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A traversodontid cynodont of African affinity in the South American Triassic

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The Traversodontidae represent one of the most diverse and abundant families of non-mammaliaform cynodonts, particularly in Gondwanan faunas of Middle to Late Triassic age. Although a great diversity of traversodontids is known for South American (approximately nine species) and African (six to seven species) Triassic faunas, the record of the group in these continents does not show similarities beyond the family level. Here we describe a new traversodontid, *Luangwa sudamericana*, from the Santa Maria Formation of southern Brazil, which is most similar to the Anisian traversodontids *Luangwa drysdalli* from the upper portion of the Ntawere Formation in Zambia, and *Scalenodon angustifrons* from the Manda Formation in Tanzania. Features in common with these African taxa are oval-outlined upper postcanines presenting an anterior labial cingulum. The new species is similar to *L. drysdalli* in a number of features, including the presence of a posterior cingulum in the upper postcanines, anterior cingulum in front of the transverse crest in the lower postcanines, short snout, enormous orbits and short temporal region. Differences with *L. drysdalli* are the less developed posterior cingulum behind the upper transverse crest that does not extend along the entire posterior border of the tooth, and the presence of a well-defined posterior accessory cusp on the sectorial crest of the upper postcanines. The comparison of the quadrate, preserved *in situ* in the squamosal notch of the new taxon, and that from other traversodontids, suggests that the quadratojugal is involved in the formation of the lateral condyle of the traversodontid suspensorium. *Luangwa* represents the first genus of traversodontid, and the second of non-mammaliaform cynodont shared by South American and African faunas. A significant biochronological implication of this finding is that part of the Santa Maria Formation may now be considered Anisian in age, and thus older than generally recognized for the unit.

Keywords: Traversodontidae, Middle Triassic, Brazil, Zambia, Cynodontia, *Luangwa.*

INTRODUCTION

The southern Brazilian Santa Maria Formation is well known for its record of an important continental Triassic vertebrate fauna. Pioneering studies in this unit were performed by Friedrich von Huene, a German palaeontologist who in 1928 conducted a six-month field trip to various localities in the Rio Grande do Sul State, southern Brazil. Huene discovered and published many species of tetrapods, including *Gomphodontosuchus brasiliensis,* the first traversodontid cynodont ever described (Huene 1928; Hopson 1985). He later identified other species of the Traversodontidae in his seminal work on the Brazilian Triassic reptile fauna (Huene 1936). Barberena (1974, 1981a,b) reinterpreted some of the traversodontid materials previously studied by Huene (1936) and, based on new discoveries, described new species of this group (Barberena 1981a).

Many traversodontid species have been described from Triassic faunas from Brazil and Argentina (Bonaparte 1982; Abdala *et al.* 2002) and genera such as *Massetognathus* (Romer 1967; Barberena 1981a; Abdala & Giannini 2000) and *Exaeretodon* (Bonaparte 1962; Abdala *et al.* 2002) were recognized from Ladinian and Carnian faunas of both countries. This family is also well diversified in Triassic deposits of Africa (including Madagascar), where it is represented by six to seven species (Crompton 1955; Brink 1963; Kemp 1980; Gow & Hancox 1993; Flynn *et al.* 2000). Despite this relatively high diversity of the group in South America and Africa, the faunas of these continents do not show similarities beyond the family level, with the carnivorous *Cynognathus* being the only genus evidencing faunal commonality between these continents. This taxon has been recorded in the fauna biostratigraphically known as the *Cynognathus* Assemblage Zone, from strata of the Burgersdorp Formation, Karoo Basin, South Africa (Kitching 1995; Hancox 2000), and in the Puesto Viejo Formation, Argentina (Bonaparte 1969; Abdala 1996).

In this report, we describe *Luangwa sudamericana* sp. nov. from the Santa Maria Formation of southern Brazil. One of the specimens included in the new species (UFRGS 267PV) was previously described as *Luangwa* sp. by Teixeira (1995). The new species is most similar to *Luangwa drysdalli* from the upper beds of the Ntawere Formation, Zambia, and to *Scalenodon angustifrons* from the Manda Formation, Tanzania, in eastern central Africa (Crompton 1955, 1972; Brink 1963; Kemp 1980), and thus demonstrate traversodontids of African affinity in the South American Middle Triassic. This finding also has important chronological implications, because both the Manda Formation and the upper portion of the Ntawere Formation are considered Anisian in age (Cox 1991; Battail 1993), and, as a consequence, some of the outcrops of the Santa Maria Formation in southern Brazil could be older than the Ladinian age usually recognized for its oldest fauna.

Institutional abbreviations. BP: Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg; MCP: Museo de Ciências e

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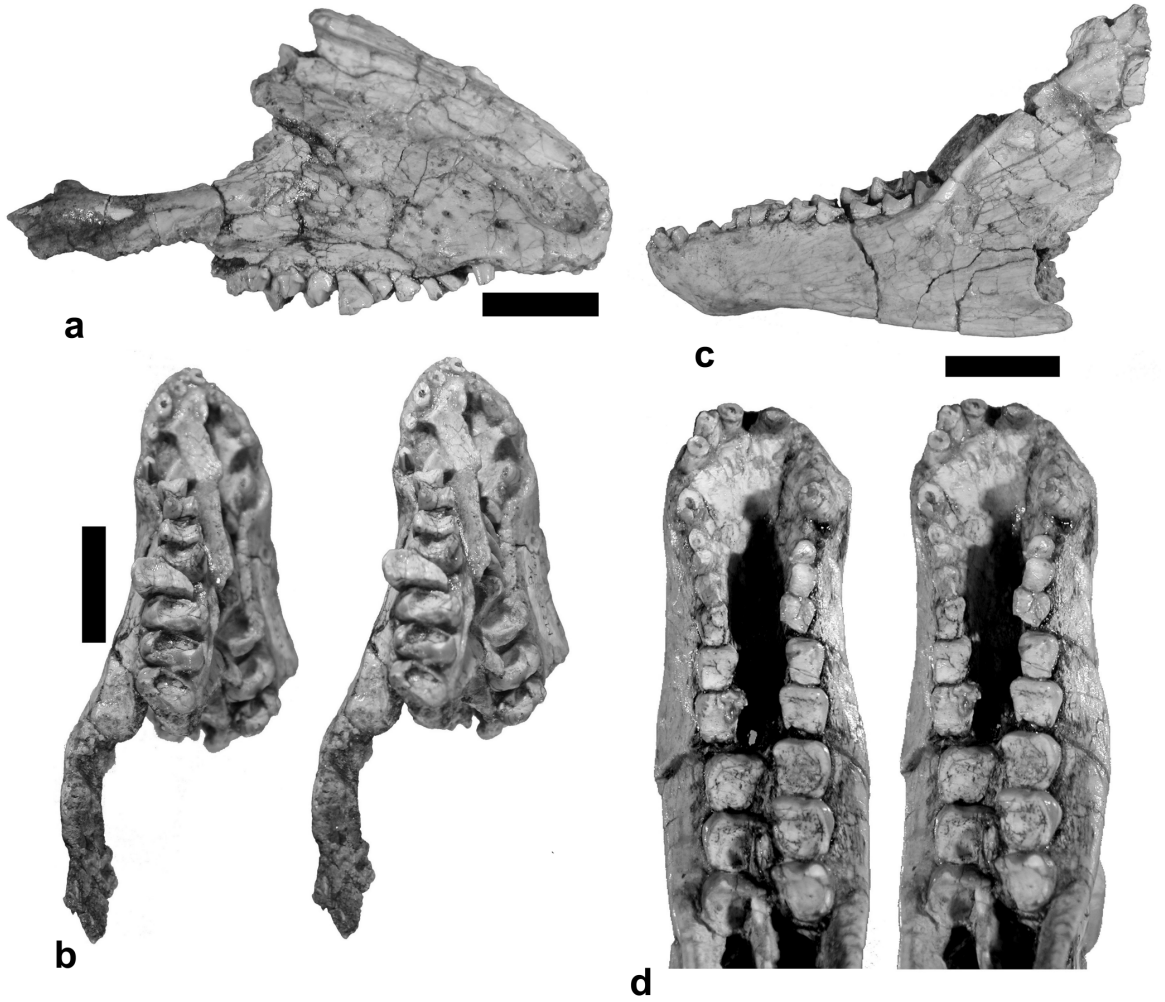

Figure 1. *Luangwa sudamericana,* holotype (MCP 3167PV); **a**, lateral view of snout; **b**, stereopair of upper dental series; **c**, lateral view of mandible; **d**, stereopair of lower dental series. Scale bars = 20 mm.

Tecnología, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachussets; NMQR: National Museum, Bloemfontein; OUMNH: Oxford University Museum of Natural History; SAM: South African Museum, Cape Town; UFRGS: Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre; UMZC, University Museum of Zoology, Cambridge.

SYSTEMATIC PALAEONTOLOGY

Therapsida Broom 1905
Eucynodontia Kemp 1982
Traversodontidae von Huene 1936
Luangwa Brink 1963

***Luangwa sudamericana* sp. nov.**, Figs 1–5

Etymology. Sudamericana refers to the first record for South America of a genus of Traversodontidae previously known only in east Africa.

Holotype. MCP 3167PV, a well-preserved partial skull and mandible. The skull includes the rostrum and rim of the right orbit, with complete dentition, and an isolated portion of the basicranium, and the most posterior portion of the zygoma, including the quadrate *in situ* (Figs 1, 4 & 5).

Referred material. UFRGS 267PV, a well-preserved partial skull and a fragment of the left lower jaw with three postcanines (Figs 2 & 3).

Horizon and locality. Santa Maria Formation, Middle to Upper Triassic. Specimen MCP 3167PV is from an unknown locality; specimen UFRGS 267PV comes from an unknown outcrop located on the border between the districts of Candelaria and Vera Cruz, Rio Grande do Sul State, Brazil. Many outcrops are present in this area, and recent field trips to the various outcrops yielded only fragmentary remains. Thus, the exact locality remains uncertain.

Comparative material. BP/1/3731, skull with articulated mandible and some postcranial bones, probably of the manus, attached to the snout; holotype of *Luangwa drysdalli* (Brink 1963; Fig. 6); BP/1/3733, poorly preserved anterior portion of the skull with dentition. Specimen smaller than the type, most likely a juvenile of the same species; OUMNH TSK121, partial skull with mandible (Fig. 7) and postcranial elements assigned to *Luangwa drysdalli* by Kemp (1980). These specimens come from outcrops of the upper beds of the Ntawere Formation in the Luangwa Valley, Zambia (Drysdall & Kitching 1963; Kemp 1975).

UMZC T.907, partial skull with lower jaw, holotype of *Scalenodon angustifrons* (Parrington 1946; Crompton 1955;

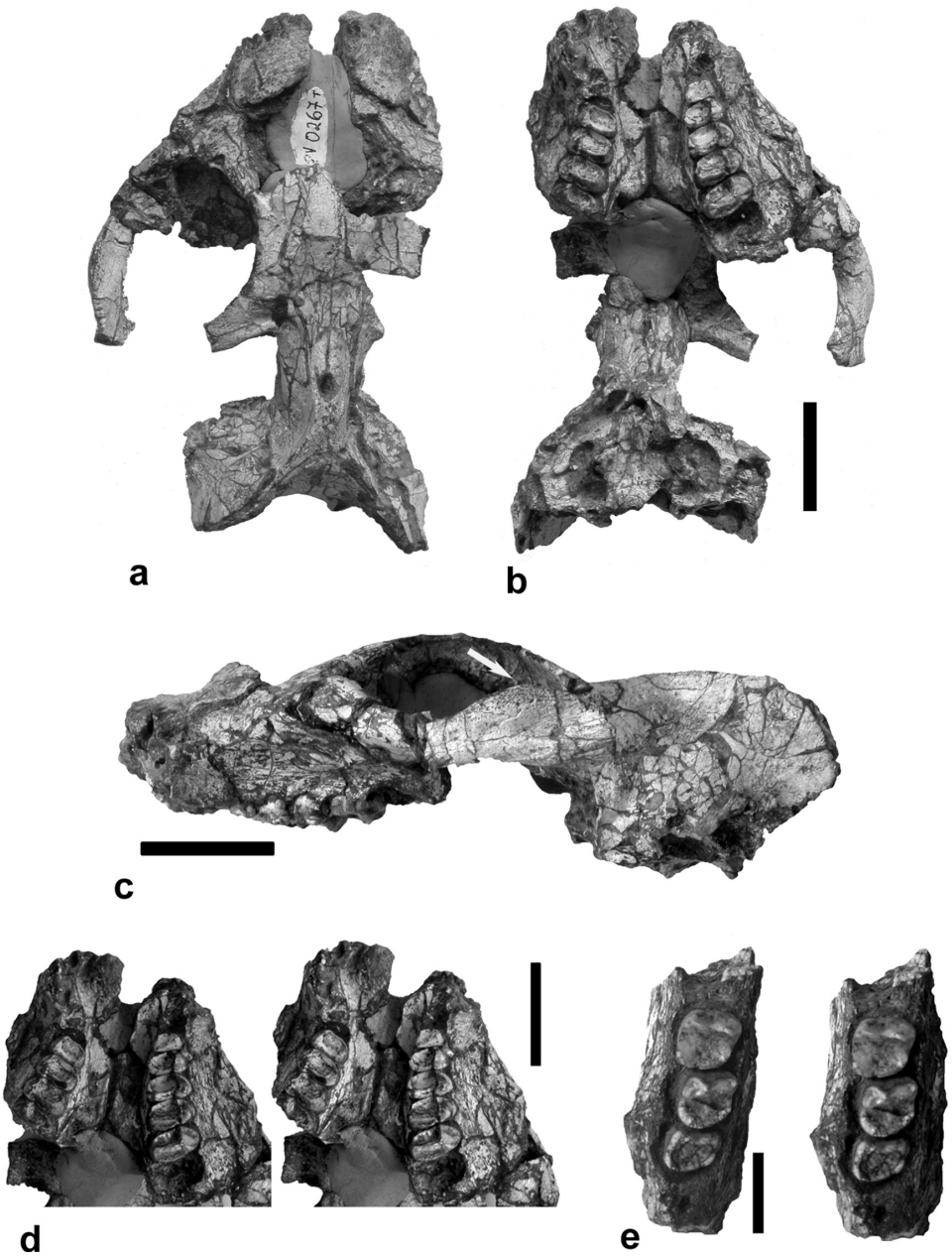

Figure 2. *Luangwa sudamericana,* UFRGS 267PV; **a**, dorsal, **b**, ventral and **c**, left lateral views of skull; **d**, stereopair of the upper postcanines; **e**, stereopair of lower postcanines. Scale bars = 20 mm (a, b, c, d) and 10 mm (e).

Fig. 8a,b); UMCZ T.908; T.909; T.910; T.911; T.912; T.913; T.914; T.915; T.916; T.917; T.918. All these specimens are skull and/or lower jaw fragments, with UMCZ T.910 showing the best-preserved upper and lower postcanines (Fig. 8c,d). They come from the locality B 29 of Stockley (1932), between Gingama and Tschikonge, Ruhuhu Valley, Tanzania and were described by Crompton (1955) as *S. angustifrons.*

Diagnosis

A traversodontid most similar to *Luangwa drysdalli* Brink 1963 and *Scalenodon angustifrons* (Parrington 1946). As in these species the upper postcanines are oval-outlined and feature an anterolabial cingulum. As in *L. drysdalli* the new species has a posterior cingulum with tiny cuspules behind the transverse crest of the upper postcanines, but less developed in *L. sudamericana* where it does not extend along the entire posterior border of the tooth. It also has tiny cuspules in front of the anterior transverse crest of the lower postcanines forming an incipient cingulum. Other similarities with *L. drysdalli* include a short snout and temporal region, large orbits and angle of the dentary slightly projected posteriorly. Differentiating *L. sudamericana* from *L. drysdalli* and *S. angustifrons* is a well-defined posterior accessory cusp on the labial crest of the upper postcanines. The presence of one anterior accessory cusp on the labial (sectorial) crest of the upper postcanines is a difference with the holotype of *L. drysdalli* (BP/1/3731), but not with OUMNH TSK 121.

Description

Specimen MCP 3167PV preserves the snout and part of the right orbit, while UFRGS 267PV is an almost complete skull, lacking the anterior and dorsal part of the snout, and showing an incomplete right orbit and temporal region on both sides. The snout is notably short, while the orbits

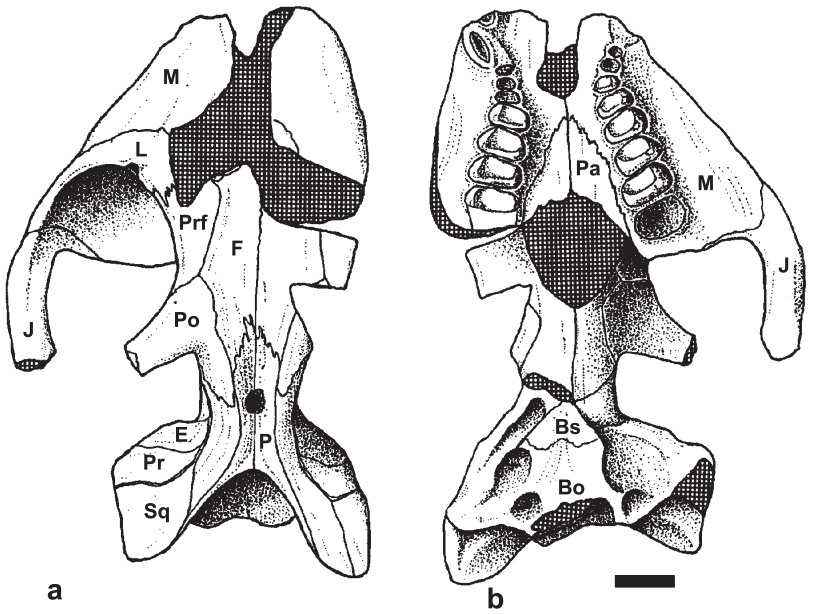

Figure 3. *Luangwa sudamericana,* UFRGS 267PV; **a**, dorsal and **b**, ventral view of skull. Abbreviations: Bo, baisoccipital; Bs, basisphenoid; E, epipterygoid; F, frontal; J, jugal; L, lacrimal; M, maxilla; P, parietal; Pa, palatine; Po, postorbital; Pr, prootic; Prf, prefrontal; Sq, squamosal. Scale bar = 10 mm.

are large in both specimens (Figs 1a, 2a, 3a). A well-developed ascending process of the premaxilla is present in MCP 3167PV (Fig. 1a). The right maxilla in the specimen is displaced from its original position, and the vertical vomer separating the nasal canals is visible. The maxillary labial platform is well developed in UFRGS 267PV (Figs 2b, 3b) and seems to be comparatively less developed in MCP 3167PV, but deformation in the specimen prevents certainty of the platform's original extent (Fig. 1b). The temporal region is remarkably short in UFRGS 267PV,

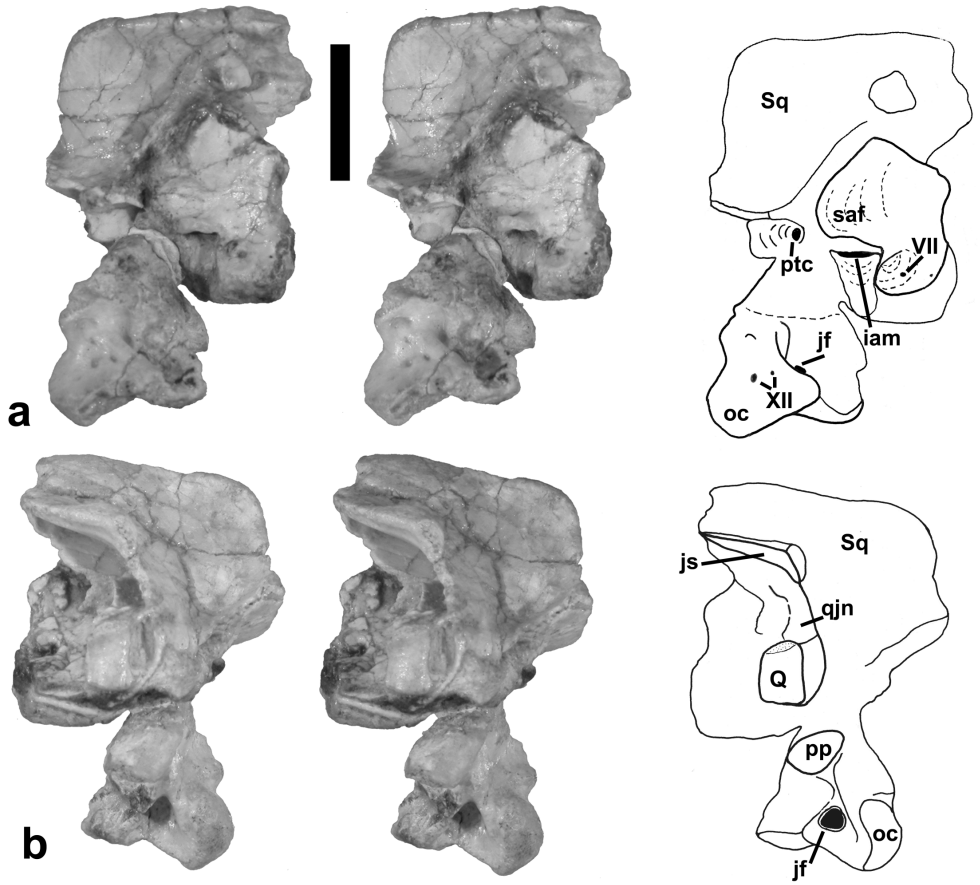

Figure 4. *Luangwa sudamericana,* holotype (MCP 3167PV); **a**, stereopair of medial view of braincase; **b**, stereopair of suspensorium and part of basicranium in ventrolateral view. Abbreviations: iam, internal auditory meatus; jf, jugular foramen; js, squamosal sutural surface for the jugal; oc, occipital condyle; pp, paroccipital process; ptc, posttemporal canal; qjn, notch in the squamosal for the quadratojugal; saf, subarcuate fossa; Sq, squamosal; VII, foramen for the exit of the facial nerve; XII, foramina for the exit of the hypoglossal nerve. Scale bar = 10 mm.

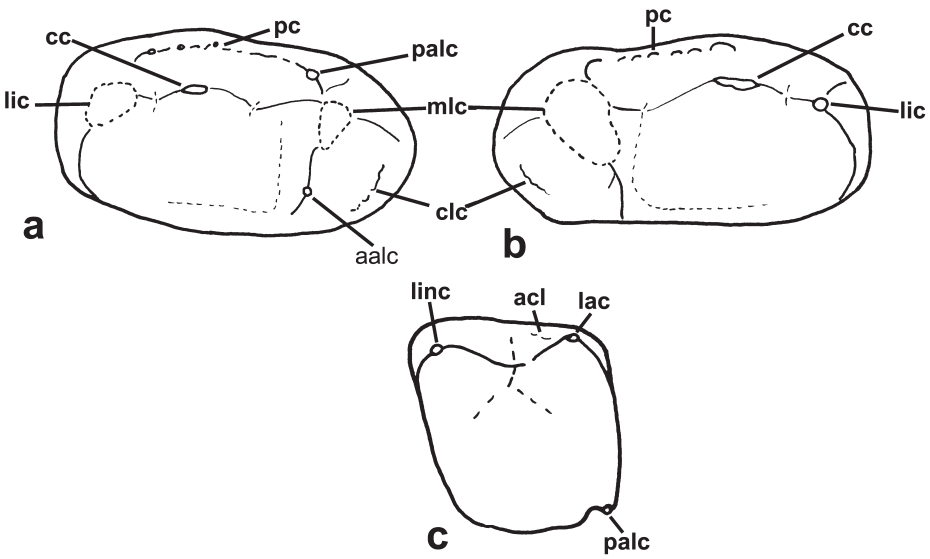

Figure 5. Postcanines of *Luangwa sudamericana,* MCP 3167PV; **a**, occlusal view of eighth upper right postcanine with some traits added considering also the ninth tooth (labial, right; anterior, bottom); **b**, occlusal view of ninth upper left postcanine (labial, left; anterior, bottom); **c**, occlusal view of seventh lower right postcanine (labial, right; anterior, top). The anterior cingulum represented in figure (**c**) was observed in UFRGS 267PV; Abbreviations: aalc, anterior accessory labial cusp; acl, anterior cingulum of the lower postcanines; cc, central cusp; clc, cingular labial crest; lac, labial cusp; lic, lingual cusp; linc, lingual cusp of the lower postcanine; mlc, main labial cusp; palc, posterior accessory labial cusp; pc, posterior cingulum.

displaying a wide parietal crest with the pineal foramen in the middle of the extension of the crest (Figs 2a, 3a). A slight ventral projection of the broken ventral edge of the zygomatic arch below the orbit in MCP 3167PV (Fig. 1a), suggests the presence of a descendant process of the jugal. This is confirmed in UFRGS 267PV where a portion of the right zygomatic arch was mistakenly glued upside down to the left side. The 'dorsal' border of the zygoma shows an extended and convex descendant process (arrow in Fig. 2c).

In the left cranio-mandibular joint region of MCP 3167PV, the squamosal accommodates the quadrate and shows a deep notch for the quadrato-jugal. Close to this notch, the squamosal shows a ventromedial surface for articulation with the posterior extension of the jugal (Fig. 4b). Another small surface on the posterior extremity of the squamosal appears to be for supplementary articulation with the surangular of the lower jaw. The posterior portion of the squamosal sulcus behind the quadrate is shallow compared with that of BP/1/3731. In anterior view, the quadrate shows a high dorsal plate directed dorso-laterally, ending in a pointed dorsal angle. The trochlea is wide anteroposteriorly (Fig. 4b), slightly convex ventrally, and the medial trochlear condyle is not medially projected from the body of the quadrate. The lateral condyle and the quadrato-jugal are not preserved.

A small portion of the lateral wall of the skull, corresponding to the prootic, is preserved medial to the

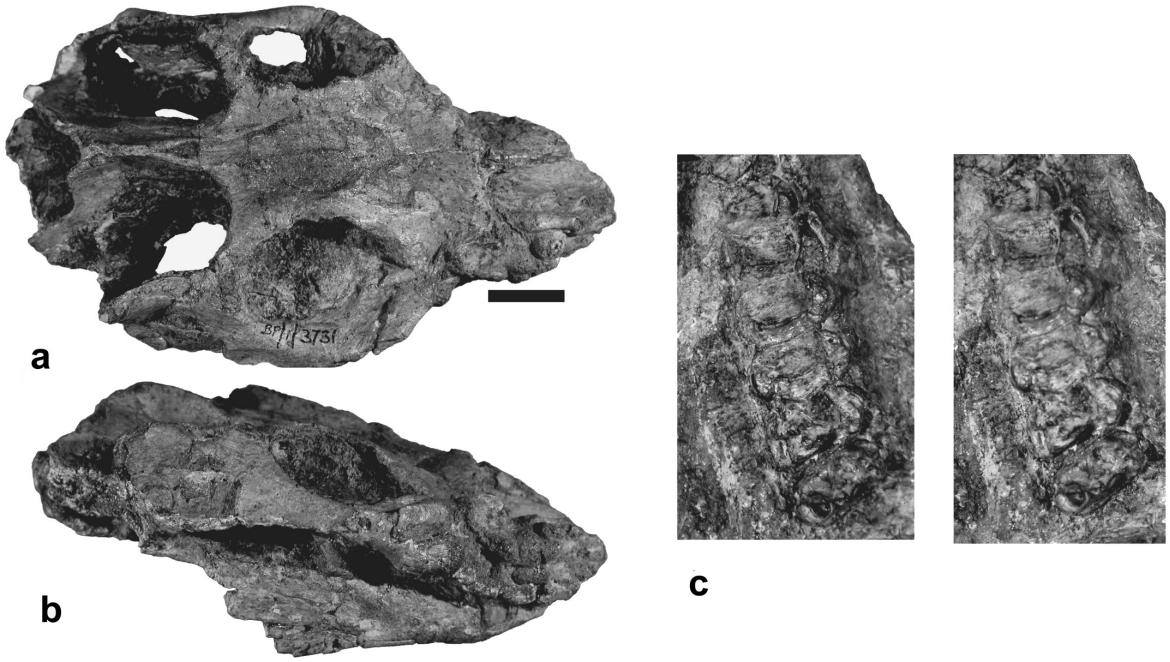

Figure 6. *Luangwa drysdalli* holotype (BP/1/3731); **a**, dorsal, **b**, right lateral view of skull; **c**, stereopair of left upper postcanine series. Scale bar = 20 mm.

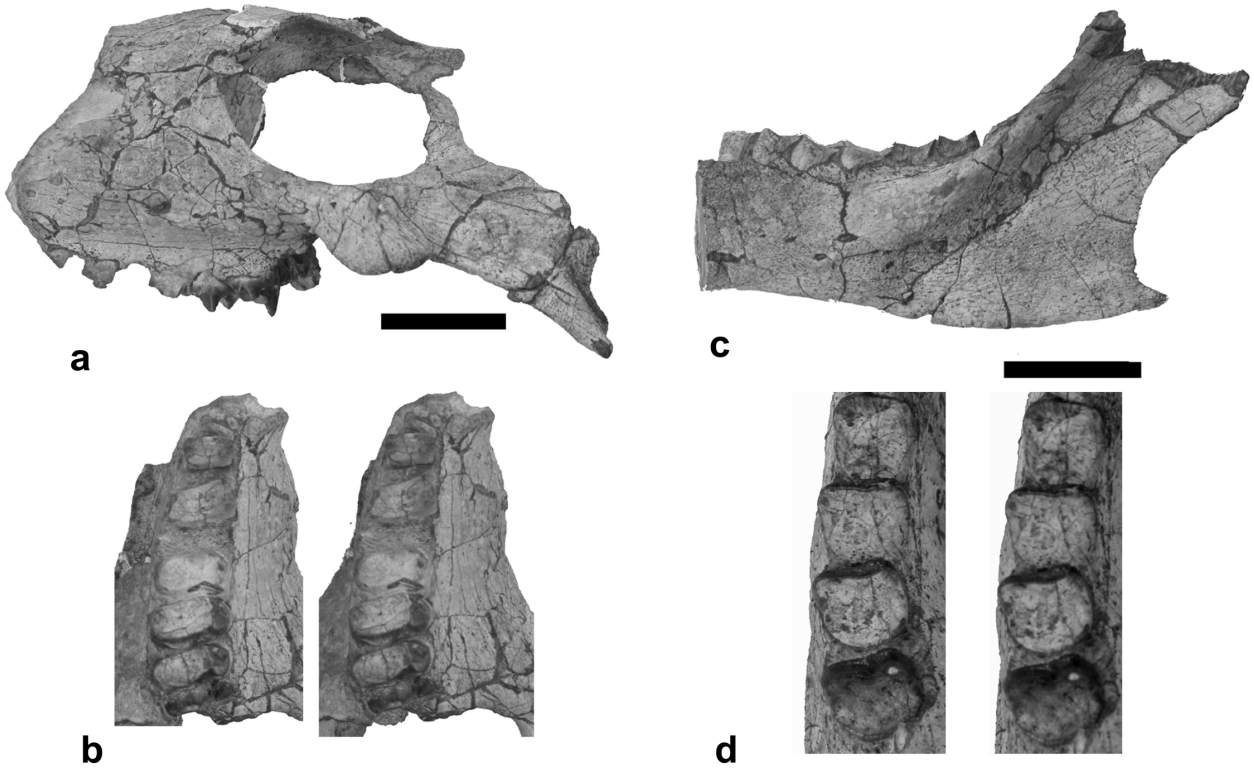

Figure 7. *Luangwa drysdalli,* OUMNH TSK121; **a**, left lateral view of snout and orbit; **b**, stereopair of left upper postcanine series; **c**, lateral view of the left mandibular ramus; **d**, stereopair of the four last right lower postcanines. Scale bars =20 mm

zygomatic process of the squamosal. Only the inner part of the wall is visible (Fig. 4a), with the fossa subarcuata, separated from the internal auditive meatus by a strong horizontal ossification. There exists a high vertical crest that separates the internal auditive meatus from a recess containing a foramen, probably for the facial nerve (VII). Part of the left basicranium, including the occipital condyle and paroccipital process, is also preserved (Fig. 4). Immediately above the condyle is a swelling probably for articulation with the proatlas, while medially there are two foramina for the hypoglossal nerve (XII). The paroccipital process is well developed with its distal end ventrally directed, and without division into anterior and posterior processes.

The dental formula in MCP 3167PV is 4/3 incisors, 1/1 canine and 9-10/8-9 postcanines, while 7–8 upper postcanines are present in UFRGS 267PV. Most of the upper incisors are broken, with the roots showing that the first, second and fourth are rounded in outline, while the third is more ellipsoid (Fig. 1b). The crown of the left third incisor is partially preserved, being canine-like, with a thick enamel layer labially that seems to be absent lingually. Faint denticulations are present on the posterior edge of this tooth, while the anterior edge appears to be smooth. A small diastema exists between the fourth incisor and the canine, the paracanine fossa being anteromedial with respect to the upper canine (Fig. 1b). This tooth is ellipsoid and is erupting on both sides. The enamel layer covers the canine both labially and lingually, and well-developed serrations are present on its anterior and posterior edges. The upper postcanines are ovoid in outline, and increase progressively in size posteriorly (Figs 1b; 2b,d; 3b). Shouldering (i.e. the anterolabial border of the upper postcanine extending forward, and producing a 'shoulder'-like process on the preceding tooth) is absent and the tooth series diverge slightly posteriorly (Figs 2b,d; 3b). The six anterior teeth in MCP 3167PV are badly worn, and the original structure of the postcanines can be seen in the posterior elements of the row (Fig. 5a,b). A main labial cusp, located posteriorly, and smaller anterior and posterior accessory cusps form the sectorial crest of the postcanine, which is positioned medially with respect to the labial border of the crown. A cingular crest occurs antero-labially, lateral to the anterior accessory cusp. Three cusps form a transverse crest of the tooth: a main labial cusp, a wide central cusp and a closely positioned small lingual cusp (Fig. 5a,b). The crest is situated near the posterior border of the tooth and a poorly developed posterior cingulum exists behind it.

The mandible displays a fused symphysis, a well-developed ascending ramus that partially covers the last postcanine in lateral view, and an incipient backward-projected angle of the dentary (Fig. 1c). The masseteric fossa in the dentary extends anteriorly to the level of the sixth or seventh postcanine. The lower incisors are roughly circular (Fig. 1d), and a thick enamel layer apparently disposed only laterally, is observed on the second left tooth. A reduced diastema is present between the third incisor and the canine. The canine is oval-shaped, slightly larger than the incisors, and covered by enamel both labially and lingually. It is not possible to see whether serrations occur on its edges. There is no diastema between the canine and the first postcanine. As in the upper series, the six anterior postcanines are badly worn (Fig. 1d). The last ones show the anterior crest formed by a wide lingual cusp and a narrow, taller labial one (Fig. 5c). An accessory labial cusp is present on the

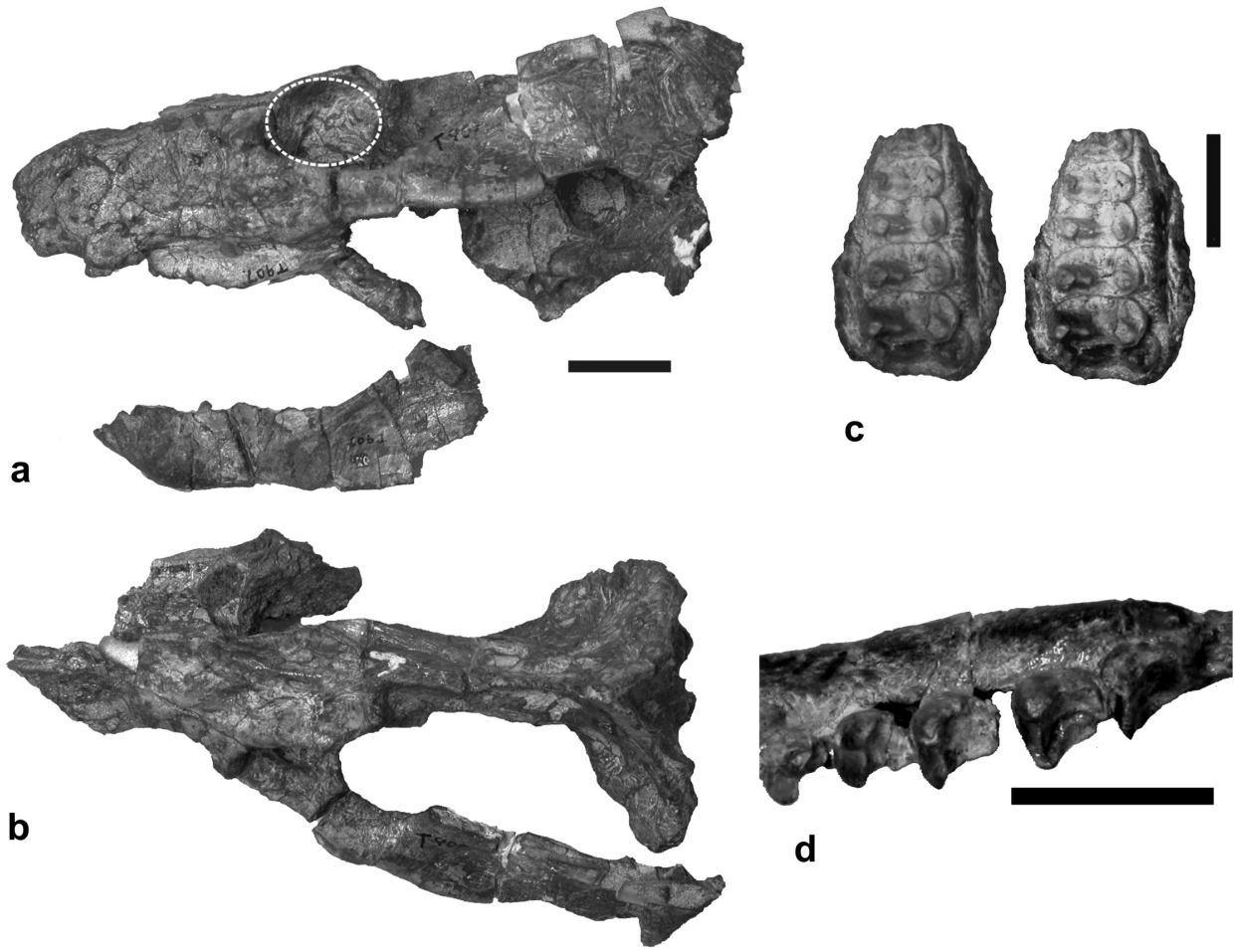

Figure 8. *Scalenodon angustifrons*; **a**, lateral view of the skull and mandible of holotype (UMCZ T.907), with the orbit outlined; **b**, dorsal view of the same skull; **c**, stereopair of left upper postcanine series (UMCZ T.910); **d**, dorsolateral view of right lower postcanine series (UMCZ T.910). Scale bars = 20 mm (a, b) and 10 mm (c, d).

posterior border of the tooth. There is no indication of an anterior cingulum in front of the transverse crest in MCP 3167PV, but two tiny cuspules occur anterior to the labial cusp of the transverse crest in the most anterior lower postcanine preserved in UFRGS 267PV (Figs 2e, 5c).

DISCUSSION

Two species of Anisian traversodontid from east Africa, *Luangwa drysdalli* from the Upper Ntawere Formation and *Scalenodon angustifrons* from the Manda Formation, appear to be more similar to the new South American traversodontid. These African species were proposed as co-generic by Battail (1991), but two recent phylogenetic analyses suggest that they do not form a monophyletic group (Hopson & Kitching 2001; Abdala & Ribeiro 2003).

Skull features of *L. sudamericana* similar to *L. drysdalli* - include a short snout, enormous orbits, and a short temporal region, while the lower jaw displays a high coronoid process with its antero-dorsal edge strongly reflected laterally, and the angle of the dentary slightly projected posteriorly from the ventral edge (Figs 1, 2, 3, 6 & 7). Proportions of the skull regions in *S. angustifrons* (UMCZ T.907) are different, with comparatively less developed orbits, longer snout and particularly longer temporal region (Fig. 8a,b). The lower jaws in the sample of *S. angustifrons* at the UMCZ are poorly preserved and not complete enough to allow a close comparison. The only specimen of *S. angustifrons* with an almost complete skull is the holotype (UMCZ T.907, Fig. 8a,b; see also Parrington 1946: fig. 8). The skull length is estimated at 13 cm and it bears nine postcanine alveoli. Considering the growth series proposed for the species by Crompton (1955: fig. 12), the maximum number of postcanines attained in specimens somewhat larger than the holotype is eleven. The holotype of *L. drysdalli,* approximately the same size as the *S. angustifrons* holotype (see Table 1), presents seven postcanines, while the specimen described by Kemp (1980) is somewhat larger than the holotype and features nine postcanines. The two individuals of the new Brazilian species are small compared to *L. drysdalli* (see Table 1), but present the same number of upper postcanines (between seven and nine).

The incisors of the new Brazilian taxon show some common traits with the African species, such as thick external enamel layer, while lingually this layer is thin in *Luangwa drysdalli* (Kemp 1980) and *S. angustifrons* (F. Abdala, pers. obs.), and absent in *L. sudamericana.* Incisors lacking enamel lingually were also reported in the Carnian traversodontid *Exaeretodon* (Chatterjee 1982; Abdala *et al.* 2002). *L. sudamericana* features serrated edges, weak on the incisors and more developed on the canines. Serrated edges are present on incisors and canines of

Table 1. Measurements (in mm) of *Luangwa* specimens.

	MCP 3167PV	UFRGS 267PV	BP/1/3731	OUMNH TSK121
Basal length of the skull		*94	136	
Dorsal length of the skull, to end of the parietal crest		*86	126.3	
Snout length	50.2	*32	60	
Length from the tip of the snout to the posterior border of the orbit		*65	93.9	
Orbital region length		22.9	38.7	
Length of the row of upper postcanines	33.6	33.7	38.6	41.1
Length from the anterior tip of the dentary to the articular process	*84.3		116.5	
Length from the anterior tip of the dentary to the angle	69.6		*88	94.2
Maximum vertical height of dentary	*53.9		*58.2	59.1
Height of dentary at anterior postcanines	13		15.7	19
Length of the row of lower postcanines	37.9/35.2			49.1

*Estimated.

S. angustifrons (Crompton 1955) and are also described for incisors of *L. drysdalli* (Kemp 1980). The holotype of the latter species shows serrated edges on the tips of the emerging canines (F. Abdala, pers. obs.). Other traversodontids from the Manda Formation, such as *'Scalenodon' hirschsoni* and *'S.' attridgei,* present instead smooth-edged incisors and canines (Hopson & Kitching 2001; F. Abdala, pers. obs.).

In the upper postcanines the new species is comparable to *L. drysdalli* and *S. angustifrons* in that the general outline of the teeth is somewhat ovoid, with the labial border slightly longer anteroposteriorly than the lingual border (Fig. 9a,b,e). This outline resembles the pattern of the teeth of *Diademodon* and the trirachodontid *Cricodon* (Crompton 1955, 1972), and is different from the more rectangular or trapezoidal teeth observed in late traversodontids (e.g. *Massetognathus, Exaeretodon,* contra Abdala & Ribeiro 2003: character 7). The external cingulum lateral to the anterior accessory cusp, recorded for the first time in a South American traversodontid, is also known in

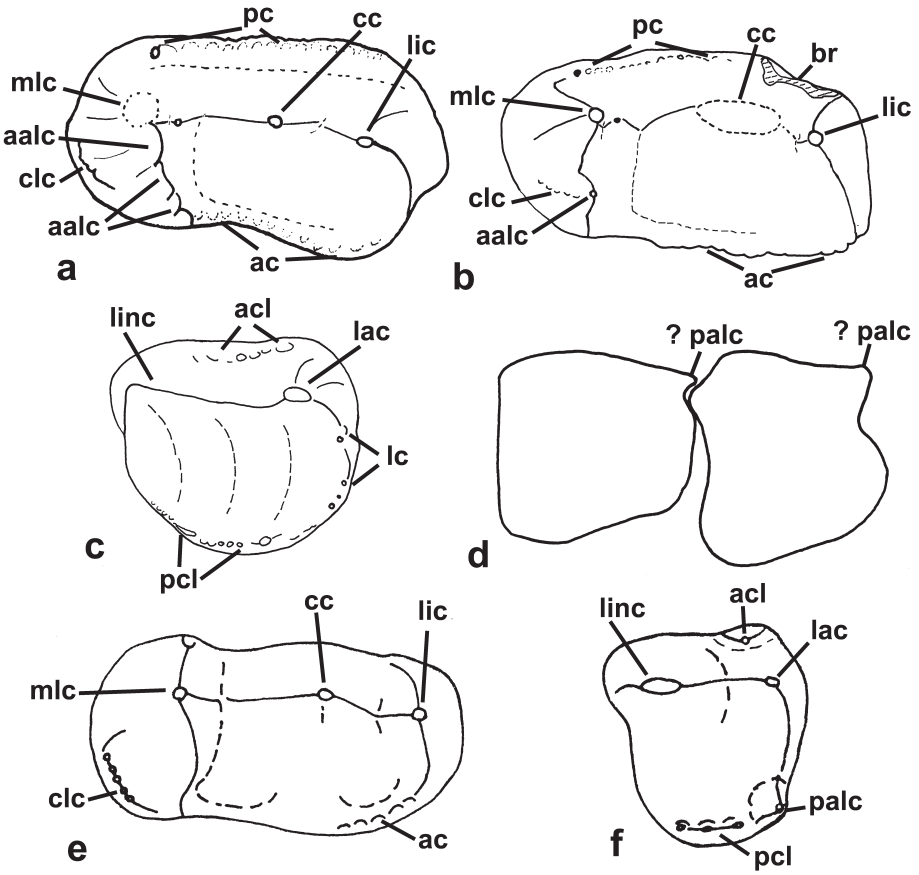

Figure 9. **a**, *Luangwa drysdalli,* BP/1/3731; occlusal view of last (seventh) left upper postcanine (labial, left; anterior, bottom); **b**, *Luangwa drysdalli,* OUMNH TSK121, occlusal view of last (ninth) left upper postcanine (in eruption process); hatching and 'br' indicate broken surface (labial, left; anterior, bottom); **c**, *Luangwa drysdalli,* OUMNH TSK121, occlusal view of last right lower postcanine (labial right, anterior up); **d**, *Luangwa drysdalli,* OUMNH TSK121, outline of lower right postcanines sixth and seventh to show the suggested posterior accessory labial cusps (labial up, anterior left); **e**, *Scalenodon angustifrons,* occlusal view of left upper postcanine; **f**, *Scalenodon angustifrons,* occlusal view of right lower postcanine. Abbreviations: aalc, anterior accessory labial cusp; ac, anterior cingulum; acl, anterior cingulum of the lower postcanines; cc, central cusp; clc, cingular labial crest; lac, labial cusp; lc, labial cingulum; lic, lingual cusp; linc, lingual cusp of the lower postcanines; mlc, main labial cusp; pc, posterior cingulum; pcl, posterior cingulum of the lower postcanines. Figures (e) and (f) from Crompton (1972).

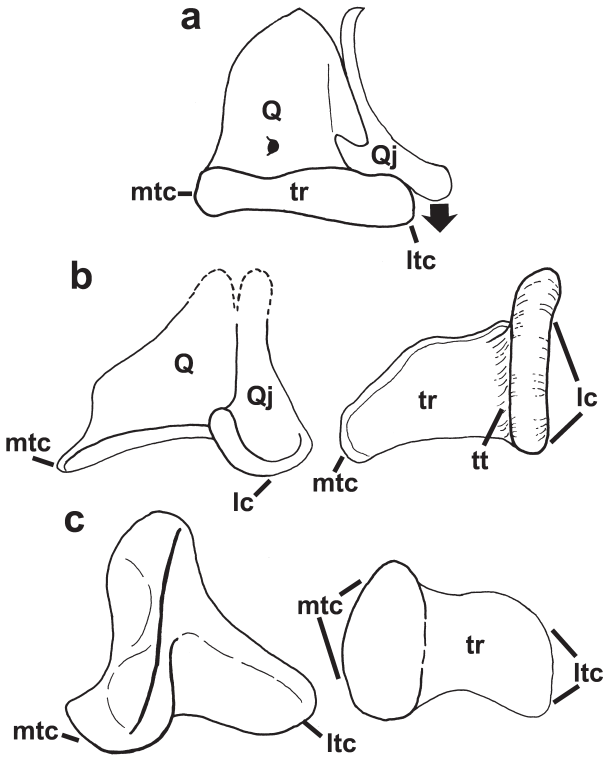

Figure 10. **a**, Anterior view of left quadrate/quadratojugal of *Thrinaxodon* (modified from Luo & Crompton 1994); **b**, anterior and anteroventral view of the left quadrate/quadratojugal of *Massetognathus.* In the anteroventral view the dorsal process of the quadrate was omitted (modified from Luo & Crompton 1994); **c**, anterior and ventral view of the left quadrate of *Lystrosaurus* (modified from Cluver 1971). Abbreviations: ltc, lateral trochlear condyle; lc, lateral condyle; mtc, medial trochlear condyle; Q, quadrate; Qj, quadratojugal; tr, trochlea; tt, trochlear trough. Arrow in (a) indicates the downward extension of the quadratojugal hypothesized to have produced the lateral condyle in *Massetognathus* (b).

L. drysdalli, S. angustifrons and in the recently described traversodontid *Dadadon isaloi* from Madagascar (Flynn *et al.* 2000; Abdala & Ribeiro, 2003). Others features of the upper postcanines of the new traversodontid similar to *L. drysdalli,* are the anterior accessory cusp on the labial crest, and the posterior cingulum with tiny cuspules behind the transverse crest (Figs 5a,b; 9a,b). Poorly developed anterior and posterior cingula were also described for *S. angustifrons,* probably based on specimen UMCZ T.910 (Crompton 1972, but see Crompton 1955). However, F.A. was not able to recognize cuspules or crenulations on the edges of the specimen at first hand examination. As in *L. drysdalli* and other traversodontids (e.g. '*Scalenodon' attridgei*: Crompton 1972: Plate 6; *Scalenodontoides macrodontes*: Gow & Hancox 1993: fig. 2), the upper tooth series curves slightly postero-laterally (Figs 2b, 3b). Features of the upper postcanines in *Luangwa drysdalli* not observed in the Brazilian material include: the presence of four cusps on the transverse crest, with a small cusp between the central and external cusps (Fig. 9a,b). The posterior cingulum in *L. sudamericana* is less developed and extends partially on the posterior border of the teeth (compare Figs 5a,b with 9a). Some traits of the upper postcanines are different in the two specimens of *Luangwa drysdalli.* BP/1/3731 presents four anterior accessory labial cusps in the last left upper postcanine, the only well preserved tooth in the specimen (Fig. 9a). In contrast, OUMNH TSK121 features one anterior accessory cusp (Fig. 9b; Kemp 1980), the same condition that characterizes *L. sudamericana* (Fig. 4a,b).

The lower postcanines of *L. sudamericana* (UFRGS 267PV) present a cingulum comprising two minute cuspules in front of the anterior transverse crest, while in *L. drysdalli* the cingulum is composed of many tiny cuspules (Fig. 9c; Kemp 1980) and a comparatively larger cusp in *S. angustifrons* (Fig. 9f). This anterior cingulum is also present in *'S.' hirschsoni* where the single cusp is extremely robust (Crompton 1972), and in the South American traversodontid *Andescynodon mendozensis* (Goñi & Goin 1988). The new species shows a narrow labial cusp and a transversely wide lingual cusp on the anterior transverse crest (Figs 1d, 5c), a trait also present in *Scalenodon angustifrons* (Figs 8d, 9f). It also has a well-differentiated accessory cusp on the postero-labial border of the tooth, a feature also present in *S. angustifrons* (Fig. 9f), '*S.' hirschsoni, Massetognathus* (Crompton 1972) and, apparently, in *L. drysdalli* (Fig. 9d, but see Fig. 9c). The absence of additional cusps on the sectorial border of the lower tooth is common to the new species and *S. angustifrons,* while *L. drysdalli* can present additional cusps, apart from the posterior one (Fig. 9c,f).

The quadrate morphology in traversodontid cynodonts

The quadrate in *L. sudamericana* is similar to that of *Massetognathus,* in the presence of a large, laterally directed dorsal plate ending in a pointed dorsal angle, and of an anteroposteriorly extended trochlea, (see Figs 4b, 10b). The dorsal plate is directed dorsally in *Procynosuchus* and *Thrinaxodon* (Fig. 10a) and slightly laterally in *Probainognathus,* while the trochlea is cylindrical in most non-mammaliaform cynodonts and in *Morganucodon* (Luo & Crompton 1994). Distinctive features in *Massetognathus* are the strong fusion of the quadratojugal with the quadrate, the presence of an anteroposteriorly elongated trochlea and a ventrally projected lateral condyle that limits externally the anteroposteriorly running trochlear trough (Fig. 10b; Luo & Crompton 1994). Besides *Massetognathus* and *L. sudamericana,* an anteroposteriorly-elongated trochlea is also present in the traversodontid *Exaeretodon* (Allin 1975: fig. 21). In addition, the latter genus also shows a well-developed ventrally projected lateral condyle delimiting the trochlear trough (MCZ 4493), a trait that is incipient in the carnivorous cynodont *Cynognathus* (NMQR 1444, SAM-PK-11264). When describing the suspensorium of the traversodontid *Massetognathus,* Luo & Crompton (1994: 348–349) interpreted the quadratojugal as fused to the dorsal plate of the quadrate, and the ventrally projected lateral condyle as produced by the quadrate trochlea. In *L. sudamericana* the quadratojugal is missing, and the trochlear trough and the lateral condyle are absent. This condition suggests that the quadratojugal was probably ventrally projected, fused at the level of the quadrate trochlea, and thus formed part of the trochlear trough and the lateral condyle. This is in agreement with the ventral location of the horizontal section of the quadratojugal in close apposition to the trochlear portion of the quadrate in

Thrinaxodon (Fig. 10a). In this scenario, the lateral trochlear condyle of *Thrinaxodon* and many other cynodonts would not be homologous with the lateral condyle of cynognathid and traversodontid cynodonts. Luo & Crompton (1994: 360) also pointed out that dicynodonts exhibited the same configuration of the trochlea as *Massetognathus.* A close inspection of the suspensorium in dicynodonts shows, however, that even when superficially similar because of the presence of an anteroposteriorly-oriented trough, the condition is reversed to that of traversodontids. Thus, in many dicynodonts (e.g. *Lystrosaurus*) the trough is located medially (Fig. 10c), limited by the quadrate medial condyle, which is directed downward, and the lateral condyle forms a long sheet that extends laterally (Cluver 1971). The pattern of the suspensorium in dicynodonts and traversodontid cynodonts seems to be oriented toward increasing the safety of the craniomandibular joint in relation to the anteroposterior movement of the lower jaw, extensive in the case of dicynodonts (Crompton & Hotton 1967; King 1990), and more restricted in traversodontids (Crompton 1972). While the two larger adductor externus muscles in dicynodonts tended to exert most of their force in the same line as the jaw ramus (Crompton & Hotton 1967), the pterygoideus, 'pterygoideus' posterior and pseudotemporalis, even when small (Crompton & Hotton 1967; King 1990), may have generated some medial traction on the lower jaw, opposed by the presence of the ventrally projected medial condyle. In most non-mammaliaform cynodonts, the zygoma is flared outward allowing for the presence of the powerful masseter complex, originated in the medial and ventral portion of the zygomatic arch, and inserted on the extensive masseteric fossa of the dentary (Barghusen 1968; Crompton 1995). The ventrally projected lateral condyle in traversodontid cynodonts is possibly related to balance forces directed laterally, generated by masseter muscles during lower jaw movements. In addition, the well-developed transverse process of the pterygoid in non-mammaliaform cynodonts, constrains severely any medially directed force exerted by muscles on the lower jaw, rendering unnecessary the presence of a ventrally projected medial condyle as in dicynodonts.

Biostratigraphic comments

Apart from the traversodontid cynodont *Luangwa,* the fauna of the upper levels of the Ntawere Formation includes the dicynodonts *Sangusaurus* and *Zambiasaurus* (Cox 1969, 1991; Cox & Li 1983), fragments of archosauriforms (Cox 1969, 1991), the mastodonsauroid temnospondyls (*sensu* Damiani 2001a) *Eryosuchus* and *Cherninia* (Chernin & Cosgriff 1975; Damiani 2001b) and the brachyopid temnospondyl *Batrachosuchus* (Chernin 1977). In addition, two cynodonts were reported from the same locality where the amphibians were recovered: 'the smaller perhaps belonging to the genus *Trirachodon* and the larger a *Scalenodon*-like form' (Chernin 1977: 90). The small cynodont mentioned by Chernin is probably BP/1/3733, a fragmentary snout of a juvenile *Luangwa drysdalli* (F. Abdala, pers. obs), while the 'Scalenodon-like form' is presumably the *L. drysdalli* holotype.

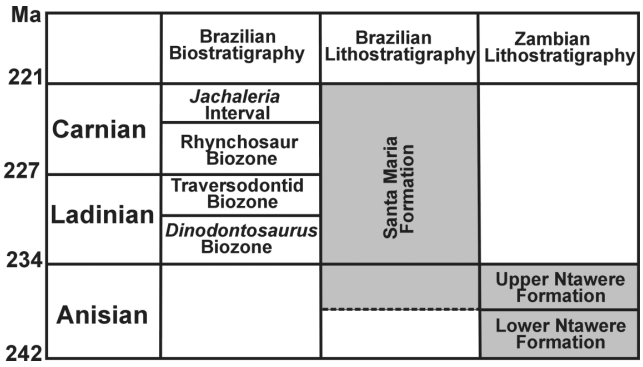

Figure 11. Stratigraphic chart showing the different faunas proposed for the Santa Maria Formation and the faunas from the Ntawere Formation in the Karoo System from Zambia. Time scale based on Gradstein & Ogg (1996). Brazilian faunas based on Abdala *et al.* (2001) and Zambian faunal ages based on Battail (1993).

Most authors interpret the upper portion of the Ntawere Formation as Anisian in age (Cox 1969, 1991; Anderson & Cruickshank 1978; Keyser & Cruickshank 1979; Anderson & Anderson 1993; Battail 1993; King 1993; but see Ochev & Shishkin 1989). The amphibian *Eryosuchus* has a Middle Triassic record (Damiani 2001a), being known also in the Manda Formation (Anisian, Tanzania), the Yerrapalli Formation (Anisian, India), and in the upper part of the Donguz formation (?Anisian-Ladinian, Russia). In addition, the dicynodont *Sangusaurus* is also present in the Manda Formation (Cox 1991).

The Santa Maria Formation of southern Brazil has been the subject of different biostratigraphical schemes of subdivision, all based largely on the tetrapod fauna (Barberena *et al.* 1985; Scherer *et al.* 1995; Schultz 1995; Schultz *et al.* 2000; Abdala *et al.* 2001; Lucas 2002). Four units were recently recognized for the Santa Maria Formation: the *Dinodontosaurus,* Traversodontid and Rhynchosaur biozones, plus the *Jachaleria* Interval, ranging from the Ladinian to the end of the Carnian (Abdala *et al.* 2001). The oldest of these faunas, the *Dinodontosaurus* Biozone, is chrono-correlated to the Chañares fauna from the Ischigualasto-Villa Union Basin in northwestern Argentina (Bonaparte 1982; Barberena *et al.* 1985; Schultz *et al.* 2000), and thus probably Early Ladinian in age (Rogers *et al.* 2001).

The presence of *Luangwa* in the Santa Maria Formation represents the second record of non-mammaliaform cynodonts that link Triassic faunas from South America and Africa. Previously, the carnivorous cynodont *Cynognathus,* a typical representative of the Late Scythian/Early Anisian *Cynognathus* Assemblage Zone of the South African Karoo (Kitching 1995; Hancox 2000), had been recorded from the Puesto Viejo Formation in western Argentina (Bonaparte 1969). Besides being the first traversodontid cynodont genus shared by Middle Triassic faunas of South America and Africa, the record of *Luangwa sudamericana* suggests an older Anisian age for some faunas of the Brazilian Middle/Upper Triassic (Fig. 11). Schultz (1995) and Scherer *et al.* (1995) also recognized a Late Anisian/Early Ladinian fauna for the Santa Maria Formation at the locality of Mariante, based on the record of a primitive rhynchosaur (Schultz & Azevedo 1990).

Nevertheless, in a more recent contribution, these authors (Schultz *et al.* 2000) regarded the afore-mentioned fauna as Ladinian.

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