Reevaluation of *Therioherpeton cargnini* Bonaparte & Barberena, 1975 (Probainognathia, Therioherpetidae) from the Upper Triassic of Brazil

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ABSTRACT

Material previously assigned to the Late Triassic cynodont *Therioherpeton cargnini* Bonaparte & Barberena, 1975 from the upper Santa Maria Formation (late Carnian) is reevaluated. A phylogenetic analysis groups *Therioherpeton* Bonaparte & Barberena, 1975 and *Riograndia* Bonaparte, Ferigolo & Ribeiro, 2001 in a monophyletic group, although support for this hypothesis is weak. Therioherpetidae are distinguished from all other probainognathians by upper teeth with the imbrication angle increasing in the posterior postcanines. In addition, upper and lower postcanine teeth are labio-lingually narrow. The Therioherpetidae are the sister group of the Tritheledontidae by virtue of characters such as the presence of some enlarged incisors, lower incisor 1 enlarger and the others small, and by the presence of simple longitudinal facet in most of the crown length. In contrast to previous phylogenetic analyses, therioherpetids and tritheledontids compose with *Brasilitherium* Bonaparte, Martinelli, Schultz & Rubert, 2003 and *Brasilodon* Bonaparte, Martinelli, Schultz & Rubert, 2003 a monophyletic group, which in turn is the sister-group of an unresolved group including *Prozostrodon* Bonaparte & Barberena, 2001 and Mammaliaformes.

KEY WORDS
Probainognathia,
Therioherpetidae,
Cynodontia,
Therioherpeton,
Late Triassic,
Carnian,
skull,
humerus,
Brazil.

RÉSUMÉ

Réévaluation de Therioherpeton cargnini *Bonaparte & Barberena, 1975 (Probainognathia, Therioherpetidae) du Trias supérieur du Brésil.*

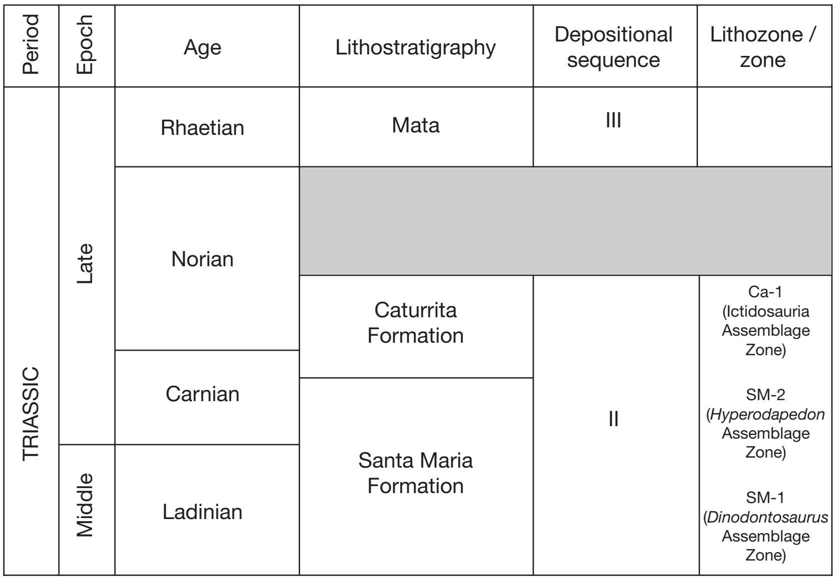
Le matériel attribué au cynodonte *Therioherpeton cargnini* Bonaparte & Barberena, 1975 (Probainognathia, Therioherpetidae), du Trias supérieur de la Formation de Santa Maria supérieure (Carnien du Sud du Brésil) a été réévalué. L'analyse phylogénétique rassemble *Therioherpeton* Bonaparte & Barberena, 1975 et *Riograndia* Bonaparte, Ferigolo & Ribeiro, 2001 dans un groupe monophylétique, mais cette hypothèse n'est que faiblement soutenue. Les Therioherpetidae diffèrent des autres Probainognathia par l'obliquité croissante de l'implantation des postcanines supérieures, d'avant en arrière dans la série dentaire. Les dents supérieures et inférieures sont comprimées labio-lingualement. Les Therioherpetidae apparaissent comme le groupe-frère des Tritheledontidae sur la base de caractères tels que l'agrandissement de certaines incisives, ou le développment de facettes d'usure. À la différence des analyses phylogénétiques antérieures, les Therioherpetidia et les Tritheledontidae apparaissent comme formant, avec *Brasilitherium* Bonaparte, Martinelli, Schultz & Rubert, 2003 et *Brasilodon* Bonaparte, Martinelli, Schultz & Rubert, 2003, un groupe monophylétique qui est lui-même le groupe-frère d'un groupe non résolu incluant *Prozostrodon* Bonaparte & Barberena, 2001 et Mammaliaformes.

MOTS CLÉS
Probainognathia,
Therioherpetidae,
Cynodontia,
Therioherpeton,
Trias supérieur,
Carnien,
crâne,
humérus,
Brésil.

INTRODUCTION

Crompton & Luo (1993) remarked that the lack of morphological information has made it difficult, if not impossible, to determine the relationships between advanced cynodonts and early mammals. The small carnivorous cynodont *Therioherpeton cargnini* Bonaparte & Barberena, 1975, from the Upper Triassic Santa Maria Formation of Brazil, was described by Bonaparte & Barberena (1975) and referred to the family Therioherpetidae. Later, Bonaparte & Barberena (2001) described unpublished postcranial material of *Therioherpeton* Bonaparte & Barberena, 1975. However, a fragment of a distal right humerus originally included in the hypodigm was briefly described and never figured. Despite Bonaparte & Barberena's (2001) considerations of the cranial morphology, many points were poorly explored, mainly concerning the dental morphology.

Therioherpeton appears to occupy an important place in the phylogeny of advanced cynodonts (Martinelli *et al.* 2005). Several studies on anatomy and phylogenetic relationships of advanced cynodonts and early mammals have been performed (Kemp 1983; Battail 1991; Shubin *et al.* 1991; Hopson 1991; Crompton & Luo 1993; Lucas & Luo 1993; Luo *et al.* 2002; Bonaparte *et al.* 2005; Sidor & Hancox 2006), but some enigmatic questions remain unsolved (e.g., the affinities of *Therioherpeton*). Based on the literature, different views on the affinities of *Therioherpeton* have emerged: the first considered it a stem mammal (Bonaparte & Barberena 1975); other views related it to the primitive cynodonts such as chiniquodontids or *Prozostrodon* Bonaparte &



Period	Epoch	Age	Lithostratigraphy	Depositional sequence	Lithozone / zone
TRIASSIC	Late	Rhaetian	Mata	III	
		Norian	▨	▨	▨
			Caturrita Formation	II	Ca-1 (Ictidosauria Assemblage Zone)
		Carnian	Santa Maria Formation		SM-2 (*Hyperodapedon* Assemblage Zone)
	Middle	Ladinian			SM-1 (*Dinodontosaurus* Assemblage Zone)

FIG. 1. — Correlation of the tetrapod assemblages from depositional sequences II and III with lithostratigraphic units and global ages. Based on Rubert & Schultz (2004). Abbreviations: **Ca-1**, Caturrita 1; **SM-1**, Santa Maria 1; **SM-2**, Santa Maria 2.

Barberena, 2001 (Carroll 1988; Bonaparte *et al.* 2005), the tritheledontids (Kemp 1982; Shubin *et al.* 1991), or to dromatheriids (Hahn *et al.* 1984; Battail 1991; Godefroit & Battail 1997). Sigogneau-Russell & Hahn (1994) recognized the Therioherpetidae as being composed of *Therioherpeton* and *Meurthodon gallicus* Sigogneau-Russel & Hahn, 1994. However, Abdala & Ribeiro (2000) did not confirm this concept of Therioherpetidae because *Meurthodon* Sigogneau-Russel & Hahn, 1994 has narrower crowns and roots that are completely divided. Datta *et al.* (2004) remarked that because of the limited known materials and plesiomorphic features of dromatheriids their phylogenetic relationships to other advanced cynodonts remain uncertain.

Classically, *Therioherpeton* has been attributed to the Rhynchosauria or *Hyperodapedon* Assemblage Zone, from latest Ladinian-early Norian age (Barberena *et al.* 1985; Schultz *et al.* 2000), or late Carnian (Lucas 2001). But several new data promote an urgent age reevaluation of the small probainognathians-bearing beds from southern Brazil (see e.g., Lucas 2002; Langer *et al.* 1999).

In this paper, I reanalyze some cranial and dental characters, describe a partial humerus and offer a reconstruction of the *Therioherpeton* skull. A new hypothesis of relationships of *Therioherpeton* and other small probainognathians described from the Late Triassic of southern Brazil is proposed. In addition, a catalogue number for the holotype is published for the first time.

ABBREVIATION

MVP	Museu Vicente Pallotti, Santa Maria, RS, Brazil.

PROVENANCE AND CORRELATION OF LATE TRIASSIC THERIOHERPETIDS

The taxa analyzed are from flood-plain mudrocks and fluvial channel sandstones of the classical "upper Alemoa Member of the Santa Maria Formation" (Schultz *et al.* 2000) and from fluvial massive sandstones of the "Caturrita Formation" (e.g., Rubert & Schultz 2004). An analysis of the tetrapod occurrences from Candelaria City reveals that stratigraphic interpretations are contradictory. For example, Scherer *et al.* (1995) refers the Botucarai assembage ("*Jachaleria*" Interval, but see Lucas 2001 and Rubert & Schultz 2004) from Candelaria as belonging to the uppermost Santa Maria Formation, and Rubert & Schultz (2004) as pertaining to the Caturrita Formation. However, based on sequence stratigraphy (Faccini *et al.* 1995) both litostrathigraphic units compose the uppermost Sequence III (Fig. 1), which is elevated to the early Norian. A key element of the assemblage from the Caturrita Formation (Candelaria locality or Botucaraí local fauna) appears to be the stratigraphic provenance of *Ischigualastia* Cox, 1962 (previously identified as *Jachaleria* Bonaparte, 1970, see Rubert & Schultz 2004), which is from the same level as are the dinosaurs and small tetrapods (see below). Other tetrapods recovered from the Candelaria locality such as the protherochampsid *Proterochampsa nodosa* Barberena, 1982, the cynodont *Exaeretodon* Cabrera, 1943 and the therioherpetid "*Charruodon*" Abdala & Ribeiro, 2000, referred as from the Caturrita assemblage (Lucas 2001, 2002), are from the upper Alemoa levels, occurring in a geographic area very close to the levels of the Caturrita Formation.

The type specimen of the genus *Therioherpeton* was collected in the upper "Santa Maria Formation", from the upper "Alemoa Member" (Bonaparte & Barberena 1975). At present, radioisotopic age data are unavailable for this southern Brazil Upper Triassic sequence. Previous workers (e.g., Barberena *et al.* 1985; Schultz *et al.* 2000; Rubert & Schultz 2004) have correlated the Alemoa beds to the Ladinian-Carnian Ischigualastian age of Argentina on the basis of its general fauna content. On the basis of Triassic global tetrapod biochronology and correlation with Ischigualasto Formation from Argentina, Lucas (1998, 2002) suggested a late Carnian (Adamanian) age for the upper Santa Maria Formation, which is followed by Langer *et al.* (1999). The upper part of the Alemoa beds, cropping out around the city of Santa Maria, has yielded a tetrapod fauna (Assemblage 5; Schultz 1995) that includes *Therioherpeton*, *Prozostrodon*, traversodontids, the rhyncosaur *Hyperodapedon* Huxley, 1859, the aetosaur *Stagonolepis* Agassiz, 1844, the proterochampsids *Cerritosaurus* Price, 1946, *Hoplitosuchus* Huene, 1942, and *Rhadinosuchus* Huene, 1942, the rauisuchian *Rauisuchus* Huene, 1942, the theropod *Staurikosaurus* Colbert, 1970 and the sauropodomorph *Saturnalia* Langer, Abdala, Richter & Benton, 1999, which are commonly assigned to the *Hyperodapedon* Assemblage Zone (Schultz *et al.* 2000; Lucas 2002).

Herein, the proposal that *Therioherpeton* is more closely related to *Riograndia* Bonaparte, Ferigolo & Ribeiro, 2001 from the Caturrita Formation assemblage than to the cynodonts from the underlying *Dinodontosaurus* Assemblage Zone, suggests that the "assemblage 5" from the upper Alemoa beds is at least Carnian in age (see also Lucas 1998, 2001). Interestingly, the absence of a significant hiatus between the upper Santa Maria and the Caturrita formations (Schultz *et al.* 2000; Rubert & Schultz 2004) provides strong evidence for a closer temporal proximity between these two units than normally considered. This linkage is also suggested by the recent discovery of "*Charruodon*", from the upper Alemoa "Assemblage 6" (Schultz 1995), in levels very close to that of *Riograndia*, in the Candelaria locality from the Santa Maria Formation (Abdala & Ribeiro 2000). In addition, on the basis of rhynchosaurs and sauropodomorph dinosaurs (Langer *et al.* 1999) and because of the presence of *Hyperodapedon* and *Stagonolepis* (Lucas 2001, 2002) a latest Carnian age for the upper Alemoa beds is suggested.

Riograndia occurs in massive siltstone and sandstone lenses (Caturrita Formation, Botucaraí locality), which is stratigraphically associated with: 1) *Ischigualastia* (Araújo & Gonzaga, 1980); 2) a phytosaur (Kischlat & Lucas 2003); 3) a not yet described new species of the cosmopolitan (see Sues & Reisz 1995) genus *Clevosaurus* Swinton, 1939 (J. F. Bonaparte pers. comm.); 4) a tritheledontid closely related to *Pachygenelus* Watson, 1913 from Africa and North America and to *Diarthrognathus* Crompton, 1958 from Africa (Martinelli *et al.* 2005); and 5) to the prosauropod *Guaiabasaurus* Bonaparte, Ferigolo & Ribeiro, 1999 (Bonaparte *et al.* 1999). This assemblage of the Caturrita Formation is considered latest Carnian-early Norian in age because of its faunal content and stratigraphic position (Rubert & Schultz 2004). Another assemblage temporally correlative to that of Candelaria is from the locality of Faxinal do Soturno (Rubert & Schultz 2004), at which were recorded the very small brasilodontids *Brasilodon* Bonaparte, Martinelli, Schultz & Rubert, 2003 and *Brasilitherium* Bonaparte, Martinelli, Schultz & Rubert, 2003, which are considered as very advanced cynodonts, closer to Mammalia or Mammaliaformes (Bonaparte *et al.* 2003, 2005). In the phylogenetic analysis (see below), these taxa are placed as non-mammalian cynodonts, closely related to therioherpetids and tritheledontids.

Although distinct taxa have been recovered in recent years, the main criterion for recognizing a new temporal interval ("Ictidosauria Assemblage Zone") in the upper Sequence II appears to be the changes of the anastomosed/meandering pattern of the upper Santa Maria Formation to the braided to low confinement fluvial system of the Caturrita Formation (Rubert & Schultz 2004); furthermore, in Candelaria and adjacent areas distinct facies associations are recorded from the lower (Alemoa beds) to the upper (Caturrita Formation) Depositional Sequence II. Although probable, the proposed subdivision of the faunal assemblages from the upper part of Sequence II is tenuous. More than three distinct taxa are recorded in relation to the upper Alemoa beds, but *Ischigualastia* constitutes an index taxon of the Ischigualastian, late Carnian in age (Lucas 1998). Other taxa from Candelaria (dinosaur, tritheledontid, *Riograndia*) appear to be more plesiomorphic than latest Triassic and Early Jurassic correlatives (e.g., Bonaparte *et al.* 2001) and another index taxon, *Clevosaurus*, is ambiguously recorded either from the Norian or Early Jurassic (?Elliot or Clarens formations) from South Africa (Sues & Reisz 1995). In any case, the fossil horizons of the Caturrita Formation as well as those of the Santa Maria Formation are paleontologically distinct lithozones (*sensu* Walsh 2000), whose boundaries are defined by lithologic contacts and facies analysis (Fig. 1).

The overlying Mata Sandstone (Sequence III), which is unconformable with the Sequence II, appears to be Rhaetian or Early Jurassic. The main aspects of these analyses are presented in Figure 1.

SYSTEMATICS

PROBAINOGNATHIA Hopson, 1990

Family THERIOHERPETIDAE
Bonaparte & Barberena, 1975

Therioherpetontidae Bonaparte & Barberena, 1975: 931.

Therioherpetidae Battail, 1991: 78.

Riograndidae Bonaparte, Ferigolo & Ribeiro, 2001: 624.

DEFINITION. — The clade including the most recent common ancestor of *Therioherpeton* and *Riograndia*, and all its descendants.

INCLUDED GENERA. — *Therioherpeton* Bonaparte & Barberena, 1975, "*Charruodon*" Abdala & Ribeiro, 2000, and *Riograndia* Bonaparte, Ferigolo & Ribeiro, 2001.

Genus *Therioherpeton*
Bonaparte & Barberena, 1975

Therioherpeton cargnini
Bonaparte & Barberena, 1975

HOLOTYPE. — MVP 05.22.04, partial skull lacking the basicranium, with the right maxilla bearing complete PC4, with alveolar portion of the canine, PC1 and PC5 and with incomplete PC2-3 and PC6-7. An isolated lower postcanine (pc5 or 6); a fragment of the right dentary; 29 articulated, partial vertebrae including 4 cervicals, 15 dorsals and (separated by a gap) 4 sacral and 6 caudal vertebrae; several incomplete ribs; left scapular blade; distal half of the right humerus; partial right radius and ulna; incomplete ilia; complete pubis; right ischium; complete left and partial right femur; fragments of tibia and fibulae and partial pes.

TYPE LOCALITY. — A roadcut on the BR-216 highway (outcroup BR-14 in Bortoluzzi & Barberena 1967), 200 m northwest of Cerriquito, Santa Maria, State of Rio Grande do Sul, Brazil.

HORIZON. — Upper Depositional Sequence II (Santa Maria Formation, upper Alemoa Beds), Late Triassic.

REVISED DIAGNOSIS. — Potential apomorphies include humerus without ectepicondylar foramen, with radial and ulnar condyles dorsoventrally flattened and laterally expanded. Differs from all other probainognathians in the following combination of features: frontals

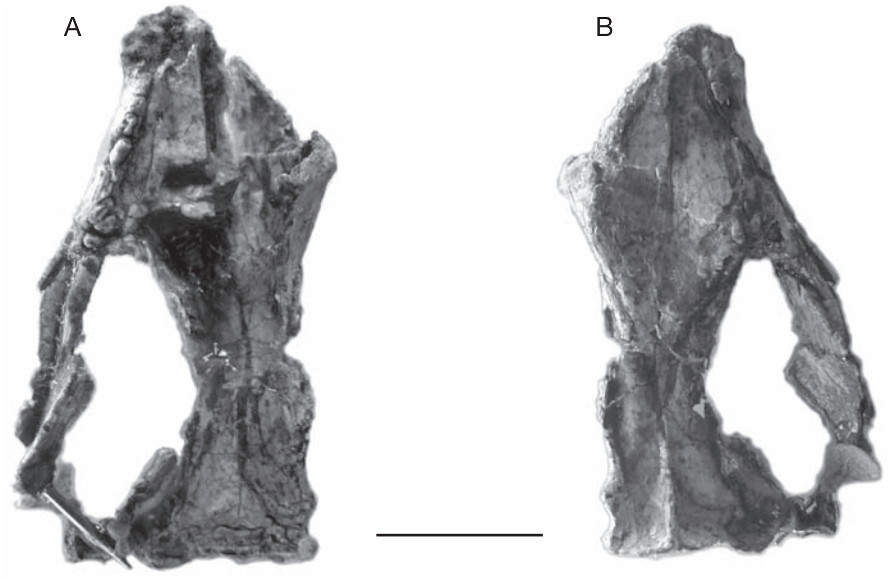


FIG. 2. — Photographs of the incomplete skull of *Therioherpeton cargnini* Bonaparte & Barberena, 1975: **A**, ventral view; **B**, dorsal view. Scale bar: 1 cm.

posteriorly wedge-shaped, with anterolateral projection that contacts the lacrimal and anterolaterally project to the lacrimals, vertebrae without anapophyses, vertebrae with cervical centra anteroposteriorly short, transversely wide and dorsoventrally low (Bonaparte & Barberena 2001), femur with lesser trochanter situated on medial surface of femoral shaft. Differs from "*Charruodon*" in the moderate crown development, approximately 1/3 of the tooth length, and from *Riograndia* in the lesser number of cusps.

REMARKS. — Other potential apomorphies related to iliac blade and femur listed by Bonaparte & Barberena (2001) are controversial because they occur in closely related groups such as tritheledontids.

DESCRIPTION

Cranial morphology

As preserved, the holotype skull (Fig. 2) is approximately 33 mm in length. Although incomplete, preserved areas of the skull permit a minimal reconstruction of the general dorsal outline (Fig. 3; see also Bonaparte & Barberena 2001: fig. 1b), palatal region (Fig. 4) and upper tooth row configuration (Fig. 5). Despite taphonomic problems such as deformation, the skull outline appears to be *Sinoconodon* Patterson & Olson, 1961 or *Brasilodon*-like in having a similar proportion of the preorbital and orbitotemporal length and straight skull posterior border. In dorsal view, reconstruction includes the distribution of the parietals, frontals, lacrimals and maxillae (see also Bonaparte & Barberena 1975). A very important preserved element is the squamosal, which on the right side preserves the most lateral and the most internal portions (Bonaparte & Barberena 1975). The reconstruction probably approximates that of *Sinoconodon*, with a well developed squamosal that contacts the parietal medially. This contrasts with the pattern seen in *Probainognathus* Romer, 1970 and chiniquodontids. The nasals are wide posteriorly and narrower anteriorly. Their posterior border is in line transversely with the anterior margin of the orbit. The lacrimal shows a clear suture with the frontal, nasal, and maxilla (Bonaparte & Barberena 1975). The lacrimal and the descending process of the frontal can be seen to form a part of the medial wall of the orbit. Anteriorly, the frontal is wide, and posteriorly it is wedged-shaped, as in *Pachygenelus* and *Brasilodon*, but not *Sinoconodon*. The parietal is posteriorly wide and bears a high sagittal crest.

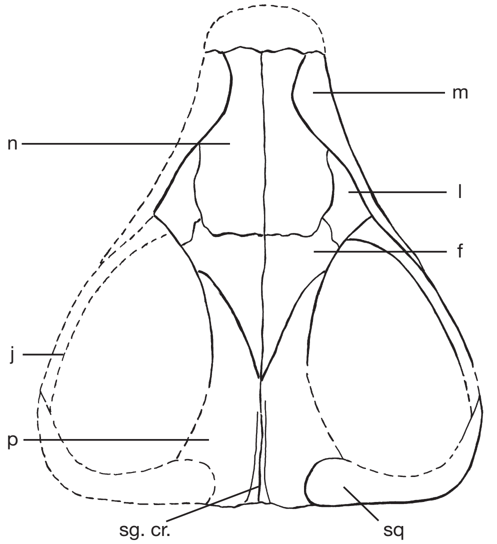


FIG. 3. — *Therioherpeton cargnini* Bonaparte & Barberena, 1975 skull reconstruction in dorsal view based on MVP 05.22.04. Abbreviations: **f**, frontal; **j**, jugal; **l**, lacrimal; **m**, maxilla; **n**, nasal; **p**, parietal; **sg. cr.**, sagittal crest; **sq**, squamosal.

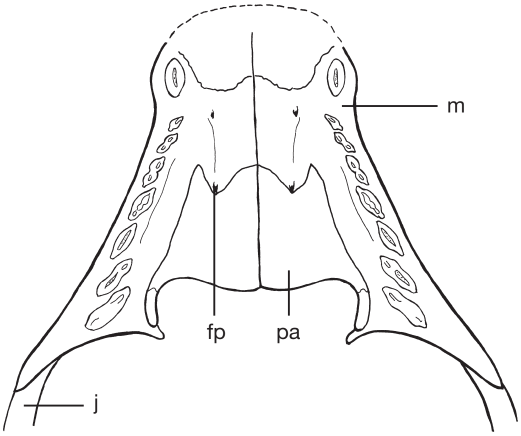


FIG. 4. — *Therioherpeton cargnini* Bonaparte & Barberena, 1975 skull reconstruction in ventral view based on MVP 05.22.04. Abbreviations: **fp**, palatine foramen; **j**, jugal; **m**, maxilla; **pa**, palatine.

The location of the pineal foramen, as suggested by a small notch (Bonaparte & Barberena 1975), is obscured. In lateral view, the lacrimal and the frontal form a part of the medial wall of the orbit, similar to *Sinoconodon*.

A large part of the palatine can be seen in lateral view. In ventral view (Fig. 4), the preservation of the right palatine is remarkable, which permits the restoration of the secondary palate. The posterior margin of the palatine ends approximately at the level of the last postcanine (see also Bonaparte & Barberena 2001). The length of the secondary palate relative to the anterior border of orbit is about equal. The palatine suture with the maxilla is similar to that of *Pachygenelus* in having a V-shaped inflexion, bearing the palatine foramen. In *Probainognathus* and chiniquodontids, this suture is straight. As observed by Bonaparte & Barberena (1975), a deep groove medial to the tooth row is present, and it is deeper posteriorly (Fig. 4). The right maxilla is well preserved and clearly shows a posterior acute projection on the jugal. The premaxilla is incomplete, but a damaged area medial to the canine probably constitutes the contact between the maxilla and premaxilla. The length of the palatine relative to the maxilla in the secondary palate appears to be slightly longer.

Dentition

Measurements of the teeth are given in Table 1. The new study of the dentition reveals some characters previously poorly explored by Bonaparte & Barberena (1975, 2001). The number of postcanine teeth (Fig. 5) is very probably seven and not eight, as concluded by Bonaparte & Barberena (1975). But this character appears to be quite variable in tritheledontids (Sidor & Hancox 2006) and also in *Riograndia* (Soares 2004). One of the most remarkable characters is the imbrication of the postcanines, which show a crescent imbrication angle posteriorly. This situation is similar to that described by Bonaparte *et al.* (2001) for *Riograndia*, which is reported to have a crescent imbrication angle ranging from about 5° on the anterior postcanines to 30° in postcanine 7. In *Pachygenelus* and *Riograndia*, the imbrication is evident, although the number and the size of the teeth are sometimes variable (Soares 2004). The tooth size in *Therioherpeton* increases rapidly from

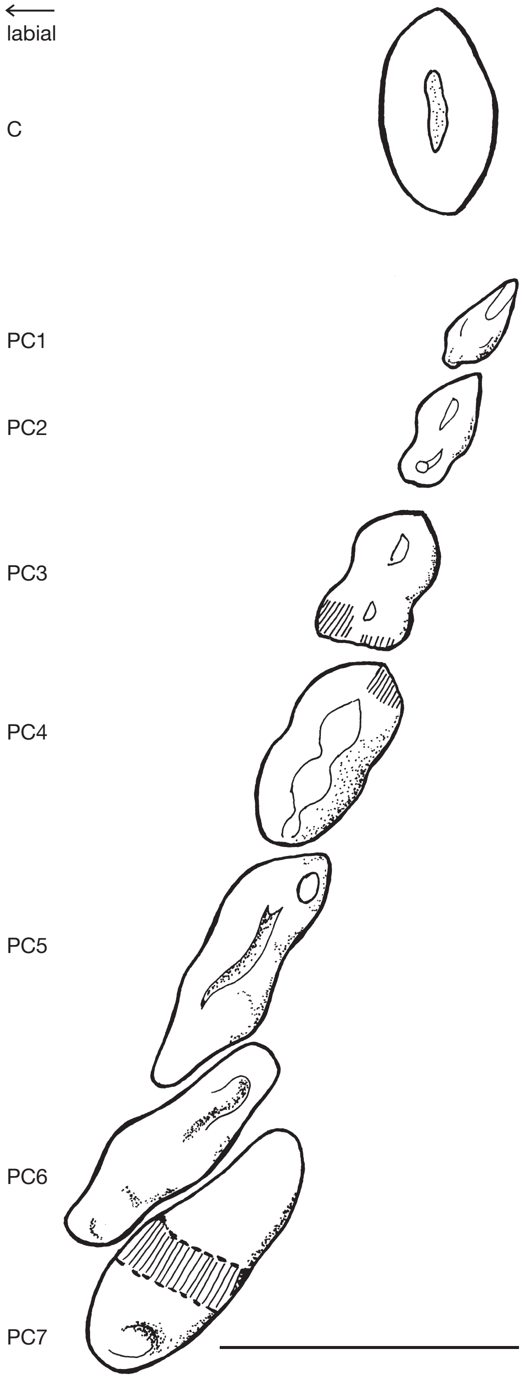


FIG. 5. — Right upper dentition (C-PC7) of *Therioherpeton cargnini* Bonaparte & Barberena, 1975 (MVP 05.22.04). Scale bar: 2 mm.

the first to the last molariform. A substantial difference between the cheek teeth of *Therioherpeton* and chiniquodontids is that the latter lacks a clear distinction between crown and root regions. The tooth morphology as represented by the "PC4" (Fig. 6A) shows long roots and a notably high and large crown, approximately 1/3 of the tooth length. The enamel of the crown is clearly distinguished from the root enamel in being wrinkled on both labial and lingual faces. An incipient root division occurs in *Therioherpeton* just below the level of the gum-line, a condition similar to that seen in early mammals (*Morganucodon* Kuehne, 1949 and *Sinoconodon*). The tooth bears four cusps in line and there is no evidence of a cingulum (Bonaparte & Barberena 1975). The main cusp A, which is longer than the others, is coincident with the axis of the bifurcation furrow (Fig. 6A). On the labial side the wear is absent and the tooth shows only a strong depression that separates cusps A and C. Relatively advanced tooth wear is evident on the crown apex and on the lingual side of the PC4 as well as in all remaining teeth, except PC5, which is strongly worn. In occlusal view the upper teeth are ovate to elliptical and the lower are elliptical, slightly more labio-lingually compressed.

The "PC4" of *Therioherpeton* differs from dromatheriids in the main postcanine cusp only slightly higher than the others (see also Battail 1991), less compressed individual cusps in cross-section and in having larger crown length in relation to the roots length.

The upper postcanines of tritheledontids (Gow 1980; Martinelli *et al.* 2005) differ from those of *Therioherpeton* in having bulbous tooth bearing a prominent main cusp. In addition, the upper teeth of *Pachygenelus* and *Diartrognathus* have a thick buccal cingulum (Gow 1980).

Humerus

The distal end of the humerus (Fig. 7) shows almost symmetrically developed ent- and ectepicondyles. Although broken, the humerus appears to bear only the entepicondylar foramen, which is oval and moderate in size, similar to that of *Morganucodon*. There is no indication of the ectepicondylar ridge. The entepicondylar ridge is long and is separated by a narrow groove from the ulnar condyle. In *Irajatherium* Martinelli, Bonaparte, Schultz & Rubert, 2001 the groove is wider. The entepicondyle is acute in ventral view and not truncated as in *Irajatherium* or *Luangwa* Brink, 1963 (Kemp 1983; Martinelli *et al.* 2005). The ulnar and radial (capitulum) articulations are well differentiated and extend onto both the medial and lateral surfaces. Both are flat, and the radial condyle is slightly more developed than the ulnar one.

PHYLOGENETIC RELATIONSHIPS OF *THERIOHERPETON*

I added three characters to the phylogenetic analysis of Martinelli *et al.* (2005), and three taxa, *Brasilodon*, *Brasilitherium* and *Elliotherium* Sidor & Hancox, 2006 (see Appendix 1).

The following character-states are reinterpreted from Martinelli *et al.*'s (2005) original list of characters.

– Character 17 (see Appendix 1) follows Bonaparte *et al.* (2005) and is regarded for *Therioherpeton* as having the character state 1: axis of posterior part of maxillary tooth row directed toward center fossa.

– Character 23 (see Appendix 1) follows Bonaparte *et al.* (2005) and is regarded for *Riograndia* as having the derived state: presence of anterolateral projection of the frontal contacting medially the nasal.

– Character 29 (see Appendix 1) is reinterpreted as unknown in *Therioherpeton*.

– Character 31 is defined as: length of secondary palate relative to anterior border of orbit shorter (0), about equal (1) or longer (2), and is regarded as longer for *Prozostrodon*. According to Bonaparte & Barberena (2001), the left palatine of *Prozostrodon* is well preserved; it is anteroposteriorly elongated and extends posterior to the last postcanine, a situation similar to *Probelesedon* Romer, 1969, *Morganucodon* and tritheledontids.

– Character 49 follows Bonaparte *et al.* (2005) and is defined as: foramen and passage of prootic sinus: absent (0) or present (1).

– Character 50 relative to the presence of the postorbital bar is regarded as absent in *Prozostrodon*.

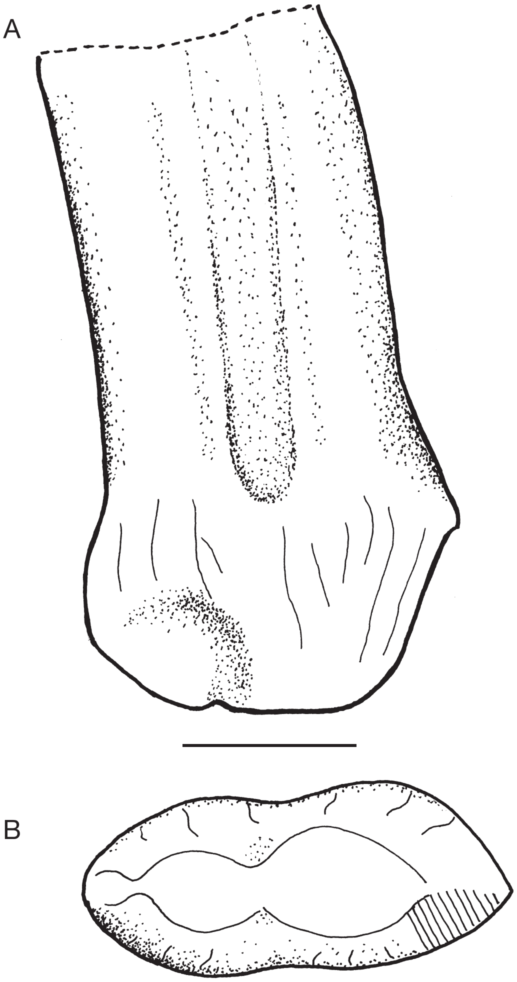


FIG. 6. — Right "PC4" of *Therioherpeton cargnini* Bonaparte & Barberena, 1975 (MVP 05.22.04): **A**, labial view; **B**, occlusal view. Scale bar: 1 mm.

– Character 54 relative to the humerus ectepicondylar foramen was considered absent in *Therioherpeton*.

The revised matrix (Appendix 2) was analyzed using the Tree Gardener 2.2 program (Ramos 1996), which was developed based on Hennig86 version 1.5 (Farris 1989). All characters were treated as unordered and given equal weight. The exhaustive method of implicit enumeration (ie) for finding the parsimonious trees was used. Twelve equally parsimonious trees (159 steps; consistency index:

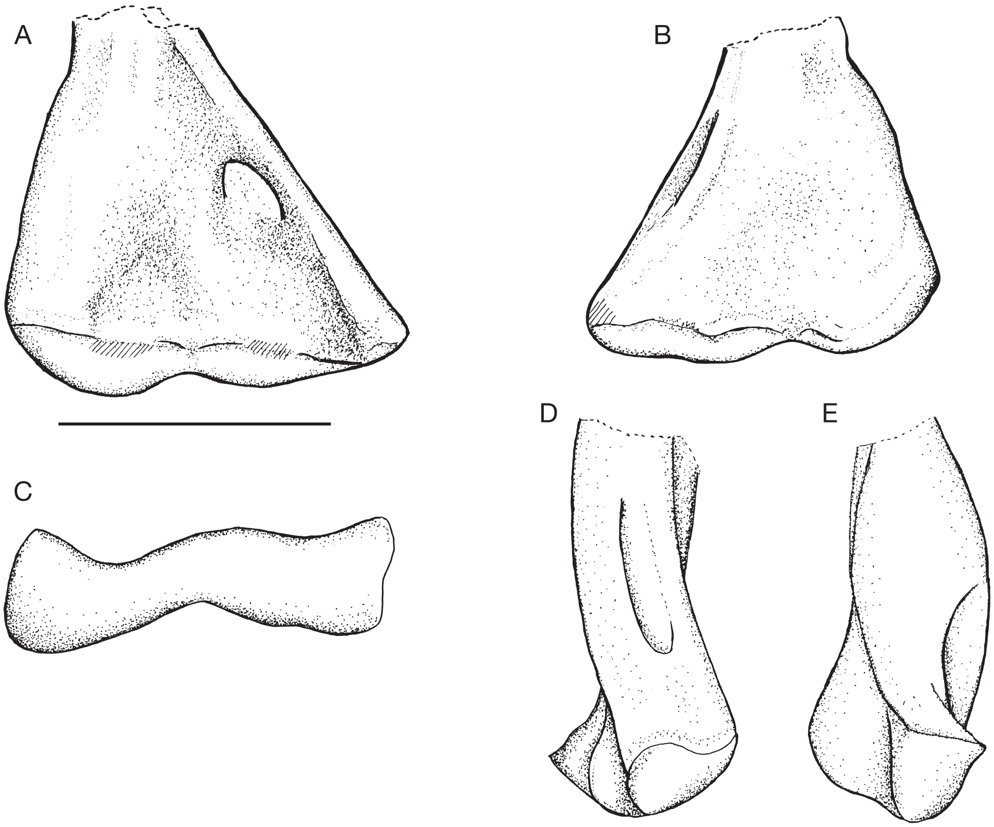


FIG. 7. — Right humerus of *Therioherpeton cargnini* Bonaparte & Barberena, 1975: **A**, ventral view; **B**, dorsal view; **C**, distal view; **D**, medial view; **E**, lateral view. Scale bar: 5 mm.

0.57; retention index: 0.72) were obtained. The strict consensus (nelsen command) produced one tree of 161 steps, a consistency index of 0.56 and a retention index of 0.71. Figure 8 illustrates the strict consensus cladogram.

DISCUSSION

ON THE MATURITY OF THE HOLOTYPE OF *THERIOHERPETON CARGNINI*

In earlier papers two very different opinions on the ontogenetic condition of the holotype of *Therioherpeton cargnini* were proposed: Bonaparte & Crompton (1994) considered it a juvenile individual and Bonaparte & Barberena (2001) an adult individual. However, the maturity of this specimen is evident as revealed by the state of ossification of the postcranium (Bonaparte & Barberena 2001) and by characters such as: the 1) strong development of the sagittal crest; and 2) evident tooth wear on the crown of the "PC4" and "pc5 or 6". Bonaparte & Barberena (1975) suggested for *Therioherpeton* an alternate tooth replacement pattern similar to plesiomorphic cynodonts. According to Luo (1994), the presence of wear facets suggests that the functional life of the individual teeth must have been quite long relative to the life span of the animal, a similar condition verified for tritheledontids and brasilodontids. Thus, judging by tooth wear it is very probable that the rate of tooth replacement in *Therioherpeton* would have been slower than in more plesiomorphic cynodonts.

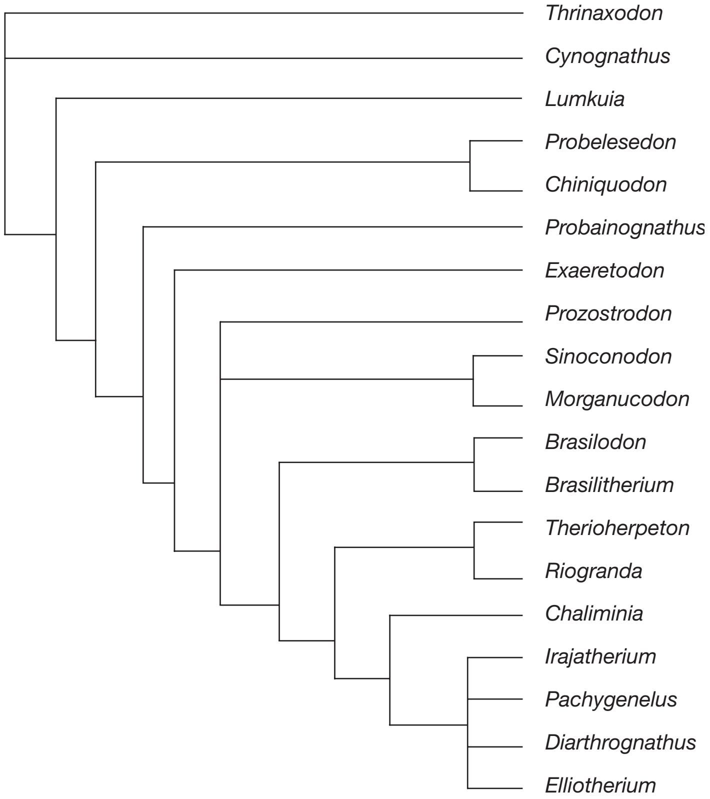


FIG. 8. — Cladogram showing the phylogenetic relationships of *Therioherpeton* Bonaparte & Barberena, 1975 among probainognathians.

PHYLOGENY

In all the trees *Probelesedon* and *Chiniquodon* Huene, 1936 share two synapomorphies: the length of secondary palate relative to anterior border of orbit longer (character 31), and posterolateral end of maxilla forms a right angle ventral to jugal contact (character 46, unequivocal).

In contrast to the results presented by Martinelli *et al.* (2005), the present analysis has recognized the Probainognathia by the following synapomorphies: parietal foramen absent (character 28) and frontal-palatine contact in the orbit present (character 38, reversed in *Exaeretodon*). In previous studies (Rubdige & Sidor 2001; Martinelli *et al.* 2005; Sidor & Hancox 2006), *Exaeretodon* is excluded from the Probainognathia (but see Rowe 1993). *Exaeretodon* is a member of non-mammalian cynodonts characterized by dental and cranial autapomorphies (characters 19, 33 and 35). Advanced features found in *Exaeretodon*, with a similar extension to those of morganucodontids (see Abdala *et al.* 2002), suggest that the relationships of traversodontids are part of an unsolved question. In the present analysis, the grouping of *Exaeretodon* and advanced cynodonts is weakly supported by synapomorphies such as the presence of ulna olecranon process (character 55) and presence of lesser trochanter location near the level of the femoral head (character 62).

The clade including Chiniquodontidae, *Probainognathus*, *Exaeretodon*, *Prozostrodon*, Mammaliaformes, Brasilodontidae, Therioherpetidae, and Tritheledontidae is supported by only one synapo-

TABLE 1. — Measurements (in mm) of the teeth of *Therioherpeton cargnini* Bonaparte & Barberena, 1975 (MVP 05.22.04). Abbreviations: **c**, lower canine; **L**, anteroposterior length; **pc**, lower postcanine; **PC**, upper postcanine; **W**, greatest width; *****, approximately.

		c	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**
Upper teeth	L	1.8*	0.7*	1.0	1.2	1.7	2.0*	1.8	2.1
	W	1.6	0.5*	0.7	0.8	0.9	0.9*	0.8	1.0
							pc5?		
Lower teeth	L						2.1		
	W						0.9		

morphy: frontal-palatine contact in the orbit present (character 38).

Prozostrodon is unresolved in this analysis, forming a polytomy with the Mammaliaformes (Fig. 8). In the analysis of Sidor & Hancox (2006), *Prozostrodon* is placed as the sister-group of Mammaliaformes, an alternative arrangement seen in at least six trees of the present phylogenetic analysis. The clade including *Prozostrodon*, Mammaliaformes, Brasilodontidae, Therioherpetidae, and Tritheledontidae is supported by the following synapomorphies: mode of occlusion unilateral (character 1; unequivocal), direction of mandibular movement during occlusion posterodorsal (character 2; reversed in *Sinoconodon*), wear facets on postcanines absent at eruption but developed later by wear (character 18), symphysis unfused (character 21; unequivocal), presence of anterolateral projection of the frontal contacting medially the nasal (character 23; reversed in *Sinoconodon*), and postorbital absent (character 26; unequivocal).

Mammaliaformes, Brasilodontidae, Therioherpetidae, and Tritheledontidae form a clade in which they share the absence of the postorbital bar (character 50; unequivocal), in at least six trees of the present phylogenetic analysis.

Recent phylogenetic studies based on new small probainognathians from southern Brazil grouped *Therioherpeton* as a sister-taxon to *Prozostrodon* (Bonaparte *et al.* 2005). However, the sister-taxon relationship of *Therioherpeton* to *Prozostrodon* is supported by the disputable identification of the length of the secondary palate relative to the anterior border of orbit as about equal in both taxa. As seen above, it is about equal in *Therioherpeton* and longer in *Prozostrodon*. In other studies (Martinelli *et al.* 2005; Sidor & Hancox 2006) *Therioherpeton* is placed as a sister-taxon to Mammaliaformes and Tritheledontidae. Data from the present phylogenetic analysis (Fig. 8) suggest that Therioherpetidae constitutes the sister-group to the Tritheledontidae by virtue of characters such as the presence of some enlarged incisors (character 5), lower incisor 1 enlarger and the others small (character 7), and presence of simple longitudinal facet in most of the length of crown (character 19; also in *Prozostrodon*). The characters 5 and 7 are unknown in *Therioherpeton*. Nevertheless, therioherpetids differ from tritheledontids in having posteriorly divergent tooth rows, upper and lower postcanine teeth labiolingually narrow, and upper teeth bearing four to nine aligned cusps.

The clade Therioherpetidae, composed of *Therioherpeton* and *Riograndia* (Fig. 8), is supported by only one synapomorphy: the imbrication angle of the posterior postcanines increases posteriorly (character 64). Another taxon included in the Therioherpetidae is "*Charruodon*" *tetracuspidatus*. In this respect, "*C.*" *tetracuspidatus*, as described by Abdala & Ribeiro (2000), might be a junior synonym of *Therioherpeton*. The great similarity between these two genera is suggested by the crown morphology, which bears four mesiodistally aligned cusps and essentially the same size relationship of cusps (a > c > b > d). However, "*Charruodon*" *tetracuspidatus* differs from *T. cargnini* in having a larger size, and higher crown development, which is approximately 1/2 of the tooth length. "*Charruodon*" *tetracuspidatus* is very important because it provides new data on the dentary morphology of therioherpetids, which is high, with a thick and anteriorly truncated symphyseal area, similar to the dentary morphology in *Riograndia* (see Bonaparte *et al.* 2001: fig. 5). Furthermore, a very important character previously not recognized is present in the teeth of "*C.*" *tetracuspidatus*: the tooth crown is very large and reveals the main evolutionary tendency in therioherpetids, which is represented by a large development of the crown. As seen above, in *Therioherpeton cargnini* the crown development is moderate, approximately 1/3 of the tooth length and in "*C.*" *tetracuspidatus* the crown is higher, approximately 1/2 of the tooth length. In *Riograndia*, is observed a large development of the crown, which is coupled with a proliferation of cusps and cuspules. This situation appears to represent a morphocline of crown elongation.

A taxa referred by some authors (Hahn *et al.* 1984; Battail 1991) as closely related to *Therioherpeton* is the family Dromatheriidae. Based on the absence of the postcanine cingulum, Battail (1991) suggested that the Therioherpetidae is the sister-group of the Dromatheriidae. The Dromatheriidae are represented by very incomplete materials, which are insufficient for a parsimony analysis of their relationships to the other cynodonts. However, the dromatheriids appear to be related to the clade including Therioherpetidae, Tritheledontidae and Brasilodontidae in having labial and lingual vertical grooves extended for the full length of the root. Therioherpetids differ from dromatheriids in the main postcanine cusp being only slightly higher than the others and in having a larger crown length in relation to that of the roots. These features are evident in the lower postcanines of *Therioherpeton* (see Abdala & Ribeiro 2000: 22, fig. 4C, D) and in the upper postcanine "PC4" (Fig. 6A). Additional differences between *Therioherpeton* and Dromatheriidae include postcanine cusps labio-lingually less compressed in *Therioherpeton* (Fig. 6B). In this context, the presence of high cusps and large central cusp (A) in the upper teeth of the dromatheriids resemble *Brasilitherium* and *Brasilodon*. The lower postcanines of dromatheriids are most similar to the anterior postcanines of *Brasilitherium*.

The concept of Tritheledontidae according to Martinelli *et al.* (2005) includes *Riograndia*, and is supported by three synapomorphies: 1) presence of three upper incisors (character 3); 2) some incisors enlarged (character 5); and 3) presence of an interpterygoid vacuity (character 29). On the basis of the present phylogenetic analysis, one alternative hypothesis is that character 29 constitutes a synapomorphy of the monophyletic group including Brasilodontidae, Therioherpetidae and Tritheledontidae, and character 5 constitutes a synapomorphy of the clade composed of Therioherpetidae and Tritheledontidae (see above). Tritheledontidae is here identified by five synapomorphies: presence of dominant central bulbous main cusp on upper postcanines (reversed in *Chaliminia*), lower middle and posterior postcanines with four cusps aligned decreasing size backwards (unequivocal), lower teeth much larger than the upper ones (reversed in *Chaliminia*), posterior portion of the maxillary tooth row extends medially to the temporal fossa (also in *Exaeretodon*) and axis of posterior part of maxillary tooth row directed toward medial rim (also in *Exaeretodon*).

In contrast to the phylogenetic results presented by Bonaparte *et al.* (2005), therioherpetids and tritheledontids constitute the sister-group to *Brasilitherium* and *Brasilodon*, which is supported by the presence of an interpterygoid vacuity between the pterygoid flanges in the adult (character 29; unknown in *Therioherpeton*) and by the absence of an upper postcanine lingual cingulum (character 11; reversal). Furthermore, the presence of incipient root division in therioherpetids, tritheledontids and brasilodontids, as indicated by vertical grooves on the root, could be a derived character of this group (but see Bonaparte *et al.* 2005). The presence of this character state in *Prozostrodon* could be interpreted as independently achieved. Furthermore, *Prozostrodon* appears to be a highly derived taxon, judging by the development of cingula on the upper teeth, the reduced unossified area between frontal, orbitosphenoid, and alisphenoid, and the anteroposteriorly long palatines (see Bonaparte & Barberena 2001). In the last lower postcanines of *Prozostrodon*, the root is deeply grooved, probably indicating a greater degree of root bifurcation than in therioherpetids, tritheledontids and brasilodontids.

The present phylogenetic analysis introduces new data to the identification of the sister-group of mammaliaforms, a crucial issue related to the origin of mammals (Luo 1994). On the basis of small probainognathians from southern Brazil, Bonaparte *et al.* (2005: 41) conclude that "*Brasilodon* and *Brasilitherium* are more closely related to mammaliaforms than are the Tritheledontidae, different from previous phylogenetic inferences". The present analysis supports that therioherpetids and tritheledontids compose with *Brasilitherium* and *Brasilodon* a monophyletic group, which in turn is the sister-group of an unresolved group including *Prozostrodon* and Mammaliaformes.

Regarding the origin of mammals, the new systematic position of brasilodontids and tritheledontids herein reported suggests that the question involving the postulation of the sister-group of mammals remains unsolved. The poorly understood status of the dromatheriids, considered by some authors as closely related to therioherpetids, appears to be an important factor in understanding the origin of mammals. Further studies as for example the establishing of tooth homology of dromatheriids with that of brasilodontids or with that of mammals (Lucas *et al.* 2001) is urgently needed.

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APPENDIX 1

List of characters used in the phylogenetic analysis following Martinelli *et al.* (2005). Characters 1, 2, 8, 9, 18, 19, 21, 22, 47-50 are from Luo (1994); characters 3, 4, 10, 11, 16, 17, 24-26, 28-46, 51-61 are from Hopson & Kitching (2001); characters 20 and 27 are from Martinez *et al.* (1996) and 5-7, 12-15, 23, 62, 63 are from Martinelli *et al.* (2005). New characters and characters modified from Martinelli *et al.* (2005) are indicated in parentheses after the number.

1. Mode of occlusion: bilateral (0); unilateral (1).
2. Direction of mandibular movement during occlusion: orthal (0); posterodorsal (1); dorsomedial (2).
3. Upper incisor number: 5 or more (0); 4 (1); 3 (2); 2 (3).
4. Lower incisor number: 4 or more (0); 3 (1); 2 (2).
5. Some incisor enlarged: absent (0); present (1).
6. Upper incisor size: all small (0); incisor 1 enlarger and the others small (1); incisor 2 enlarger and the others small (2).
7. Lower incisor size: all small (0); incisor 1 enlarger and the others small (1).
8. Postcanine replacement: alternate (0); partial (1); sequential addition posteriorly (2).
9. (modified) Roots of postcanines: single (0); incipient root division as indicated by vertical grooves on the root (1); incomplete separation of roots (2); complete separation of roots (3).
10. Upper postcanine buccal cingulum: absent (0); present (1).
11. Upper postcanine lingual cingulum: absent (0); narrow (1); lingually expanded (2).
12. A dominant central bulbous main cusp on upper postcanines: absent (0); present (1).
13. Upper posterior postcanines with cusps B and C buccally displaced and bulbous, prominent cusp A: absent (0); present (1).
14. Lower middle and posterior postcanines with four cusps aligned decreasing size backwards: absent (0); present (1).
15. Lower teeth much larger than the uppers: absent (0); present (1).
16. Posterior portion of the maxillary tooth row extends medial to the temporal fossa: absent (0); present (1).
17. Axis of posterior part of maxillary tooth row: directed lateral to temporal fossa (0); directed toward center fossa (1); directed toward medial rim (2).
18. Wear facets on postcanines: absent (0); absent at eruption but developed later by wear (1); wear facets present at eruption (2).
19. Relationships of wear facet to main cusps: absent (0); simple longitudinal in most of the length of crown (1); two distinctive facets (2); multiple cusp, with each cusp bearing one or two transverse facets (3).
20. Tooth row: divergent posteriorly (0); parallel to subparallel from the axial plane of the cranium (1).
21. Symphysis: fused (0); unfused (1).
22. Squamosal glenoid for the dentary: absent (0); formed by small and medially facing facet (1); formed by broad and anteroventrally facing glenoid (2); glenoid facing ventrally and separated from cranial moiety by neck (3).
23. Anterolateral projection of the frontal contacting medially the nasal: absent (0); present (1).
24. Premaxilla forms posterior border of the incisive foramen: absent (0); present (1).
25. Prefrontal: present (0); absent (1).
26. Postorbital: present (0); absent (1).
27. Parietals: fused (0); unfused (1).
28. Parietal foramen: present (0); absent (1).
29. Interpterygoid vacuity in adult between pterygoid flanges: absent (0); present (1).
30. Length of secondary palate relative to tooth row: shorter (0); about equal (1); longer (2).
31. Length of secondary palate relative to anterior border of orbit: shorter (0); about equal (1); longer (2).
32. Ventral surface of basisphenoid depressed below occipital condyles: less than 1/4 occipital height (0); greater than 1/4 occipital height (1).
33. Zygomatic arch dorsoventral height: slender (0); moderately deep (1); very deep (2).
34. Zygomatic arch dorsal extent: below middle of orbit (0); above middle of the orbit (1).
35. Jugal depth in zygomatic arch relative to exposed squamosal depth: less than twice (0); greater than twice (1).
36. Jugal suborbital process: absent (0); present (1).
37. Squamosal groove for external auditory meatus: moderately deep (0); very deep (1); shallow (2).
38. Frontal-palatine contact in the orbit: absent (0); present (1).
39. Descending flange of squamosal lateral to quadratojugal: present not contacting surangular (0); present contacting surangular (1); absent (2).
40. Internal carotid foramina in basisphenoid: present (0); absent (1).
41. Groove on prootic extending from pterygoparoccipital foramen to trigeminal foramen: open (0); enclosed as a canal (1).
42. Trigeminal nerve exit via foramen: between prootic and epipterygoid (0); via two foramina (1).
43. Quadrate ramus of pterygoid: present (0); absent (1).
44. Greatest width of zygomatic arches: near middle of arch (0); at posterior end of arch (1).
45. Length of palatine relative to maxilla in secondary palate: shorter (0); about equal (1); longer (2).
46. Posterolateral end of maxilla: passes obliquely posterodorsally into suborbital bar (0); forms right angle ventral to jugal contact (1).
47. Fenestra rotunda separation from jugular foramen: confluent (0); partially separated by finger-like projection from posterolateral wall of jugular foramen (1); completely separated (2).
48. Stapedial muscle fossa: absent (0); present (1).
49. (modified) Foramen and passage of prootic sinus absent (0); present (1) (Bonaparte *et al.* 2005).
50. Postorbital bar: present (0); absent (1).
51. Scapular elongation between acromion and glenoid: present (0); absent (1).
52. Procoracoid in glenoid: present (0); barely present or absent (1).
53. Procoracoid contact with scapula: greater than coracoid contact (0); smaller than coracoid contact (1).
54. Humerus ectepicondilar foramen: present (0); absent (1).
55. Ulna olecranon process: absent (unossified) (0); present (1).
56. Length of anterior process of ilium anterior to acetabulum (relative to diameter of acetabulum): less than 1.0 (0); 1.0-1.5 (1); greater than 1.5 (2).
57. Length of posterior process of ilium posterior to acetabulum (relative to diameter of acetabulum): greater than 1.0 (0); less than 0.5 (1).

58. Dorsal profile of ilium: strongly convex (0); flat to concave (1).
59. Greater trochanter separated from the femoral head by distinct notch: absent (0); present (1).
60. Lesser trochanter position: on the ventromedial surface of femoral shaft (0); on medial surface of femoral shaft (1).
61. Vertebral centra: amphicoelous (0); platycoelous (1).
62. Greater trochanter location at the level of the femoral head: absent (0); present (1).
63. Lesser trochanter location near the level of the femoral head: absent (0); present (1).
64. (new) Imbricating upper teeth: absent (0); with equal imbrication angle in all teeth (1); with imbrication angle increasing in posterior postcanines (2).
65. (new) Development of the ulnar and radial articulations: both high and medially situated (0); both are flat and laterally expanded (1).
66. (new) Outline of lower and upper teeth: equal, both subcircular (0); equal, both transversely narrow (1); different, upper narrower to subtriangular and lower narrow (2).

APPENDIX 2

Character matrix used in the phylogenetic analysis

Thrinaxodon	0011000000000000000000?0000000000000000000000000000000000000000000
Cynognathus	011100020000000001?000?0001000000101101100110000000000001000000000
Exaeretodon	012100020020?001223100??001100111111101111110010000100120100010000
Lumkuia	0011000000000000000000?000011010000000100010000000010??????????000
Probelesedon	0011000000000000000000?1000101200000011000101110000100020100000000
Chiniquodon	0011000000200000000000??0001022000000110001021?0000100?20100001000
Probainognathus	0011000000100000100001?1000101100000011000100010100???020100000000
Prozostrodon	120000001010000011101?11?1???22?0??0?1??????1????0???0??????0??0?1
Therioherpeton	?2?????0100000001110??1?1101?11?0000?1?????01????1???1?21101011211
Riograndia	122112101000000011101?1111??122?0??0?1??????2????1?????????????2?1
Chaliminia	??2111100??001012??1?0??1101122?000????????0?????1?????????????0??
Irajatherium	12?????01001111??1101????????????????????????????????0????01?110?2
Pachygenelus	1232121011111111211112?11101122000002120001020200111101211111111?2
Diartrognathus	12321110?1010111210112??1101122000?021?O?0102?0001?????????????0?2
Sinoconodon	10000002211000001000130011010220000021?011100?2111?????????????0?1
Morganucodon	121000113110000011211310110102200000212011100021211111121111111001
Brasilitherium	121100011000000011201?1?11011220000021?0010000??11???0????????10?1
Brasilodon	12??0?001000000011201?1?11011120000021?00?0000??11???1????????10?1
Elliotherium	?????????0?10??12111????11?1?12??0?0?1????1??0???1?????????????0??