) same width throughout; (2) widest in the middle. HK39*. Hopson & Kitching (2001: character 39) considered the ‘greatest width of zygomatic arches at posterior end of arch’ (interpreted here as similar to the state temporal fenestra widest posteriorly) as a synapomorphy of Cynognathia. We, however, documented some variation in this character in the group. *Trirachodon*, *Langbergia*, *Luangwa* (Brink, 1963: fig. 15A), *Massetognathus*, and *Exaeretodon* (Bonaparte, 1962: fig. 3) show the same width from the anterior to the posterior margins of the fenestra (state 1), whereas in *Scalenodontoides* it seems to be widest in the middle of the fenestra (Gow & Hancox, 1993: fig. 2).

34. Incisor cutting margins: (0) serrated; (1) smoothly ridged; (2) denticulated. HK55, SS47. Denticulated refers to mediodistally enlarged incisors or ‘chisel-shaped incisors with longitudinal striations’, as in *Massetognathus* (Romer, 1967: 7). The same state is also scored for *Santacruzodon*, in which the incisors are enlarged mediodistally, but arrowhead-shaped, with nine to 11 marginal cuspules (Abdala & Ribeiro, 2003: 533). Incisors with marginal cuspules are also known in the Laurasian traversodontid *Arctotraversodon plemmyridon* (Hopson, 1984). Hopson & Kitching (2001: character 55) scored a question mark for *Diademodon*, but a serrated margin of incisors is present in BS1934 VIII 14.

35. Canine serrations: (0) present; (1) absent. HK59, SS49. Hopson & Kitching (2001: character 59) scored a question mark for *Diademodon*. Serrated margins of the canine are, however, recorded in AM 3753 (Broom, 1919). In addition, BMNH R3588 (a partial lower jaw) shows a serrated anterior margin and smooth posterior (Watson, 1911), whereas in BMNH R2578 the posterior margin of the upper canine and anterior margin of the lower canine are serrated.

36. Axis of the posterior part of maxillary tooth row: (0) directed towards the lateral rim of the subtemporal fenestra; (1) directed towards the centre of the fenestra; (2) directed towards the medial rim of the fenestra. R80*, M12*, HK78, B13. Hopson & Kitching (2001: character 78) formulated this character. We agree with the scores they proposed for the taxa common in both analyses. The plesiomorphic condition is present in *Cynognathus* and *Diademodon*, whereas state (1) is typical of the three trirachodontids. The axis of the posterior part of the maxillary tooth row directed towards the medial rim of the fossa was scored for all the traversodontids in this analysis. The latter condition is also present in tritylodontids (e.g. *Kayentatherium*; Sues, 1986: fig. 6) and in the tritheledontid *Pachygenelus* (Bonaparte *et al*., 2003: fig. 19).

37. Postcanine tooth row in adults: (0) formed by sectorial; (1) conical, gomphodont, and sectorial; (2) gom-

phodont and sectorial; (3) gomphodont. The states of this character are clear-cut between the three group members of the Gomphodontia. Conical, gomphodont, and sectorial postcanine teeth characterize the adult dentition of *Diademodon* (Hopson, 1971), gomphodont and sectorial teeth seem to be typical of trirachodontid adults, although with some exceptions (see Tables 3 and 4), and only gomphodont (= traversodont) teeth are known in adults of traversodontids (Battail, 1983).

38. Posterior cingulum in the lower postcanines: (0) present; (1) absent. A posterior cingulum is present in the lower postcanines of trirachodontids, *Diademodon*, *Massetognathus*, *Scalenodon angustifrons*, '*Scalenodon*' *hirschsoni*, *Luangwa*, and *Santacruzodon* (Crompton, 1972a; Grine, 1977; Abdala & Ribeiro, 2003; Abdala & Teixeira, 2004).

39. Anterior cingulum in the upper postcanines: (0) present; (1) absent. Although less extended than in trirachodontids, an anterior cingulum is present in the upper postcanines of *Diademodon* (Crompton, 1972a; Grine, 1977). A restricted anterior cingulum is also observed in *Santacruzodon* and *Massetognathus* (Crompton, 1972a; Abdala & Ribeiro, 2003).

40. Deep occlusal basins in the postcanines: (0) absent; (1) present. The presence of deep occlusal basins is characteristic of traversodontids (Crompton, 1972a: 66), contrasting with the shallow basins of *Diademodon* and trirachodontids.

41. Postcanine occlusion: (0) absent; (1) present. M8. The presence of buccolingually expanded postcanines in gomphodont cynodonts ensures the presence of rudimentary postcanine occlusion (Crompton, 1972a; Hopson, 1984), a synapomorphy of gomphodonts developed by parallelism in tritylodontid cynodonts.

42. Shearing planes between the outer surface of the main cusp of the lower and the inner surfaces of the main cusps of the upper postcanines: (0) present; (1) absent. In his study of occlusion in cynodonts and tritylodontids, Crompton (1972a: 66) pointed out that small matching shearing planes are produced on the outer surface of the main cusp of the lower postcanines and the inner surface of the main cusp of the upper teeth in *Diademodon*. The same pattern of contact between upper and lower postcanines, but more effective because of the high crests and deep occlusal basins, is recognized in traversodontids. On the contrary, trirachodontids have alternate occlusal patterns between the transverse crest of the upper and lower postcanines, but no other complex occlusal pattern. Considering the similarity in the tooth pattern for all trirachodontids, the same pattern is scored for *Langbergia*.

APPENDIX 3

DATA MATRIX

	01234567891	1111111112	2222222223	3333333334	44
	0	1234567890	1234567890	1234567890	12
Cynognathus	0000000?0??	??0?00????	0000000000	0000000??0	0?
Diademodon	00000010000	?00?0100?0	00010A0000	0000001000	10
Trirachodon	000000100B1	A00?2201?0	01A100010?	0010012000	11
Langbergia	00000010001	000?0201?0	0001010100	0010012000	11
Cricodon	01000010001	100?0201?0	01??010?0?	0??0012000	11
Andescynodon	00000020010	?10?131011	01120?010?	??01123111	10
Massetognathus	00111121A21	1100031002	0112000111	0112123001	10
Exaeretodon	11101221120	?101031012	1111102011	1111123111	10
Luangwa	00000010021	1010A31001	01010010??	0?10023001	10
Scalenodon angustifrons	000000100B1	1110231001	010210?1??	0?00023011	10
'*Scalenodon*' *hirschsoni*	1111?020?21	1001131001	01??????01	???1123011	10
Traversodon	00000020121	1011031002	0101?0????	0??1123?01	10
Gomphodontosuchus	0011112112?	?10??31012	01???0????	1??1123111	10
Pascualgnathus	10000010000	?0?0231???	?1100001??	0?01123?01	10
Scalenodontoides	111??221?20	?10?031012	111?1021??	1?21?23111	10
Menadon	11111?21120	?1012?????	11?21020??	0??1023?1?	10
Dadadon	000??021121	11112?????	01?3??????	???1123?11	10
Santacruzodon	000??021121	1100031012	01?3?00???	???2123001	10

A = 0,1; B = 0,2.

APPENDIX 4

UNAMBIGUOUS SYNAPOMORPHIES IN THE MAJORITY-RULE CONSENSUS TREE OBTAINED UNDER EQUAL-WEIGHTED CHARACTERS

Trirachodontidae + Traversodontidae
22. Presence of a maxillary labial platform lateral to the postcanine series. Reversal in *Langbergia*.
28. Snout subequal to the temporal region. Reversal in *Luangwa*.
37. Axis of the posterior part of maxillary tooth row; directed towards the centre of the subtemporal fenestra.

Trirachodontidae
18. Three cusps in the transverse crest of the lower postcanines.
34. Temporal fenestra of the same width throughout.
43. Absence of shearing planes between the outer surface of the main cusp of the lower postcanines and the inner surfaces of the main cusps of the upper postcanines.

[Langbergia, Cricodon]
26. Coronoid process of the mandible does not cover the last postcanine in lateral view.

Traversodontidae
9. Transverse crest of upper postcanines located posteriorly. Reversal in *Pascualgnathus*.
17. Transverse crest of lower postcanines located anteriorly.
20. One or more anterolabial cuspules forming the anterior cingulum in the lower postcanine.
37. Axis of the posterior part of maxillary tooth row directed towards the medial rim of the subtemporal fenestra.
41. Presence of deep occlusal basins in the postcanines.

Clade a
6. Rectangular to trapezoidal upper postcanines in occlusal view. Reversal in *Pascualgnathus*.
35. Incisor margins smoothly ridged.
36. Absence of canine serrations. Reversal in *Menadon*.

Clade b
12. Absence of posterior cingulum in upper postcanines. Parallelism in *Scalenodon angustifrons*.
19. Anterolabial cusp higher than anterolingual in the lower postcanines. Reversal in *Massetognathus*.

Dadadon [Santacruzodon [Massetognathus [Gomphodontosuchus [Scalenodontoides [Exaeretodon, Menadon]]]]]
7. Presence of shouldering in upper postcanines.
8. Last upper postcanines oblique in relation to the longitudinal axis of the skull. Parallelism in *Traversodon*.

Santacruzodon [Massetognathus [Gomphodontosuchus [Scalenodontoides [Exaeretodon, Menadon]]]]
15. More than two cusps in the sectorial border of the upper postcanines. Reversal from state 1–0.

Massetognathus [Gomphodontosuchus [Scalenodontoides [Exaeretodon, Menadon]]]
2. Absence of diastema between upper incisors and canine.
5. Paracanine fossa medial in relation to upper canine.

Gomphodontosuchus [Scalenodontoides [Exaeretodon, Menadon]]
31. Maxilla included in the margin of the subtemporal fenestra. Reversal in *Menadon*.
39. Absence of posterior cingulum in the lower postcanines. Parallelism in *Andescynodon*.

Scalenodontoides [Exaeretodon, Menadon]
0. Three upper incisors.
1. Large incisors
5. Paracanine fossa posteromedial in relation to the upper canine.
21. Absence of internarial bar.

[Exaeretodon, Menadon]
28. Snout longer than temporal region. Reversal from state 1–0.