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DISCOVERIES IN THE LATE TRIASSIC OF BRAZIL IMPROVE KNOWLEDGE ON THE ORIGIN OF MAMMALS

*Descubrimientos en el Triásico tardío de Brasil perfeccionan nuestro conocimiento
sobre el origen de los mamíferos*

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Abstract. A new specimen of *Brasilitherium riograndensis*, which includes complete skull, lower jaws, dentition and some postcranial bones, is described, along with a redescription of the skull, lower jaws and dentition of *Minicynodon maieri*, both derived eucynodonts from the Late Triassic of Southern Brazil. The anatomical comparison confirms the close relationships of both genera with the Morganucodonta and suggest that the Trithelodontidae is the sister group of the Brasilodontidae. Some comments after the anatomical information from the brasilodontids are developed on the following subjects: the sister group of mammals, the interpterygoid vacuity, and on *Adelobasileus*, *Hadrocodium* and *Microconodon*.

Key words. Brasilodontidae, *Brasilitherium*, *Minicynodon*, Triassic, Brazil.

Resumen. Un nuevo espécimen de *Brasilitherium riograndensis*, el cual incluye un cráneo completo, mandíbulas, dentición y algunos huesos postcraneanos, conjuntamente con la descripción del cráneo, mandíbulas y dentición de *Minicynodon maieri* son descritos. Ambos son eucinodontes derivados del Triásico Tardío del sur de Brasil. La comparación anatómica confirma la cercana relación filogenética de estos géneros con los Morganucodonta y sugiere que los Trithelodontidae serían el grupo hermano de Brasilodontidae. Luego de la revisión de la información anatómica brindada por los brasilodóntidos se realizan comentarios sobre los siguientes aspectos: el grupo hermano de los mamíferos, la vacuidad interpterygoidea, y sobre los géneros *Adelobasileus*, *Hadrocodium* y *Microconodon*.

Palabras clave. Brasilodontidae, *Brasilitherium*, *Minicynodon*, Triásico, Brasil.

INTRODUCTION

Starting in the late nineteenth and early twentieth century, the problem of the origin of mammals attracted the attention of numerous paleontologists and comparative anatomists, most notably Robert Broom (1912), who in 1914 first outlined the principal stages of the transition from non-mammalian therapsids to mammals based primarily on Permo-Triassic fossils from the Karroo of South Africa. Richard Owen (1861) had first noted the similarities between certain Karroo therapsids and mammals. Broom and others established that one group, the Cynodontia, included the precursors of mammals, but extensive parallel evolution among the known cynodont taxa made it difficult to identify the closest sister-group of mammals.

Based primarily on postcranial features, Kemp (2005) considered the highly derived, rodent-like Tritylodontidae as the sister-group of mammals, an interpretation followed, as well as objected, by several paleontologists (e.g., Rowe, 1988, 1993; Luo, 1994; Sues and Jenkins, 2006). Hopson and Barghusen (1986) hypothesized the still incompletely known Tritheledontidae as the sister-group of mammals, an interpretation most recently followed by Kielan-Jaworowska *et al.* (2004). The scarcity of relevant fossil evidence, especially from the Middle and Late Triassic, has rendered testing of these hypotheses difficult.

Recent discoveries of remarkably well-preserved specimens of derived non-mammalian cynodonts from the Early Late Triassic of southern Brazil (Bonaparte and Barberena, 1975, 2001; Bonaparte *et al.*, 2003, 2005, 2010; Martinelli and Bonaparte, 2011; Bonaparte, 2012) revealed a substantial amount of new anatomical information on the cynodont-mammal transition and

promoted discussions of correlated problems of such complex anatomical change.

Two notably well preserved skulls and lower jaws were discovered in 2005 thanks to a grant from National Geographic Society to J.F. Bonaparte. One of the specimens represents a new genus and species of the non-mammalian eucynodonts, *Minicyonodon maieri* (Bonaparte *et al.*, 2010), and the second specimen corresponds to *Brasilitherium riograndensis* (Bonaparte *et al.*, 2003, 2005). During a three months visit to the Tübingen University of Germany, both specimens were carefully analyzed in cooperation with Prof. Dr. W. Maier, who was particularly interested to study in full detail the *Brasilitherium* skull, UFRGS-PV-1043-T. So, he has in preparation a paper on both external and internal anatomy of these specimens through a set of tomographies. The description of these specimens presented here is a brief, traditional description of some characters of these species not well known before.

DESCRIPTION

Brasilitherium riograndensis* Bonaparte, Martinelli, Schultz and Rubert, 2003*General aspects of the skull**

The skull of *Brasilitherium* measures 38 mm in total length, it is elongate and narrow, with little lateral bowing of the zygomatic arches, and a long, narrow snout with prominent expansion around the canine alveoli and a narrow premaxillary region (Figure 1; see also reconstruction in figures 8 and 9). Its outline resembles that of *Morganucodon*, but differs from the basal cynodont *Thrinaxodon* and other more derived cynodonts in which the zygomatic arches are often considerably bowed out

a marked constriction behind the canines, which appears to be confluent with the buccal margin of the diastema. The dorso-lateral compression of the skull affected the width of both palate and interpterygoid vacuities. However, the skull clearly was rather low and elongate, with the highest point marked by the frontal on the anteromedial rim of the orbit. Posterior to it, the reduced parietal crest extends almost horizontally to its end whereas the dorsal profile of the snout turns down anteriorly.

The zygomatic arch

The slender jugal lacks a postorbital process and it is laterally convex in transverse section. The jugal extends back to the level of the pterygo-paraoccipital foramen where it contacts a short anterior process of the squamosal. Anteriorly, the jugal overlies the posterior process of the maxilla and it is overlain by the lacrimal.

The squamosal is incompletely known in UFRGS-PV-1043-T. The posterior surface of it, where the quadrate is attached, is dorsoventrally low and bears a shallow groove that presumably formed the external auditory meatus. The ventral side of the left incomplete squamosal is anteroposteriorly wide just lateral to the quadrate, showing a glenoid-like depression delimited by a distinct border. The zygomatic arch of *Brasilitherium*; resembles that of the earliest mammals.

The left quadrate is inserted in the squamosal and firmly attached below the paraoccipital process; it has been slightly displaced from its original position. In ventral view, the quadrate trochlea is rather large, with its anteroposterior axis longer than in *Morganucodon*. The posterior border of the trochlea is slightly concave whereas the anterior margin is convex. The lateral trochlear condyle has a dorsal and posterolateral pro-

jection, which is the reverse of the condition in *Morganucodon* (Luo and Crompton, 1994), in which the lateral projection is anterolateral. The stapedial process cannot be identified in the adult UFRGS-PV-1043-T, but the process is well preserved in UFRGS-PV-0929-T (Bonaparte *et al.*, 2005), and closely resembles that of *Morganucodon* (Luo, pers. com., 2004).

Orbito-temporal region. The parietal crest is low, decreasing its height anteriorly. The frontals underlay the parietals. Anteriorly the frontals of *Brasilitherium* become wider and contact the nasals along an interdigitate suture as in *Morganucodon*. Observations on this area of the skull of *Therioherpeton* (Bonaparte and Barberena, 1975), *Prozostrodon* (Bonaparte and Barberena, 2001), and the tritheledontid *Riograndia* (Soares, 2004; Soares *et al.*, 2011), suggest that the anterolateral portion of the frontal may represent a prefrontal that became indistinguishably fused to the frontal.

Dorsally the frontal have a slightly depressed median area. A weak dorsal ridge marks the extent of the *temporalis* musculature. A supraorbital foramen of unknown function is present on the dorsolateral aspect of the frontal, near the contact with the nasal. Interestingly, a similar foramen on the same position was recorded in the primitive tritheledontid *Riograndia* (Soares, 2004; Soares *et al.*, 2011).

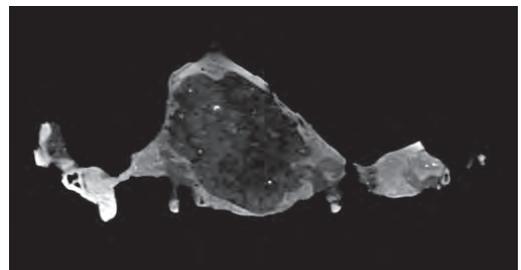


Figure 2 - *Brasilitherium riograndensis* (UFRGS-PV-1043-T). Tomographic transverse section of the posterior braincase area to show the wide cranial cavity.

In dorsal view (Figure 1), the wide braincase and the region of the olfactory bulbs of *Brasilitherium* become narrower at the level of the anterior portion of the parietals. From this point backwards, the braincase increases in width to a lesser degree than in *Morganucodon* (Kermack *et al.*, 1981), but from that point forward the width of the olfactory bulbs increases more than in *Morganucodon*. In *Brasilitherium* the braincase is proportionally smaller than in *Minicynodon* (this paper) as well as in *Morganucodon*. In *Minicynodon* the braincase is proportionally wider and shorter, more comparable in its proportions to that of *Morganucodon*.

The good preservation of the floor of the orbit and lateral side of the braincase merits further discussion. The orbital floor is composed of ventral processes of the frontal as well as a large lacrimal component. More medially the palatine is superimposed on the pterygoid. The palatine may contribute to the orbital floor but the evidence is ambiguous in this specimen as well as in UFRGS-PV-0804-T.

There is a large interorbital vacuity, with only a small piece of bone located medial to the anterodorsal border of the epipterygoid (alisphenoid), possibly representing a partially ossified orbitosphenoid (Figure 1). There is tomographic evidence of an anteriorly displaced orbitoesfenoides medially to the orbital process of the frontal. The UFRGS-PV-1043-T specimen preserves complete epipterygoid. It is longer antero-posteriorly than tall dorsoventrally, not different from *Thrinaxodon*, but broader than in *Probainognathus* (Rougier *et al.*, 1992), *Pachygenelus* (Wible and Hopson, 1993), *Sinoconodon* (Lucas and Luo, 1993), and *Morganucodon* (Kermack *et al.*, 1981). Possibly the plesiomorphic state is a broad epipterygoid which shows progressive reduction in derived non-mammalian cynodonts

and the earliest mammals. In lateral view the epipterygoid contacts the dorsomedial aspect of the quadrate ramus of the pterygoid and is exposed in ventral view participating in the contact between pterygoid and basisphenoid. This character is another one plesiomorphic feature compared with the condition in *Sinoconodon* and *Morganucodon*. A similar feature has been figured for *Procynosuchus* (Kemp, 1979) and *Thrinaxodon* (Fourie, 1974), but has not been reported in *Pachygenelus*, *Sinoconodon* and *Morganucodon*. It may be homologous with the "ventral prong of the epipterygoid bone's basal plate" recorded in *Haldanodon* (Lillegraven and Krusat, 1991).

The quadrate ramus of the epipterygoid extends posterolaterally close to the pterygoparaoccipital foramen, far from the quadrate and ventral to the prootic. There is a distinct foramen on the left epipterygoid, located anterior from the V_3 nerve exit of the prootic. The anterior border of the epipterygoid is thick and rounded, suggesting that it may have been extended in cartilage.

Both prootics are the first complete prootics known for *Brasilitherium*. They show clear sutures with epipterygoid, pterygoid, squamosal and parietal, as well, in ventral view, with the opisthotic and basioccipital. The surface structure shows that the posterodorsal region is medially twisted, contributing to the vault of the braincase; the posteroventral area projects posterolaterally, contacting the squamosal and closing the pterygo-paraoccipital foramen. Here the lateral side of the prootic forms a robust, rod-like structure dorsoventrally directed, bordering the groove for the proximal stapedia artery (Rougier *et al.*, 1992). This structure, possibly representing an autapomorphic character for *Brasilitherium*, is sharply defined anteriorly by a pronounced

step in the surface of the prootic, forming a bridge for a large, posterodorsally directed foramen, confluent with the afore mentioned groove. It may correspond to the passage of the lateral head vein in *Thrinaxodon* (Rougier *et al.*, 1992). In *Morganucodon*, a comparable foramen is present anterior to the groove for the stapedia artery (Wible and Hopson, 1993).

Posterodorsally, the prootic contacts the squamosal, contributing to the cover of the foramen for the large diploetic artery passing to the post-temporal foramen.

Two foramina for the maxillary (V_2) and mandibular (V_3) branches of the trigeminal nerve are present on the anterior lamina of the prootic. The more ventral one for the V_3 is larger than that for the V_2 , representing a derived condition (Wible and Hopson, 1993; Luo *et al.*, 2002), shared with *Adeobasileus*, *Sinoconodon* and *Morganucodon*.

Ventral view of the skull

In ventral view the prootic has a well defined exposure medial to the pterygoparaoccipital foramen, forming the lateral trough and the promontorium, and contacting the opisthotic and exoccipital posteriorly (Figures 1,3). Sutures are not clearly defined in this region. The anterior extension of the trough is more developed than in *Pachygenelus* (Wible and Hopson, 1993), more similar to *Sinoconodon* (Crompton and Sun, 1985), but less developed than in *Morganucodon* (Kermack *et al.*, 1981; Wible and Hopson, 1993). The small opening of the prootic sinus is lateral to the fenestra vestibuli and anterior to the groove of the stapedia artery. The foramen for the facial nerve (VII) opens anteromedially to the latter. Between the openings of the facial nerve and the prootic sinus, and bordering anteriorly the fenestra vestibuli, a crest extends up from the lateral border of the promontorium

to the trough on the prootic. This feature, not known in other non-mammalian cynodonts or earliest mammals may be an autpomorphy for *Brasilitherium*.

The promontorium is well developed in *Brasilitherium* (Bonaparte *et al.*, 2005), but less globular than in *Minicynodon maieri* (Bonaparte *et al.*, 2010), possibly due to dorsoventral compression. On the left promontorium of *Brasilitherium* (Figure 3), the more anterior portion of the structure, near its contact with the basisphenoid, is broken, revealing the internal chamber, which also extends anteriorly to that contact. The globular portion of the pars cochlearis (promontorium) that extends ventromedially and laterally, as seen through the broken area, is a derived character that *Brasilitherium* shares with *Sinoconodon* and more derived mammaliforms such as *Morganucodon* and *Megazostrodon* (Luo *et al.*, 2002). The promontorium is composed of the prootic and is bordered by the basioccipital medially and the basisphenoid anteromedially. It is unclear whether the basioccipital overlaps the medial side of the promontorium. The opisthotic and prootic form the crista interfenestralis. On the opisthotic this crest is well defined, distinct, directed to the posterior region of the paraoccipital process, representing another autpomorphy of *Brasilitherium*. Lateral and anterior to this crest is the "stapedial recess" (Figure 3) into which the fenestra vestibuli opens posterolaterally, towards the place occupied by the quadrate. The groove of the stapedia artery is well marked on the roof of the "stapedial recess". Medial to the latter, the perilymphatic foramen is confluent with the jugular foramen (Figure 3) in the specimen UFRGS-PV-1043-T, but separated by bone in *Minicynodon* UFRGS-PV-1030-T. The cavum epiptericum is rather large.

The ventral surface of the basioccipital is

concave anteroposteriorly and transversely except for the posterior region between the perilymphatic recesses and near the occipital condyles where it is flat transversely. Possibly the median portion of the perilymphatic recess is formed by the basioccipital; it bears three small, possibly vascular foramina. The sutures of the basioccipital are not visible, but that of the exoccipital and opisthotic is evident. The condylar foramen is quite near the jugular foramen but on a more ventral position.

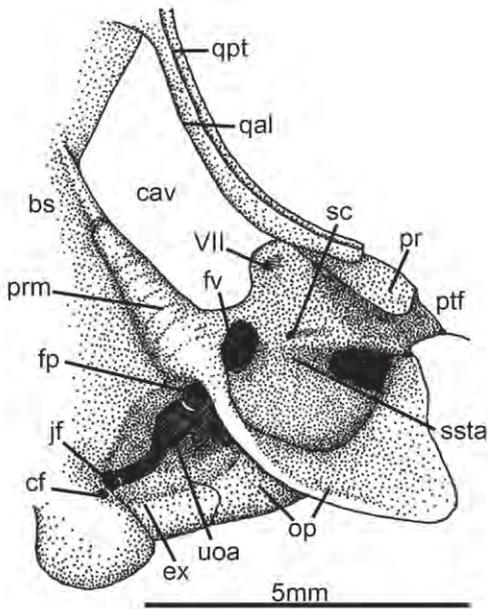


Figure 3 - *Brasilitherium riograndensis* (UFRGS-PV-1043-T). Ventral view of the left braincase area. Abbreviations as in previous figures and: **cf**, condylar foramen; **qal**, quadrate ramus of epipterygoid/alisphenoid; **sc**, sinus canal; **sta**, stapedial fossa; **uoa**, unossified area; **VII**, foramen for nerve VII.

Based on UFRGS-PV-1043-T the structure of the basicranium of *Brasilitherium* can now be interpreted. It resembles those of *Adelobasileus* (Lucas and Luo, 1993) and *Morganucodon* but differs in the confluence of the perilymphatic and jugular foramina.

In general terms it appears more derived than in *Probainognathus* and *Pachygenelus*.

The sutures between the basisphenoid, basioccipital and prootic are not evident, suggesting that these bones might be fused to each other. The lateral margins of the basisphenoid form continuous, narrow crests, "basisphenoid wings" (Crompton, 1964), which meet to the parasphenoid and form a pronounced ventral process, probably for attachment of *M. longus capitis*. This ventral process is not present in other derived cynodonts and basal mammals, and may represent an autapomorphy for *Brasilitherium*. The carotid foramina are located near the basisphenoid wing, at some distance behind the parasphenoid. Two distinct rugosities of unknown function (muscular attachment?) are present just behind the carotid foramina.

The lateral ends of the basiptyergoid processes are slightly concave, bordering the cavum epiptericum, and contact the pterygoid at almost right angles to the sagittal plane. This contact shows noticeable separation in UFRGS-PV-1043-T suggesting a no rigid union (Figure 4), permitting some kind of movement between pterygoids and basisphenoid. If so, the line of flexure appears to continue laterodorsally through the interorbital unossified area to the loose contact frontoparietal in which the former is overlain by parietal. The parasphenoid rostrum is not well preserved in either *Brasilitherium* or *Minicynodon* specimens described here.

In lateral view (Figure 4), the pterygoid forms a large, lateral, posteroventrally projecting flange and an anterior process that contacts the maxilla and palatine. The posterolateral border of the pterygoid flange is crescentic, as in *Sinoconodon* (Crompton and Luo, 1993), bordering a wide, concave and posteriorly facing area which is confluent

with the ventral surface of the wide pterygoid along the margins of the interpterygoid vacuity. It possibly served as the area of origin for part of the pterygoid musculature (Kielan-Jaworowska *et al.*, 2004). The distal end of the pterygoid flange is turned medially. The ventral face of the pterygoid is transversely wide, with the medial border turned ventrally. Near the anterior end of the interpterygoid opening, the median border of the pterygoids forms a distinct ventral step and the ventromedial process, which is large and well defined in the specimen UFRGS-PV-1043-T. This process represents the posterior end of the nasopharyngeal crest, laterally delimiting a deep nasopharyngeal passage. It slightly diverges from the internal nares with the presence of a low median keel extending into the internal nares. Lateral to this trough is the less deep concavity for the Eustachian tube (Hopson and Barghusen, 1986), laterally bordered by the pterygoid flange, and extending to the lateral margin of the internal nares. The ventromedial process of the

pterygoid was possibly for insertion of the *velum palatinum* muscles (Maier, pers. com., 2006). Except for this process, the pattern of crests and troughs is almost identical to that of *Morganucodon* (Kermack *et al.*, 1981), *Sinoconodon* (Crompton and Luo, 1993), *Riograndia* (Soares *et al.*, 2011), and *Pachygenelus* (Hopson, pers. com., 2001), but different from that in *Probainognathus* (Romer, 1970) where the medial trough is wider anteriorly, shorter posteriorly, ending in a ventromedial keel formed by the parasphenoid and pterygoids.

There is not distinct ectopterygoid. Here the pterygoid forms a broad contact with the medial and posterior side of the maxilla, participating in the border of the sub-orbital opening. Behind the internal nares, the "primary palate" (the interpterygoid region) does not exhibit any sutures between the palatines, pterygoids and vomer.

The secondary bony palate extends back to the level of the last postcanine in all specimens of *Brasilitherium*. The anterior border of the palatine is indicated by a short ex-

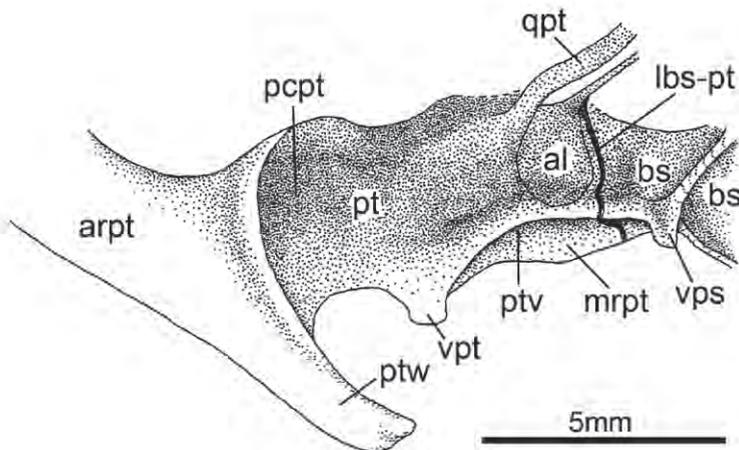


Figure 4 - *Brasilitherium riograndensis* (UFRGS-PV-1043-T). Lateral view of the left pterygoid wing and its contact with epipterygoid and basicranial bones. Abbreviations as in previous figures and: **arpt**, anterior ramus of pterygoid; **bs**, basisphenoid; **lbs-pt**, contact basisphenoid-ptyergoid; **pcpt**, posterior cavity of pterygoid; **vpt**, posterior ventral process of pterygoid.

tent of suture at the level of the fourth post-canine, indicating a rather long palatine, longer than in *Probainognathus* (Romer, 1970) and *Sinoconodon* (Crompton and Luo, 1993), but shorter than *Pachygenelus* (Hopson, pers. com., 2001) and *Morganucodon* (Kermack *et al.*, 1981).

Preorbital region

The structure of the bones on the lateral side of the antorbital region shows no differences from previously reported material of *Brasilitherium* (Bonaparte *et al.*, 2003, 2005). The paracanine fossae on the maxilla, located anteromedially to the canines, are large anteroposteriorly. The short internarial process of the small premaxilla contacts the long anterior process of the nasal.

The length of the tooth-bearing portion of the maxilla and premaxilla is less than half the total length of the skull in the specimen UFRGS-PV-1043-T (43%), but is almost half (48%) in *Minicynodon*. The corresponding ratio is 38-41% in *Probainognathus*, 52% in *Pachygenelus*, 50% in *Sinoconodon*, and 54% in *Morganucodon*.

The limited ventral exposure of the premaxilla (Figure 1) suggests it was smaller than in *Pachygenelus* (Hopson, pers. com., 2001) and *Sinoconodon* (Crompton and Luo, 1993) but more similar to *Morganucodon*.

Lower jaw

Both lower jaws with complete dentitions and without the postdentary bones are present in the UFRGS-PV-1043-T.

The dentary has a long, low horizontal ramus, with a dorsally elevated symphyseal portion (Figure 5). The posteriorly inclined ascending process is larger than the horizontal ramus and bears a large lateral depression for the masseter muscles. The articular process forms the posteriormost point of the jaw and is separated from the tip of the coronoid process by a crescentic posterior edge. The dentary condyle is incipiently developed.

The groove for the postdentary bones is large and continued anteriorly by the Meckelian groove, which extends close to the ventral border. The proportions of the horizontal ramus of the dentary show differences between *Brasilitherium* and the *Minicynodon* specimens. In the former, the length of the horizontal ramus (measured from the posterior border of the last postcanine to the anterior tip of the incisors) is less than half the length of the dentary. The ascending process is proportionally larger in *Brasilitherium*. The anterior border of the coronoid process is rather thick. On the medial side of the dentary, a short distance behind the last postcanine, there is a triangular medially directed process, possibly a coronoid boss.

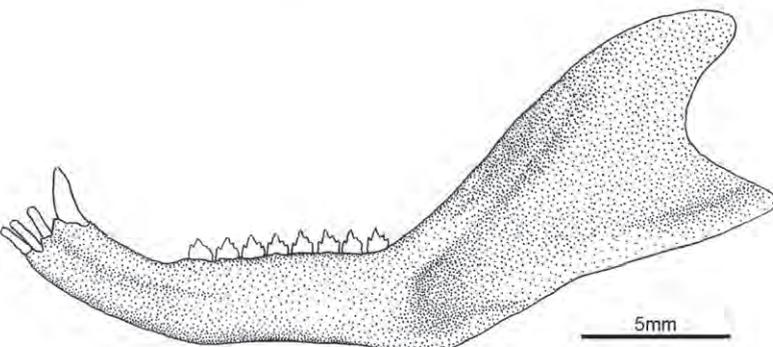


Figure 5 - *Brasilitherium riograndensis* (UFRGS-PV-1043-T). Left lower jaw without postdentary bones. Note that the cusp "a" is more mesially displaced than the center of the postcanines.

Dentition

A complete, associated upper and lower dentition has not been previously available for *Brasilitherium*. However, basic information was derived from several incomplete specimens (Bonaparte *et al.*, 2003, 2005; Figure 7). In the two skulls reported here both set of teeth are complete, although they are only adequately prepared and exposed in the *Brasilitherium* specimen.

Upper incisors

The specimen UFRGS-PV-1043-T bears three incisors. The third is thicker but shorter than the first. The incisors are bent back due to crushing but probably project-

ed ventrally in life. The third incisor is separated from the canine by a long diastem formed by the laterally expanded paracanine fossa.

Lower incisors

The specimen has three lower incisors. The first is more procumbent than the third, a condition shared with *Riograndia* (Soares, 2004; Soares *et al.*, 2011) and *Pachygenelus* (Hopson, pers. com., 2001). There is not evidence of incisors replacement.

Canines

The cross-section near the base of the crown is almost circular in the upper ca-

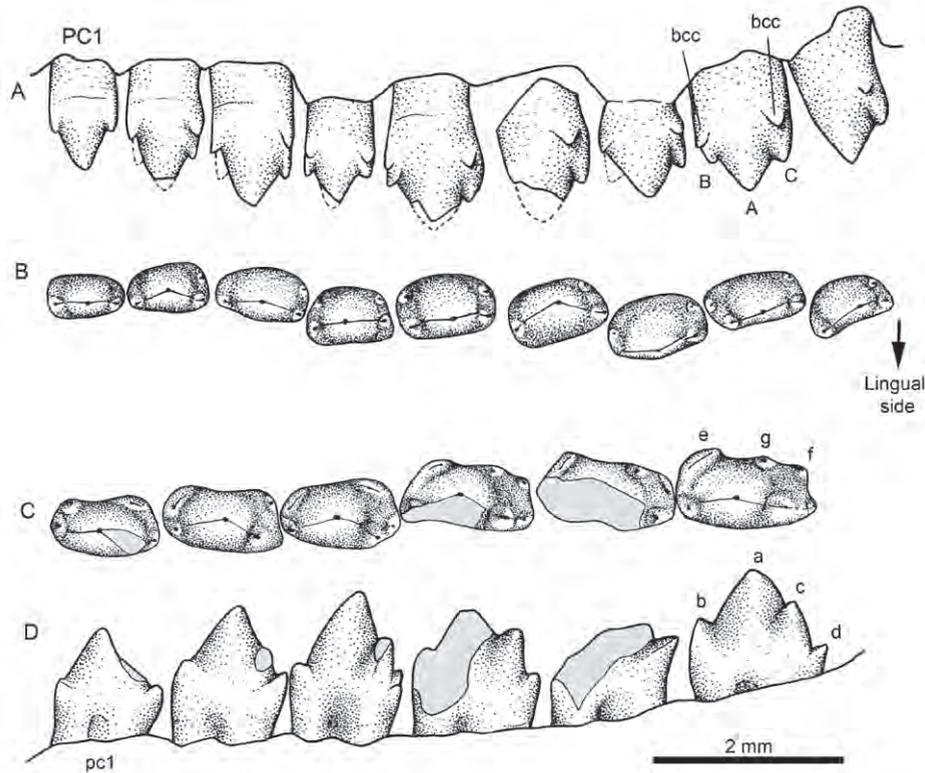


Figure 6 - *Brasilitherium riograndensis* (UFRGS-PV-1043-T). Left upper and lower postcanines as preserved in the specimen. **A**, buccal view and **B**, occlusal view of the uppers; **C**, occlusal view and **D**, buccal view of the lowers. **Abbreviations:** **bcc**, buccal cingular cusps, and those corresponding to the upper and lower cusps.

nines, and transversely narrow in the lower ones. As shown in specimens UFRGS-PV-0594-T and UFRGS-PV-0929-T, the relative size of the canines resembles that of *Morganucodon* but they are larger in the UFRGS-PV-1043-T specimen, similar to those in *Sinoconodon* (Kielan-Jaworowska *et al.*, 2004). The position of the upper canines far behind the anterior margin of the premaxilla in all specimens of *Brasilitherium*, is comparable to that in the earliest mammals, and different from that in *Probainognathus* and Chiniquodontidae, where the canine is situated more anteriorly. *Pachygenelus* appears to show an intermediate position (Hopson, pers. com., 2001).

Postcanines

In *Brasilitherium*, the diastema between canine and the first postcanine is proportionally longer in the dentary than in the maxilla. The UFRGS-PV-1043-T skull has nine postcanines in the maxilla and six or seven in the dentary (Figures 1, 6).

The structure of the postcanines of *Brasilitherium* has previously been described (Bonaparte *et al.*, 2003; 2005); the new material (Figure 6) confirms that account but

provides additional information. On previously described lower postcanines, the principal cusp "a" is slightly displaced mesially; a smaller cusp "b", two small posterior cusps "c" and "d", and two lingual cusps "e" and "g" are also present (Figure 6). There are not any evidence of "premolars" or "molars".

Tooth replacement

The *Brasilitherium* specimen shows ankylosis of the left postcanines 2, 4 and 7, and the right postcanine 7 on the maxilla. The remaining postcanines show slight separation from the alveolar margins. In the dentary, only the left tooth row is exposed; the postcanines 1, 4 and 5 are also ankylosed to the alveoli, indicating that tooth replacement worked in a rather primitive sequence (see Martinelli and Bonaparte, 2011). As noted earlier, tooth replacement in *Brasilitherium* was more frequent than in the closely related *Brasilodon*, and apparently similar to the condition in the basal eucynodont *Thrinaxodon* (Osborn and Crompton, 1973). In the primitive mammal *Sinoconodon* (Kielan-Jaworowska *et al.*, 2004) the tooth replacement was frequent but in a different way.

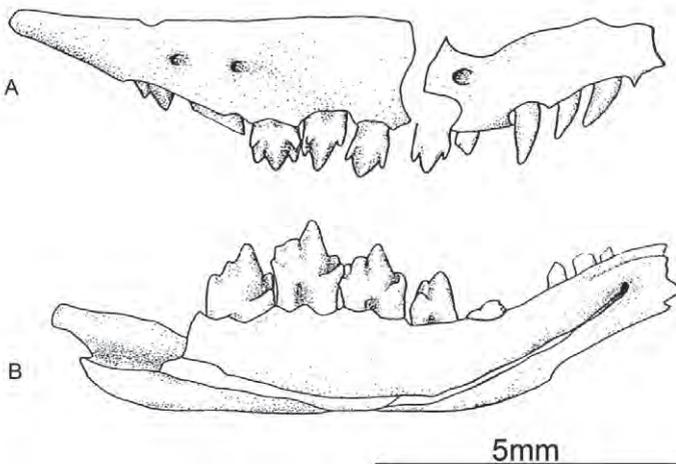


Figure 7 - *Brasilitherium riograndensis* (UFRGS-PV-0759-T). **A**, right maxilla in buccal view; **B**, left dentary in lingual view. Taken from Bonaparte *et al.* (2003).

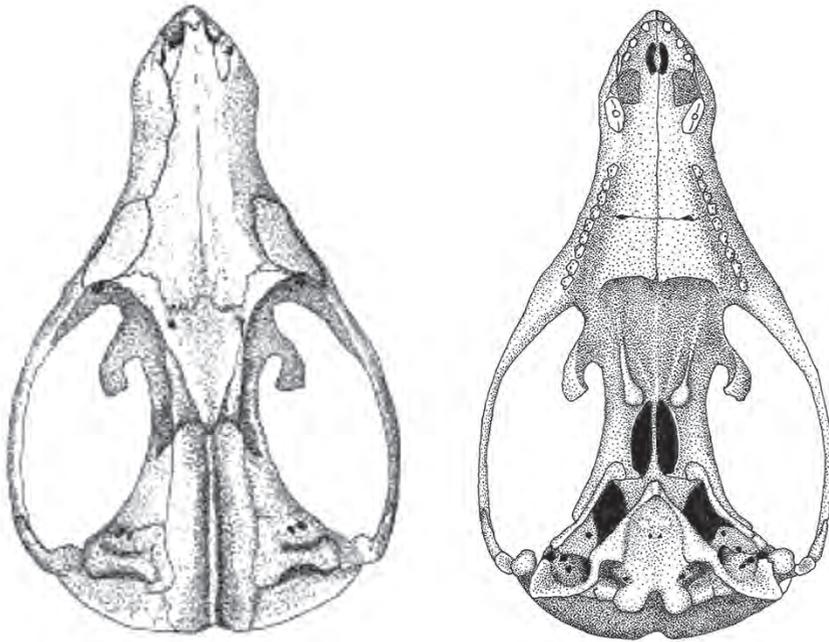


Figure 8 - *Brasilitherium riograndensis*. Reconstruction of the skull based on specimen UFRGS-PV-1043-T, in dorsal and palatal views. Total skull length 33 mm.

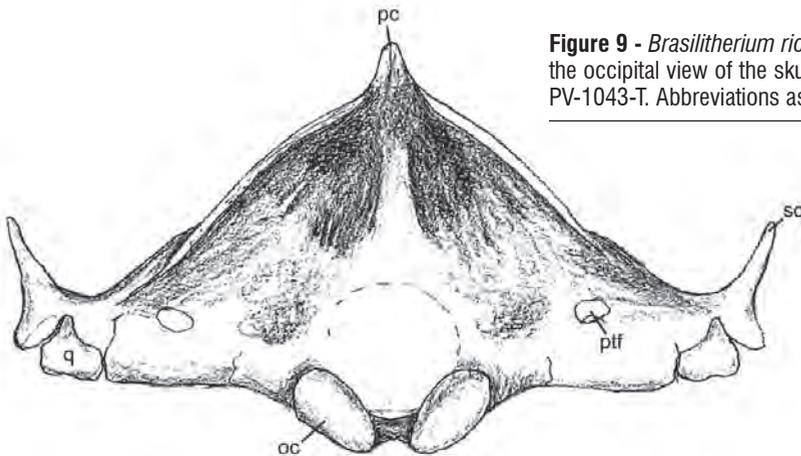


Figure 9 - *Brasilitherium riograndensis*. Reconstruction of the occipital view of the skull based on specimen UFRGS-PV-1043-T. Abbreviations as in previous figures.

Postcranial bones

A few appendicular bones of specimen UFRGS-PV-1043-T are complete, without apparent distortion: a left humerus, ulna and radius; and a right femur and tibia

(Figure 10). The humerus (Figure 10A) resembles that of *Morganucodon* (Jenkins and Parrington, 1976) but the deltoid crest is more developed distally. The humeral head is spherical, projected dorsally and separat-

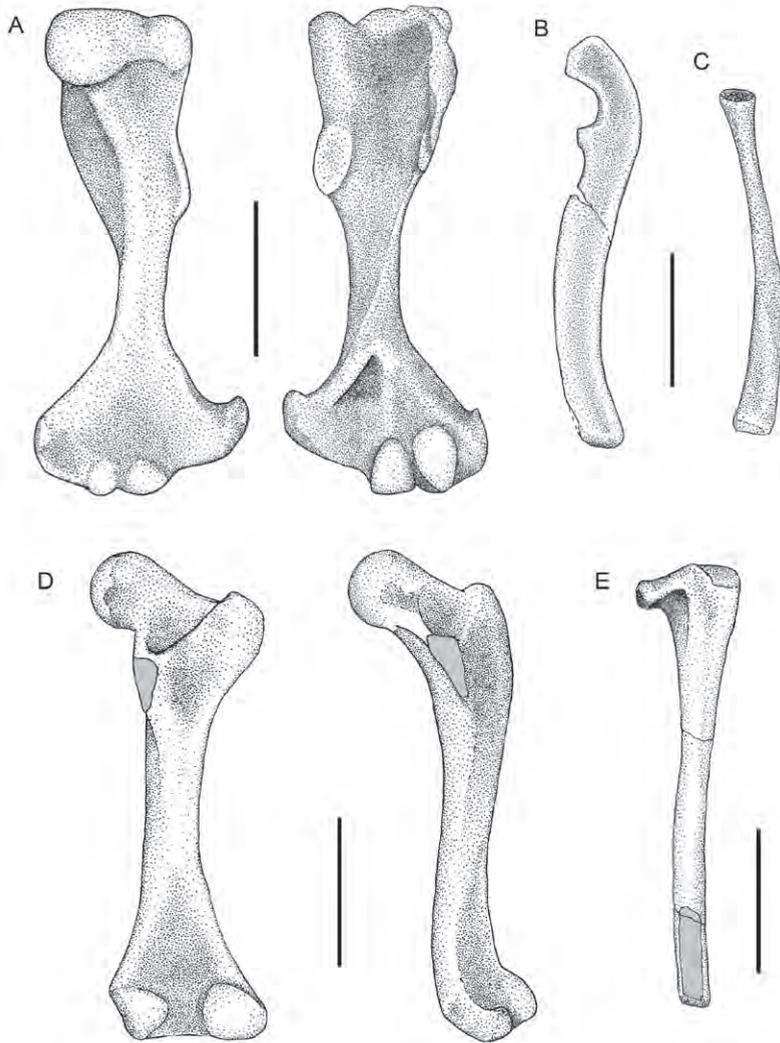


Figure 10 - *Brasitherium riograndensis* (UFRGS-PV-1043-T). **A**, left humerus in dorsal and ventral views; **B**, left ulna in lateral view; **C**, left radius in posterior view; **D**, right femur in ventral and medial views; **E**, right tibia in lateral view. Scale bar 5mm.

ed from both greater and lesser tuberosities by deep grooves. The former is smaller and more proximally placed than the latter. A pronounced dorsal, rounded ridge runs distally through a great portion of the humerus length becoming distally confluent

with the ectepicondyle. This is somewhat larger proximodistally and the shaft of the humerus shorter than in *Morganucodon*.

In ventral view the lesser tuberosity is larger than the greater tuberosity. The bicapital groove is deep, distinct up to the end

of the deltoid crest. The latter appears less developed medially than in *Morganucodon* (Jenkins and Parrington, 1976: Figure 5C). On the medial side at level with the distal end of the deltopectoral crest, there is a pronounced process for muscular attachment, resembling that of *Irajatherium* (Martinelli *et al.*, 2004; Oliveira *et al.*, 2011), larger than in *Morganucodon*. The shaft of the humerus appears better defined and longer in *Morganucodon* in ventral view. Both radial and ulnar condyles are well exposed in ventral view, the former larger and more deeply separated than the latter. In dorsal view the ulnar condyle is larger than the radial. The humerus length is 15,7 mm, the length of ulna: 15,8 mm, the length of radius: 12,7 mm.

The complete right femur is exposed in ventral view. The *Brasilitherium* femur is different from other non-mamalian cynodonts as *Thrinaxodon*, *Massetognathus*, *Exaeretodon* and *Therioherpeton* because the lesser trochanter is in a higher position, the major trochanter is separated from the femoral head by a groove, and the head of the femur is sub-spherical, with a pronounced medial scar for capital ligaments. The femoral head is deflected more medially than in *Morganucodon*. The major trochanter is noticeable larger than the lesser trochanter.

The intertrochanteric fossa is pronounced, deeper towards the lesser trochanter and separated from the fossa of the adductor muscles (Jenkins, 1971), by a rounded ridge connecting both trochanters. Distally, the lateral condyle is larger than the medial condyle. The posterior projection of them suggests an important angle was between femur and tibia–fibula. The total length of the femur is 16,5 mm and the length of tibia is 15,2 mm.

Detail description of these postcranial elements will be presented in a future contribution.

***Minicynodon maieri* Bonaparte, Schultz, Soares and Martinelli, 2010**

This species was briefly studied in a paper on the whole tetrapod records from the Late Triassic beds of the Caturrita Formation (Andreis *et al.*, 1980), corresponding to the top of the Sequence Santa Maria 2 (Zerfass *et al.*, 2003), exposed near Faxinal do Soturno, Rio Grande do Sul, Brazil (Bonaparte *et al.*, 2010). It was collected from the same levels that yielded *Brasilodon quadrangularis* and *Brasilitherium riograndensis* (Bonaparte *et al.*, 2003), *Riograndia guaibensis* (Bonaparte *et al.*, 2001), and *Irajatherium hernandezi* (Martinelli *et al.*, 2005). Originally, the senior author considered the tiny skull and lower jaws of the *Brasilitherium riograndensis* type specimen (UFRGS-PV-1030-T) as a juvenile, but after long discussions and restudy of the specimen with the Prof. Wolfgang Maier, he persuaded me that the specimen is actually an adult creature bearing several anatomical characters of its adult condition. Such experience of working together with a so trained mammalogist proved to be of important help.

General aspect of the skull

The small size of the skull with jaws in articulation, the fine preservation, the complete upper dentition exposed on one side and only some small deformation make of it an exceptional specimen of a non-mamalian cynodont. However, important fails of good preservation are seen in the palatal view because from the internal nares backwards only the right basicranial area is preserved. It has not expanded zygomatic arches, the snout is rather elongate, slender, and the braincase transversally expanded. The parietal crest is much reduced. The temporal region is axially shorter than the orbito–rostral portion of the skull. In gen-

eral terms it is very similar with the *Brasilitherium riograndensis* skull.

The zygomatic arch

The zygomatic arch is very slender as in other brasilodontids, with small contribution of the squamosal located only in the posterior section of the arch. An overlying and long contact is seen between squamosal and jugal. Because the right lower jaw and the quadrate are forwardly displaced it is not possible to observe the ventral side of the squamosal. It is inferred that an incipient glenoid fossa was present because the dentary condyle is clearly seen in the right lower jaw (Figure 11A).

Orbito temporal region

The parietal crest is reduced in a similar condition as in *Brasilitherium*. However,

the contact between the parietal and frontal bones is different. In *Minicynodon* the parietals bear an extensive facet dorsally for the overlying posterior border of the frontals. In *Brasilitherium* the parietals overlie the frontals.

The posterior area of nasals and the anterior of frontals are very intimately fused, a character not observed in *Brasilodon* or *Brasilitherium* (Bonaparte *et al.*, 2003, 2005).

The foramen supraorbital recorded in *Brasilitherium* is present on both frontals, as it is also present in *Riograndia* (Soares, 2004; Soares *et al.*, 2011), suggesting some kind of relationships between them.

In the orbit the ventral process of the frontal and the dorsal process of palatine are present contacting between them. On the floor of the orbit only small fragments of palatine and lacrimal are preserved.

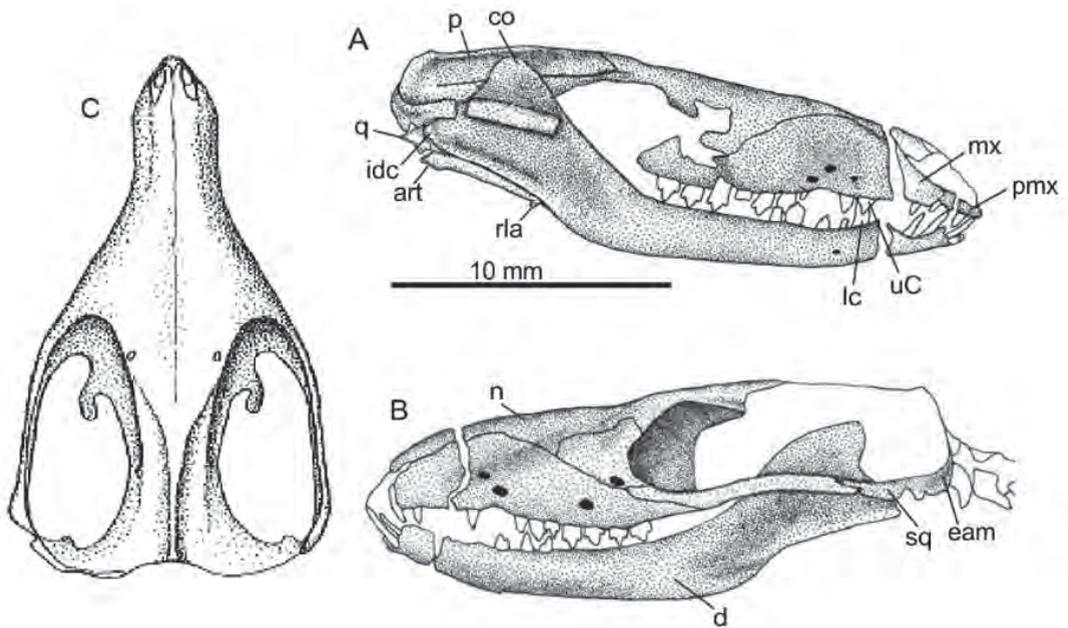


Figure 11 - *Minicynodon maieri* (UFRGS-PV-1030-T). **A**, Right lateral and **B**, left lateral views of the skull and lower jaws of the holotype specimen. **C**, reconstruction of the skull in dorsal view. Abbreviations as in previous figures.

The braincase is proportionally wider than in *Brasilitherium*, but shorter, more similar to that of *Morganucodon* (Kermack *et al.*, 1981; Kielan-Jaworowska *et al.*, 2004). Unfortunately only the right side of the braincase is preserved. It shows the large epipterygoid and a large area without ossification in the interorbital vacuity. The prootic seems similar to that of *Brasilitherium* but not details of it can be observed.

Ventral area of the braincase

The promontorium is well preserved and its volume is proportionally larger than in *Brasilitherium*. Opisthotic and prootic appear to be fused.

The jugular foramen is separated from the perilymphatic foramen by bone, different to the condition in *Brasilitherium*, in which they are confluent. The posterior area of the promontorium is connected to the interfenestral crest, not separated as it is in *Brasilitherium*.

Lower jaw

The lower jaws are in occlusion with the uppers. The left ramus lacks the postdentary bones, but the right one, which is anteriorly displaced, has the postdentary bones in the corresponding dentary groove and the articular is closely articulated to the quadrate (Figure 12).

The dentary is low and elongate, and the coronoid process rather low and posteriorly inclined. In the right lower jaw there is a distinct, incipient condyle seen in lateral view (Figure 12A) because the jaw is a bit anteriorly displaced. It was not observed in *Brasilitherium* but possibly it was present because an incipient glenoid groove was observed (Figure 1). Possibly an incipient glenoid was also present in *Minicynodon*.

The proportion between the horizontal branch of dentary and the total length of it is larger than in *Brasilitherium*.

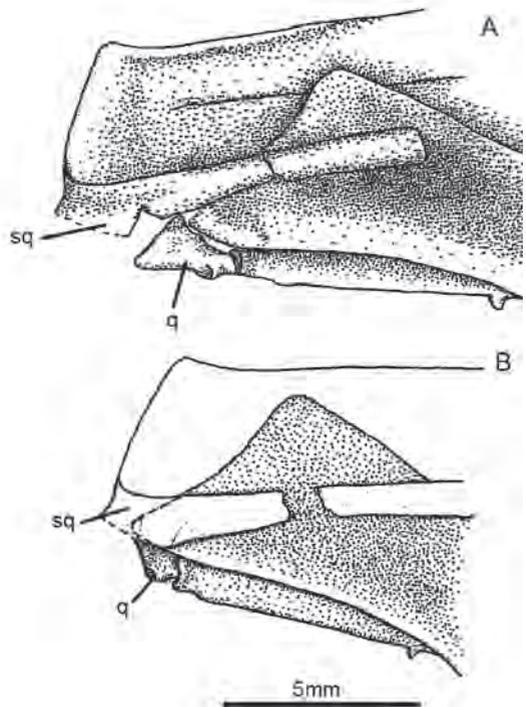


Figure 12 - *Minicynodon maieri* (UFRGS-PV-1030-T). **A**, right mandibular-skull articulation, as preserved, in lateral view; **B**, the same articular area with the bones in their anatomical position. Abbreviations as in previous figures.

Dentition

Because the lower jaws are in tight occlusion, many small details are not possible to observe. Some small but possibly significant differences can be seen between *Minicynodon* and *Brasilitherium* dentition.

Upper incisors

Minicynodon has not a diastema between canines and incisiform. It has five incisiform teeth, three in the premaxilla and two or possibly three in the maxilla. They are rather cylindrical and ventrally directed.

Lower incisors

It has four lower incisors. The fourth is thicker than the more procumbent first in-

cisor. There is not a diastema between the lower incisors and the canine.

Canines

Upper and lower canines are proportionally smaller than those of *Brasilitherium*.

Postcanines

Upper and lower postcanines are separated from the canines by a very small diastema. There are seven postcanines in the maxilla, similar with those of *Brasilitherium*, and seven or eight in the dentary. The lower postcanines show some differences with those of *Brasilitherium*, because they have the main cusp “a” on the center of the crown, not mesially displaced as in *Brasilitherium*.

Tooth replacement

The last postcanine of the left dentary was in process of eruption. Not other indication of tooth replacement was observed.

DISCUSSION

Transition eucynodonts-mammals

It seems clear that the discovery and studies on the brasilodontids have opened new opportunities to improve knowledge on the eucynodonts–mammals transition (Bonaparte, 2012a). New interpretations after new evidences improve the knowledge although usually giving room for new interpretative problems.

After the magnificent chapter on the origin of mammals in Kielan-Jaworowska *et al.*, (2004), with very much anatomical information especially, on the transformation of characters, we have the false impression that most of the knowledge on the transitional

steps between cynodonts and mammals are safely established. Actually, the anatomy of the brasilodontids suggests that there are too much to learn on this fascinating subject on the origin of mammals. On this respect it is interesting to cite an opinion by Tom Kemp included in his recent book on *The Origin and Evolution of Mammals* (2005:78): “For the moment, this mosaic of ancestral and derived mammalian characters seen among the most progressive eucynodont groups, tritylodontids, tritheledontids, therioherpetids, juvenile probainognathids, and presumably also dromatherians and their like, reveals the possibility that several lineages of Middle Triassic eucynodonts were independently evolving reduced body size with a concomitant convergence of several basic characters associated with small body size, but superimposed upon divergent characters associated with differing diets, etc. It is perhaps significant, as described in a later chapter, members of the taxon mammalian almost at their first appearance consisted of at least four distinct groups”. This statement demonstrates that the information and knowledge of these transitional stages was far from complete.

The specializations in the transitional stages between derived eucynodonts and the earliest mammals presented by Kemp (2005) seem to us that are more in accordance with the state of this fascinating subject. The evolutionary significance of the brasilodontids demonstrates that some traditional and recent ideas (Kielan-Jaworowska *et al.*, 2004; Kemp, 2005) have to be improved and update.

The sister group of mammals

For many years it was considered that Tritylodontidae (e.g., Kemp, 1982) and

then the Trithelodontidae (e.g., Hopson and Barghusen, 1986) were the sister group of mammals, ideas that are still supported by several authors (Kielan-Jaworowska *et al.*, 2004; Kemp, 2005; among others). Now, after the discoveries of *Brasilodon* and *Brasi-*

litherium (Bonaparte *et al.*, 2003, 2005) from the Late Triassic of Southern Brazil, was confirmed the interpretation by Bonaparte *et al.*, (2003) that the brasilodontids represent the sister group of mammals (Luo, 2007). The characters supporting this inter-

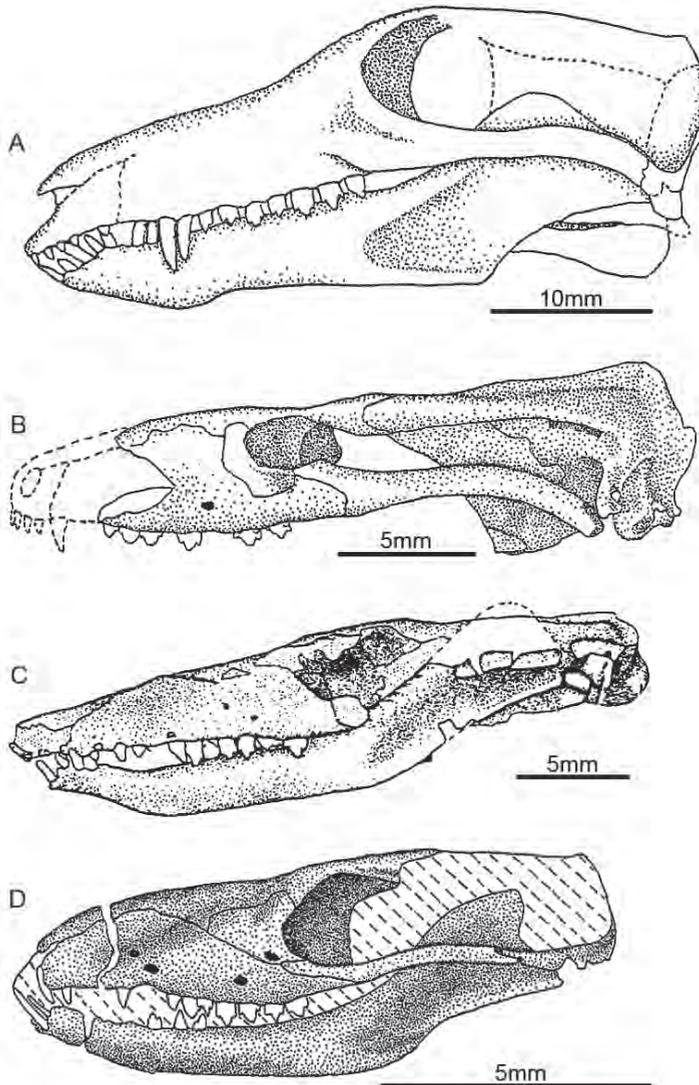


Figure 13 - The four Brasilodontidae genera. **A**, *Protheriodon* (Middle Triassic); **B**, *Brasilodon* (Upper Triassic); **C**, *Brasilitherium* (Upper Triassic); **D**, *Minicynodon* (Upper Triassic).

pretation are from almost complete skulls, lower jaws, dentitions and a few appendicular bones (this paper), from three species from the Late Triassic (Norian) and one from the Middle Triassic (Bonaparte *et al.*, 2006) from Southern Brazil (Figure 13).

Although brasilodontids clearly resemble the Morganucodonta (Kielan-Jaworowska *et al.*, 2004) a few autapomorphies of *Brasilitherium* may discard an ancestor-descendant hypothesis after the known species (McKenna and Bell, 1997).

However, Brasilodontidae was made, probably, not only by the few genera and species recorded from a small region of Southern Brazil, and possibly they were present on other latitudes of the huge Pangea supercontinent, as recently demonstrated (Bonaparte, 2012b) by the presence of *Panchetocynodon* in India (Das and Gupta 2012). At present, the hypothesis that Brasilodontidae originated the Morganucodonta appears reasonable because not reversal of characters is required for such interpretation.

The interpterygoid vacuities

The comparative anatomy of brasilodontid genera and the inferred phylogenetic relationships with procynosuchids (Bonaparte *et al.*, 2011) have shed some light on the presence or absence of the interpterygoid vacuities. The evolutionary history of the vacuities was greatly confused because most of the Early and Middle Triassic cynodonts do not present such openings and thereafter the character reappear in some Late Triassic and Early Jurassic derived cynodonts as the Tritheledontidae (Crompton, 1958; Bonaparte, 1980; Hopson and Barghusen, 1986). Such dual information have stimulated hypothesis to understand the problem. Detailed and long

discussion on the subject were published, notably, by Martinelli and Rougier (2007) who postulate that the disappear and reappearance of the character by the most diverse and hypothetical processes, including heterochronic factors.

However, the brasilodontids clearly show that the interpterygoid vacuities were a persistent primitive character inherited from the procynosuchids, present in all the four genera of Brasilodontidae and in the sister group, the Tritheledontidae.

In the earliest mammals as *Sinoconodon* (Crompton and Sun, 1985) and *Morganucodon* (Kermack *et al.*, 1981) the wide pterygoid is present on its original place but the vacuities are covered by medial growing of the lateral branch of the pterygoid, preserving the width space of the primary palate.

The process of closing the vacuities was different in Thrinaxodontidae, Probainognathidae, Chiniquodontidae, Traversodontidae and Tritylodontidae to that of Brasilodontids and mammals, because the pterygoid moved medially and become firmly appressed to the parasphenoid, making the characteristic ventromedial keel that connects the anterior with the posterior regions of the skull. Finally, the presence of the pterygoid vacuities in the Tritheledontidae is explained because they are the sister group of Brasilodontidae, retaining such primitive character.

The functional aspect of the vacuities is not discussed here, although the interpretations by Barghusen (1986) appear well founded (see also Martinelli and Rougier, 2007).

Adelobasileus, Hadrocodium, and Microconodon.

The knowledge of the Late Triassic Brasi-

lodontidae gives opportunity to discuss something more on the species *Adelobasileus cromptoni* Lucas and Hunt, 1990, *Microconodon tenuirostris* Osborn, 1886, and on *Hadrocodium wui* Luo, Crompton and Sun, 2001. *Adelobasileus* is from the Late Triassic Tecovas Formation of Texas, USA, of Late Carnian age. The only known specimen is the holotype, a very incomplete skull preserving only a partial braincase and some details of the basicranium. Several mammalian characters were observed by Luo (1994), Lucas and Luo (1993), Luo *et al.* (2001) and Kielan-Jaworowska *et al.* (2004), but they were not enough to be sure of its actual relationships because the absence of critical diagnostic characters from the dentition, lower jaw, and zygomatic arch. However its mammalian affinities were emphasized by the authors that described and discussed it. Kielan-Jaworowska *et al.* (2004) include *Adelobasileus*, tentatively within the "Earliest Stem Mammals", other authors as Rougier *et al.* (1996) and Luo *et al.* (2001, 2002) have interpreted *Adelobasileus* as intermediate between *Sinoconodon* and other stem mammals.

It is interesting to point out that most of characters indicated by Kielan-Jaworowska *et al.* (2004, p. 185), to support, even tentatively, the mammalian condition of *Adelobasileus* have been recorded in the non-mammalian cynodonts brasilodontids (Bonaparte *et al.*, 2003, 2005, 2006, 2010). They are the following:

- a) "incipient promontorium": (Promontorium well developed are present in specimens of *Brasilitherium* UFRGS-PV-1043-T and of *Minicynodon* UFRGS-PV-1030-T).
- b) "an enlarged anterior lamina of the petrosal for the lateral wall of the braincase encircling the foramina...". The same or very similar are the characters observed

and figured for *Brasilitherium* (Bonaparte *et al.*, 2003, 2005).

- c) "an ossified floor to the cavum epipitericum for the trigeminal ganglion". However, in the reconstruction of the basicranium of *Adelobasileus* presented in Kielan-Jaworowska *et al.*, (2004, Figure 4. 11C), the cavum is not totally ossified. In *Brasilitherium* the cavum epipitericum is similarly unossified as in the type specimen of *Adelobasileus* shown in the cited figure of Kielan-Jaworowska *et al.* (2004).
- d) "full enclosure of the pterygo-paraoccipital foramen (for the stapelial artery) by bone and partial enclosure of the ascending channel for the orbitotemporal...". In the specimen of *Brasilitherium* UFRGS-PV-1043-T is the same situation, but in the holotype of *Brasilodon* and one specimen of *Brasilitherium* the pterygo-paraoccipital foramen is not totally closed. The state of this character and that of the channel for the diploetica artery appear to be variable on this level of derivation toward the mammalian condition. So, both of these characters may be of doubtful value.
- e) "separation of the cochlear foramen from the jugular foramen and separation of the hypoglossal (condylar) foramen from the jugular foramen". In *Brasilitherium* specimen UFRGS-PV-1043-T the cochlear and jugular foramina are confluent, but in the type specimen of *Minicynodon* UFRGS-PV-1030-T they are separated by bone. The condylar foramen is separated from the jugular foramen in *Brasilodon*, *Brasilitherium* and *Minicynodon* available specimens.

It seems clear that these five significant characters are not enough to assume that *Adelobasileus* may be considered a stem mammal, as cited by Kielan-Jaworowska

et al. (2004). The presence of a small pterygoid vacuity (Lucas and Luo, 1993: 320), and the presence of the median pterygoid crest (Lucas and Luo, 1993: fig.9; Kielan-Jaworowska *et al.*, 2004, Figure 4. 11A and C) suggests a more plesiomorphic level of organization than both in *Sinoconodon* and *Morganucodon*, that is more in accordance with the anatomical characters present in the Late Triassic brasilodontids. So, it seems reasonable to interpret *Adelobasileus* as a member of the Family Brasilodontidae or of some other taxon of non-mammalian cynodonts.

Hadrocodium wui (Luo, Crompton and Sun, 2001) is represented only by the holotype skull, a quite small specimen, 12 mm long, which includes complete dentition and lower jaws in natural connection with the skull.

Preservation of the palatine and basicranial regions is not the best, and some deformation is also present. In 2004, the former author had the opportunity, thanks to Dr. Z.-X. Luo, to observe the specimen that was temporarily at the Carnegie Museum of Natural History. In 2005 Bonaparte *et al.* (2005) published some observations on the well

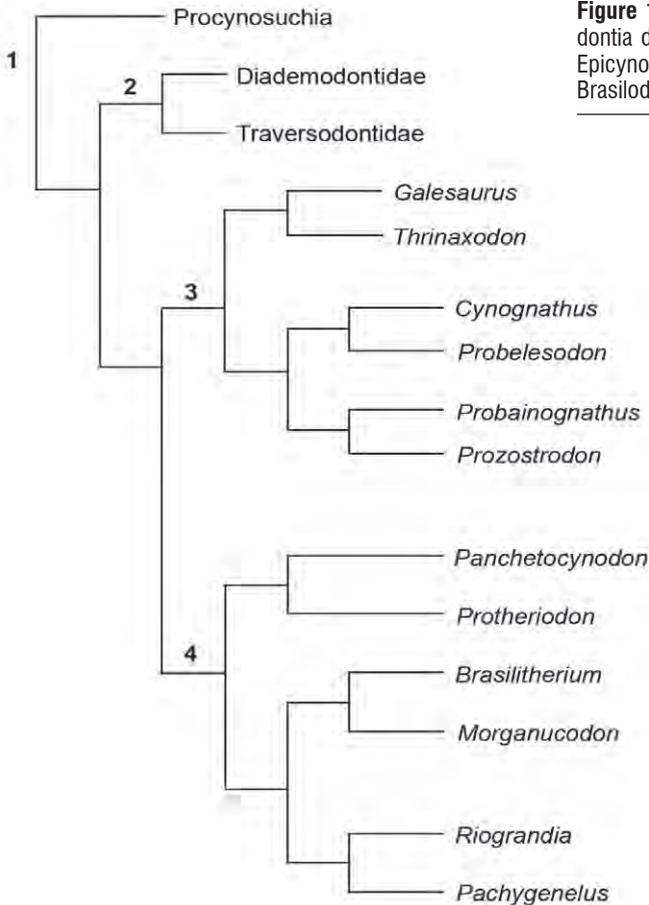


Figure 14 - Tentative cladogram of the Epicynodontia discussed in this paper. **Abbreviations:** **1**, Epicynodontia. **2**, Gomphodontia. **3**, Galesauria. **4**, Brasilodontia. Modified from Bonaparte (2012b).

developed pterygoid wing present in *Hadrocodium*. Originally, Luo *et al.* (2001: 336) indicated: "The small hamulus of pterygoid is similar to the condition in *Haldanodon*, *Ornithorhynchus* and multituberculates but more reduced than the homologous transverse flange of cynodonts...". The well developed pterygoid wing observed in the type specimen of *Hadrocodium* (Bonaparte *et al.*, 2005) is, without doubt, a functional character related to the masticatory function, indicating a level of primitive organization of some muscles controlling occlusal movements of the lower jaws. So, probably the unreduced pterygoid wings of *Hadrocodium* may shed doubts on the mammalian condition of this small Chinese genus.

At present times, after the anatomical information on Late Triassic Brasilodontidae we suggest that *Hadrocodium* may be in an intermediate evolutionary position between *Brasilitherium* and *Morganucodon*.

Microconodon tenuirostris Osborn 1886 is known by a large number of specimens. The numerous species supposedly related to it from North America and Europe were extensively and carefully analyzed by Sues (2001). *Tricuspes* (Huene, 1933), *Pseudotricodont* (Hahn *et al.*, 1984), *Lepagia* (Hahn *et al.*, 1987), *Gaumia* (Hahn *et al.*, 1987), "*Pseudotricodont*" (Lucas and Hoakes, 1988), *Therioherpeton* (Bonaparte and Barberena, 1975), and *Prozostrodon* (Bonaparte and Barberena, 2001), although of uncertain systematic interpretations, because of incomplete material, they obviously are enough to demonstrate that the variety of derived non-mammalian cynodonts taxa was very significant and of great geographical distribution on Pangea. These incompletely known taxa along with *Brasilodon*, *Brasilitherium* and *Minicynodon* (Bonaparte *et al.*, 2003, 2005, 2006, 2010) show the existence of a rich evolutionary scenario of

forms previous to the earliest known mammal. So, the ideas of Kemp (2005, p.78) that indicate: "... may be the "reptilian-mammalian" boundary was crossed several times, if such a cladistically incorrect statement may be forgiven", seems to have a real conceptual value.

CONCLUSIONS

The anatomical description and comparisons of the new specimen of *Brasilitherium riograndensis* (UFRGS-PV-1043-T) and of the holotype of *Minicynodon maieri* (UFRGS-PV-1030-T) (Bonaparte *et al.*, 2003, 2005, 2010) confirms the very close relationships of them to *Morganucodon watsoni* (Kermack *et al.*, 1981). Both genera of Brasilodontidae show a great similar morphology suggesting that the possibility of ancestor-descendent appears to be quite clear at the family level. A few autapomorphies in both genera make uncertain closer relationships. It is confirmed that the Brasilodontidae (Bonaparte *et al.*, 2005) is composed by the genera *Protheriodon* (Bonaparte *et al.*, 2006) from the Middle Triassic, and *Brasilodon* (Bonaparte *et al.*, 2003), *Brasilitherium* (Bonaparte *et al.*, 2003), and *Minicynodon* (Bonaparte *et al.*, 2010) from the Late Triassic (Norian) of Southern Brazil. Very recently Bonaparte (2012b) considered that the Early Triassic *Panchetocynodon* from the Panchet Formation of India (Das and Gupta, 2012) is a primitive Brasilodontidae although represented by an incomplete left lower jaw. The tentative cladogram in Figure 14 shows the possible phylogenetic position of the Early Triassic *Panchetocynodon*, as presented in Bonaparte (2012b).

The synonymy of *Brasilitherium* with *Brasilodon* proposed by Liu and Olsen (2010) is the result of quick and superficial

observations ignoring evolving characters of advanced eucynodonts.

It is considered that the Tritheledontidae is the sister group of Brasilodontidae, both constituting a subclade closely related to Morganucodontidae and quite separated from the remaining eucynodonts (Kemp, 1982). The small size of these taxa suggests insectivorous habits and the retention of plesiomorphic characters along with derived ones connected with mastication, hearing, olfaction and an improved nervous system as indicated by the larger braincase. On the other hand, Thrinaxodontidae, Cynognathidae, Chiniquodontidae and Probainognathidae developed several adaptive characters for a carnivorous habit.

According with Bonaparte (2012b), the subclade Brasilodontia, so different to the well know Triassic eucynodonts, opens doors for new interpretations on the origin of mammals.

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