NEW INFORMATION ON *BRASILODON* AND *BRASILITHERIUM* (CYNODONTIA, PROBAINOGNATHIA) FROM THE LATE TRIASSIC OF SOUTHERN BRAZIL

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ABSTRACT – New discoveries of articulated skulls and lower jaws of *Brasilodon* and *Brasilitherium* from the Late Triassic of Brazil provide additional information on these small cynodonts, allowing us to establish the family Brasilodontidae nov. The basicranium, lateral wall of the braincase, primary and secondary palates and the quadrate of *Brasilitherium* are described, as well as the basicranium, primary palate and lower jaw of *Brasilodon*. *Brasilitherium* exhibits more derived characters than *Brasilodon* in the periotic, the promontorium, and the articular process of the dentary. *Brasilodon* is more derived in the lower dentition, the mode of tooth replacement, and the vascular features in the "stapedial recess". Both genera have interpterygoid vacuities that are considered here as possibly derived or reversed characters of the mammalian primary palate. The new phylogenetic analysis presented here corroborates the position of both genera as sister-group of mammals as previously proposed.

Keywords: Cynodontia, Probainognathia, *Brasilodon*, *Brasilitherium*, Late Triassic, southern Brazil.

RESUMO – Novos achados, incluindo crânios com mandíbulas articuladas, de *Brasilodon* e *Brasilitherium* do Neotriássico do Brasil fornecem informações adicionais sobre estes pequenos cinodontes, permitindo a proposição de uma nova família, Brasilodontidae. São descritos o basicrânio, a parede lateral da caixa craniana, o palato primário e o secundário e ainda o quadrado de *Brasilitherium*, bem como o basicrânio, o palato primário e a mandíbula de *Brasilodon*. *Brasilitherium* apresenta caracteres mais derivados em relação a *Brasilodon* no periótico, promontório e processo articular do dentário. *Brasilodon* apresenta uma dentição mandibular mais derivada, bem como o padrão de substituição dentária e ainda o sistema vascular relacionado ao recesso estapedial. Ambos apresentam vacuidades interpterigóides, que são aqui interpretadas como uma característica derivada ou uma reversão, diretamente relacionada à organização do palato primário mamaliano. A nova análise filogenética aqui apresentada confirma a proposição deste dois gêneros constituírem o grupo-irmão dos mamíferos, como já foi proposto em trabalhos prévios.

Palavras-chave: Cynodontia, Probainognathia, *Brasilodon*, *Brasilitherium*, Triássico superior, sul do Brasil.

INTRODUCTION

The recent discovery in the Late Triassic of southern Brazil of two small and derived cynodonts bearing several mammalian features (Bonaparte *et al.*, 2003) provide new evidence to the current interpretations on the sister group of mammals (Kemp, 1982; Hopson & Barghusen 1986; Wible *et al.*, 1990; Shubin *et al.*, 1991; Hahn *et al.*, 1994; Luo, 1994; Hopson & Kitching, 2001; Luo *et al.*, 2002).

Brasilodon and *Brasilitherium* (Bonaparte *et al.*, 2003) are both based on incomplete skulls and lower jaws. However, the significance of their preserved characters provides a new insight into the complex and fascinating subject of the anatomical transition between advanced cynodonts and the earliest mammals such as *Morganucodon* (Kühne, 1949), *Sinoconodon* (Patterson & Olson, 1961), and *Kuehneotherium* (Kermack *et al.*, 1968).

New discoveries of articulated skulls and lower jaws of both Brazilian taxa, with well preserved dentitions and new information on several areas of the skull enable us to update the anatomy of these small cynodonts and to correct some misinterpretations based on fragmentary specimens. The newly available materials confirms the validity of both taxa, showing significant differences in the lower dentition, in the degree of fusion of the skull roof bones, and in some basicranial features. Perhaps the most significant information regarding these species is that they have a dentition morphologically more derived than *Morganucodon* (Kermack *et al.*, 1973; Crompton, 1974) and, in the case of *Brasilodon* its upper and lower dentition suggest some kind of morphological affinities to later "symmetrodonts" such as *Kuehneotherium* (Kermack *et al.*, 1968).

In this paper we provide further knowledge of the skull anatomy of both *Brasilodon* and *Brasilitherium*, and a discussion on their possible evolutionary relationships with the Late Triassic radiation of small and advanced cynodonts represented by *Microconodon* (Osborn, 1886; Sues, 2001); *Dromatherium* (Emmons, 1857; Sues *et al.*, 1994; Hahn *et al.*, 1994; Sues, 2001); *Pseudotriconodon* (Hahn *et al.*, 1984); *Tricuspes* (Huene, 1933); *Gaumia* and *Lepagia* (Hahn *et al.*, 1987); and *Meurthodon* (Sigogneau-Russell & Hahn, 1994), from which eventually mammals were differentiated. A phylogenetic analysis is developed in order to test the relationships of *Brasilodon* and *Brasilitherium* with Triassic cynodonts and the earliest mammals. It is possible that the phylogenetic importance of these small cynodonts from Brazil may require, in the future, more extensive studies on their anatomy.

Abbreviations
Institutional. IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MACN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **UFRGS PV-T**, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

SYSTEMATIC PALEONTOLOGY

THERAPSIDA Broom, 1905
CYNODONTIA Owen, 1861
EUCYNODONTIA Kemp, 1982
PROBAINOGNATHIA Hopson, 1990

BRASILODONTIDAE nov.

Type genus. *Brasilodon* Bonaparte, Martinelli, Schultz & Rubert, 2003.

Included genera. *Brasilodon* Bonaparte, Martinelli, Schultz & Rubert, 2003. *Brasilitherium* Bonaparte, Martinelli, Schultz & Rubert, 2003.
Diagnosis. Probainognathian cynodonts with a central, large cusp and an anterior and a posterior accessory cusp symmetrically arranged on the lingual side of the upper postcanines, different from morganucodontids, tritheledontids, probainognathids, chiniquodontids and other carnivorous eucynodonts. Similar distribution of the cusps in the lower postcanines, or bearing an additional buccal cusp posterior to the main cusp. A small cingular cusp on the anterior and on the posterior side of the upper and lower postcanines. Presence of interpterygoid vacuities; transverse contact of the wide pterygoid with basipterygoid process; low and posteriorly extended jugal; separate foramina for nerves V2 and V3; presence of prootic sinus foramen on the lateral flange of prootic; stapedial artery groove covered by prootic posteriorly; occipital condyles more posteriorly positioned than the lambdoid crest; lack of postorbital bar; topographically defined promontorium; quadrate similar to that of *Morganucodon*; pterygoparoccipital foramen open in the prootic; basicranial area ventrally wide; unfused lower jaw symphysis anterodorsally projected; medial lower incisors procumbent; articular process of dentary transversely expanded almost touching the squamosal; Meckelian groove near the ventral edge of dentary; lack of ectepicondylar foramen in the humerus; proximal articulation surface of the ulna facing anteriorly and cross section of the diaphysis in an 8 shape; presacral vertebrae with neural canal wider than the centrum.

Brasilodon quadrangularis Bonaparte,
Martinelli, Schultz & Rubert, 2003.

Emended diagnosis. Brasilodontid cynodont with the following combination of characters: Upper and lower postcanines with a large, central cusp, an anterior and a posterior small cusp on the lingual side of the uppers and on the buccal side of the lowers. Lower postcanines without cusp d which is present in *Brasilitherium*. Different from the latter with the perilymphatic and jugular foramina being partially confluent; the prootic and opisthotic are not fused; and the promontorium is less developed. Postcanine replacement delayed, less frequent than in *Brasilitherium*. Skull size is about 40% larger than in *Brasilitherium*.

Description
Besides the type specimen of *Brasilodon quadrangularis*, UFRGS PV0611T, the new materials discussed here are: UFRGS PV0628T, an incomplete skull articulated to the lower jaws (Figures 1, 2, 3, and 4); and UFRGS PV0765T, an incomplete skull associated with two incomplete lower jaws and an ulna (Figure 6). Both specimens were collected during June-July 2002 in Faxinal do Soturno, Rio Grande do Sul, Brazil (see Bonaparte *et al.*, 2003 for stratigraphical references).

Secondary osseous palate. The information on the osseous secondary palate of *Brasilodon* given in the original description has not been significantly improved with the new specimens. In UFRGS PV0628T the palatal processes of the maxilla are rather complete but the palatines are very fragmentary. Medial to the postcanine tooth row there is a well defined groove to accommodate the lower postcanines. This groove becomes deeper posteriorly, especially in the area of the junction of the anterior dorsal border of the pterygoid wing, the lateral area of the palatine and the most posterior projection of the maxilla. No ectopterygoid bones have been observed in this area.

In the type specimen the posterior border of the secondary osseous palate is partially preserved at the left side where there is a doubtful fragment of palatine plus maxilla observed (Bonaparte *et al.*, 2003, fig. 3). The posterior border of the secondary osseous palate of *Brasilodon* possibly was posterior to the last postcanine (Figure 5) such as in *Prozostrodon* (Bonaparte & Barberena, 2001, fig. 9B), and possibly more extended than in *Pachygenelus* (Hopson, pers. com., 2001).

Primary palate. The primary palate extends from the roof of the choana to the pterygoid-basisphenoid contact, including the interpterygoid vacuities. Behind the choana and in a lateral position to the median plane, the palatines bear a pronounced pterygopalatine crest which continues backwards onto the pterygoids (Figures 1, 2 and 5), ending in a sharp spine-like process which lies in line with the posterior border of the pterygoid wings. Between this crest and the lateral border of the pterygoid wing there is a transversely concave depression, anteriorly directed in relation to the more anterior and dorsal area of the pterygoid wing. The suture between the palatine and the pterygoid is not clear. However, it is possible that the pterygoid contacts the maxilla excluding the palatine from the subtemporal border of the orbit, similar to that observed in *Pachygenelus* (Hopson, pers. com. 2001).

The central portion of the primary palate is formed by the vomer extending forward from the anterior edge of the interpterygoid vacuities. The vomer appears to be transversely wide and narrows anteriorly and posteriorly. The sutures of the vomer with the palatines and with the pterygoids are partially clear. On the ventral surface of the vomer there is a small axial crest which eventually connects, inside the choana, to the dorsal surface of the secondary osseous palate by means of a septum.

The pterygoid wings are well developed, similar to the carnivorous chiniquodontids and probainognathids (Romer, 1969a, 1969b), but somewhat larger and more laterally expanded than in *Morganucodon* (Kermack *et al.*, 1981, figs. 98, 99) and *Sinoconodon* (Luo, 1994, fig 6.2). Luo *et al.* (2001, fig. 1B) indicate a great reduction of the pterygoid wing of *Hadrocodium*. However, the examination of the type specimen has revealed that *Hadrocodium* has well developed pterygoid wings (Figure 19). The relative position of the pterygoid wings of *Brasilodon* is more anterior than in the reconstruction of *Pachygenelus* (Hopson, pers. com.). Behind the pterygoid wings, the strong and transversely wide stem of the pterygoid borders laterally the interpterygoid vacuity. Its morphology is complex and not very different to *Procynosuchus* (Kemp, 1979), with a thick end for contact with the basipterygoid process of the basisphenoid. An anteroposterior ridge borders a ventrolateral area of the bone, on which a lateral process marks the more lateral point in this portion of the pterygoid. Medial to the anteroposterior ridge the pterygoid is deep.

The contact of the pterygoid with the basipterygoid process of the basisphenoid appears to be strong, mainly transversely projected as is suggested by the anterior border of the preserved basipterygoid process. The quadrate ramus of the pterygoid is not preserved. The interpterygoid vacuities, although incompletely preserved are well defined by the left pterygoid and its anterior contact with the vomer.

The morphology and position of the pterygoid suggests a well developed separation between each pterygoid forming the interpterygoid vacuities. The latter were axially elongate and possibly transversely narrow. Anteriorly, these vacuities were probably bordered by the pterygoid and the vomer, although no clear sutures are seen here. The vacuities, laterally bordered by the strong pterygoids, are posteriorly bordered by the basisphenoid-parasphenoid complex. The axial separation between the vacuities is not preserved. Possibly an anterior projection of the parasphenoid was developed there, as is seen in the *Brasilitherium* skull UFRGS PV0929T (Figure 11).

The anterior border of the vacuities are situated behind the posterior border of the pterygoid wings, while in *Pachygenelus* the anterior border lies between the pterygoid wings according to an unpublished reconstruction by Hopson (pers. com). Also in *Kayentatherium* (Sues, 1986) the vacuities are in a more anterior position than in *Brasilodon*.

Basicranium. The basicranium is incompletely preserved. Only the left half of the basioccipital, the anterior portion of the basisphenoid, both exoccipitals, and the left prootic and opisthotic are preserved (Figure 1).

A fragment of the basisphenoid is preserved which makes contact transversally with the pterygoid. On the ventral surface there is an axial rounded process, followed posteriorly by an axial low crest and laterally by smooth longitudinal, paired depressions. The small carotid foramen is present on the preserved right side of the basisphenoid, in the specimen UFRGS PV0628T (Figures 1-2).

The basioccipital shows a rather flat ventral surface. Sutures with the surrounding bones are not clear.

The exoccipital forms the posterior edge of the jugular fossa (Kielan-Jaworowska *et al.*, 1986), and the contact with the opisthotic is clear. The exoccipital bears two hypoglossal foramina for the nerve XII, these are situated close to one another and separated from the jugular foramen (Figure 7).
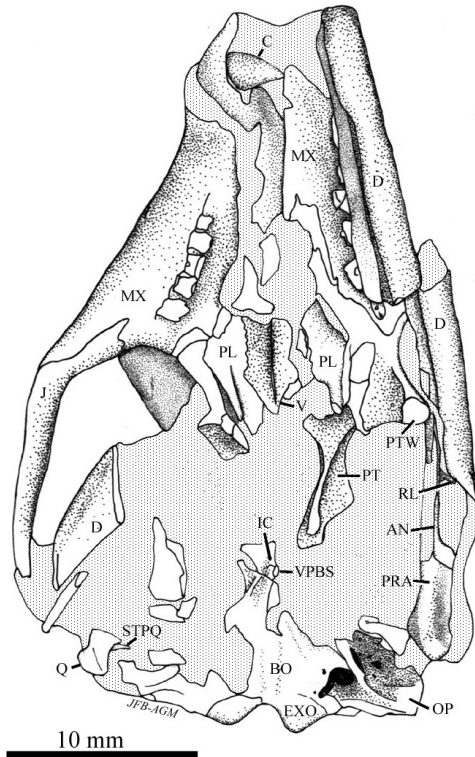
Figure 1. *Brasilodon quadrangularis.* UFRGS PV0628T, skull and articulated left lower jaw in ventral view. **Abbreviations: AN,** angular; **BO,** basioccipital; **C,** upper canine; **D,** dentary; **EXO,** exoccipital; **IC,** internal carotid foramen; **J,** jugal; **MX,** maxilla; **OP,** opisthotic; **PL,** palatine; **PRA,** prearticular; **PT,** pterygoid; **PTW,** pterygoid wing; **Q,** quadrate; **RL,** reflected lamina of the angular; **STPQ,** stapedial process of the quadrate; **V,** vomer; **VPBS,** ventral process of the basisphenoid.

One of them is located medioventrally inside the jugular fossa, and the other is anterolateral to the condyle and outside the fossa. The exoccipital condyles are rather small, ventrally convex and with a posteromedial projection. Their longest axis is posteromedially directed. A deep anterior notch separates both condyles indicating that a good portion of the basioccipital may lie between them. The opisthotic is not fused to the prootic; this is a primitive character. The jugular foramen and the perilymphatic foramen are located in the jugular fossa cited by Kielan-Jaworowska *et al.* (1986). They are confluent, only partially separated by an acute process from the posterior wall of the jugular fossa (Figure 7), not very different to the condition present in *Probainognathus* (Rougier *et al.*, 1992, fig. 7B), representing another primitive feature of *Brasilodon*. The jugular foramen is much smaller than the perilymphatic foramen and its posteromedial edge is formed by the exoccipital. The latter foramen appears to be entirely bordered by the prootic. On the jugular fossa, medial to the perilymphatic foramen there is another small opening, possibly a vascular foramen.

The crista interfenestralis is prominent and narrow, and continues posterolaterally on the ventral side of the opisthotic. Anterolateral to this crest and medial to the pterygoparoccipital foramen there is a large and deep depression, here called the "stapedial recess", bearing several foramina and a complex morphology (Figure 7).

The fenestra vestibuli is large and faces lateroanteriorly. It is located near a transversal line through the pterygoparoccipital foramen, but lies more distant to it than in *Morganucodon* and tritylodontids (Luo, 1994, fig. 6.3). The promontorium is only represented by the mid-posterior fragment of the left prootic in
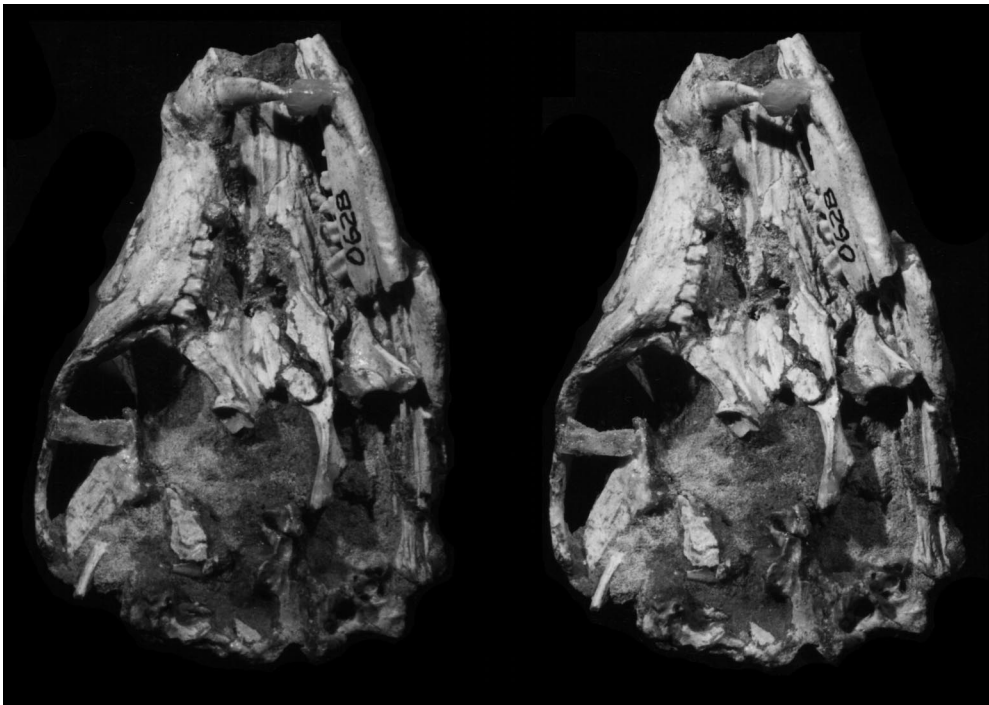

Figure 2. *Brasilodon quadrangularis.* UFRGS PV0628T, stereophotograph of the skull and left lower jaw in ventral view.

UFRGS PV0628T. An incipient structure of it was previously recognized in the holotype of *Brasilodon* (Bonaparte *et al.*, 2003).

The prootic is incompletely preserved and lacks part of the area of the cavum epiptericum and the anterior lamina. The preserved region is posterior to the cavum, and forming part of its floor, which is perforated by four foramina (Figure 7). The anteriormost opening is here interpreted as the facial foramen (nerve VII; Rougier *et al.*, 1992). A relatively large foramen that opens laterally to the fenestra vestibuli may corresponds to the tympanic opening for the prootic sinus vein (Rougier *et al.*, 1992). Anterior to the pterygoparoccipital foramen, on a slightly displaced fragment of the lateral flange of the prootic there is a small opening which possibly correspond to a vascular foramen. Medially to the pterygoparoccipital foramen there is another large foramen not identified. The area of the "stapedial recess" has more numerous foramina than in *Probainognathus*, *Brasilitherium* (Figure 15), *Pachygenelus* (Wible & Hopson, 1993, fig.5.2.A), and *Morganucodon* (Wible & Hopson, 1995, figs. 9A, 6A).

The pterygoparoccipital foramen is incomplete, bordered by the prootic. In the holotype the lateral edge of the foramen is partially closed (Bonaparte *et al.*, 2003) because the anterior and posterior projections of the prootic are displaced, superimposed on one another, due to postmorten deformation. The anterior and posterior paroccipital processes of the opisthotic are rather well defined; the former is larger than the latter resembling that of *Pachygenelus* and *Probainognathus* (Rougier *et al.*, 1992, fig.7B). The opisthotic-squamosal contact is not clear.

The quadrate is preserved on the right side (Figures 1-2). Its morphology is basically similar to that of *Morganucodon* but more derived than in *Pachygenelus* (Luo, 1994; Luo & Crompton, 1994), because of the pronounced stapedial process. **The upper dentition** (Figures 1, 2, 8).Upper incisors of *B. quadrangularis* are not available. Both canines in specimen UFRGS PV0628T are large, transversely flat with a dorsoventrally smooth sulcus on the anterolateral surface, without serrations. Their morphology and size suggest that *Brasilodon* was a predator. The canines are proportionally larger than in *Brasilitherium*. The upper postcanines (beautifully preserved) of the type specimen correspond to a subadult individual. They were described in detail in Bonaparte *et al.* (2003). Here we describe only those preserved in PV0628T because they provide significant information on the tooth replacement of *Brasilodon*.

In the right maxilla of the cited specimen the preserved postcanines are seven plus the alveolus of PC2. PC1 is quite small, medially displaced, with a rather flat worn surface showing a granulose pattern. PC2 is represented only by the alveolus. PC3 is badly preserved with no morphological information, except that the tooth is high. PC4 is badly preserved showing only the upper portion of the crown and root. The root shows an incipient bifurcation. PC5 has the central worn cusp but cusps B and C, and those of the buccal
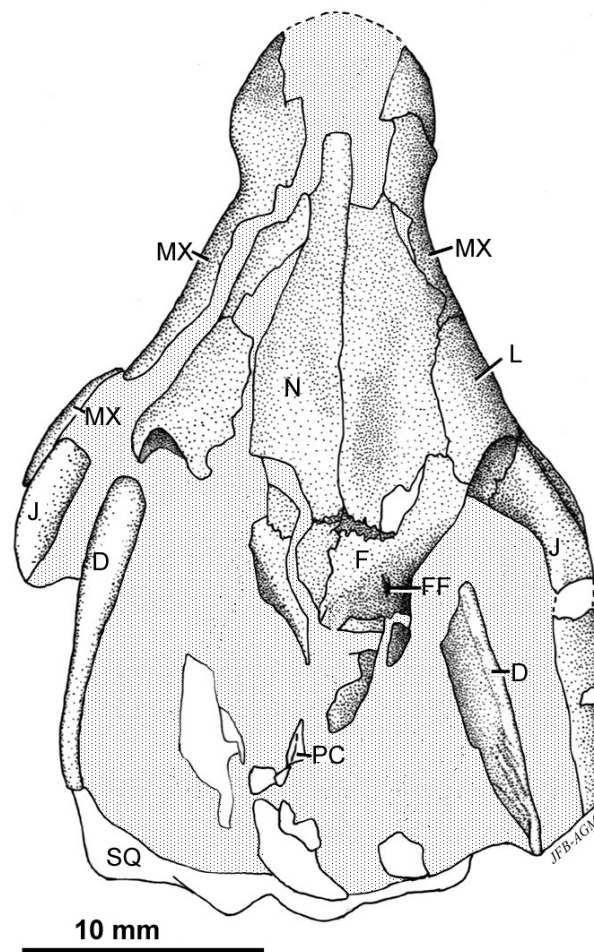

Figure 3. *Brasilodon quadrangularis*. UFRGS PV0628T, skull in dorsal view and part of coronoid process of both dentaries. **Abbreviations: D,** dentary; **F,** frontal; **FF,** foramen frontal; **J,** jugal; **L,** lacrimal; **MX,** maxilla; **N,** nasal; **PC,** parietal crest; **SQ,** squamosal.

cingulum are preserved. PC6 is strongly worn affecting the cusps A, B, C, and the anterior buccal one. This tooth shows a more pronounced wear, and it is mesiodistally the longest postcanine. PC7 is less worn than the previous one; cusps B and C are medially displaced and worn as well as the buccal accessory cusp. The posterior buccal cusp is in a lower position than the anterior one. PC8 is almost unworn, recently erupted. It shows two large and imprecise wear facets on the internal surface of the crown. No wear is present on the tip of the main cusp neither or on the remaining cusps.

On the left maxilla there is evidence for eight postcanines. PC1 and 2 are represented by broken roots in the alveoli. PC3 shows no apical wear and suggests it had recently erupted. Cusp A is almost complete with some dorsoventral wear on its medial side. This cusp represents almost the whole crown, and cusps B and C are quite small. The tooth has incipient bifurcation in the root. PC4 is broken. PC5 is strongly worn
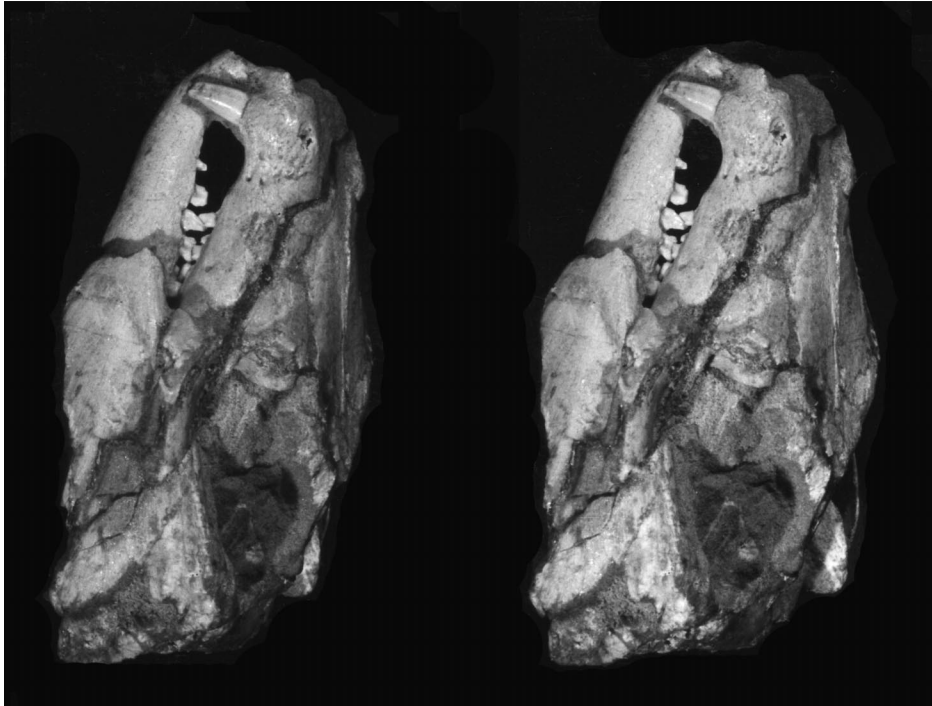
Figure 4. *Brasilodon quadrangularis*. UFRGS PV0628T, stereophotograph of the skull and lower jaw in lateral view.

but cusps B, C, and the buccal cingular cuspules are still present. Cusp B is anteromedially placed to the cusp A, and the posterior buccal accessory cusp is lower than the anterior one. PC6 is strongly worn and the buccal accessory cusps are affected by wear. PC7 has the plane of wear posteroventrally inclined, affecting cusps A and B. Cusp C is unworn as well as the cingular buccal cusps. PC8 is recently erupted as is its partner on the right tooth row. It has some lingual wear but cusps A, B, C, and the buccal ones appear to be complete.

There is not much difference of these upper postcanines with those described for the holotype of *Brasilodon quadrangularis* (Bonaparte *et al.*, 2003), except in their strong wear and the information they provide for tooth replacement. The inference from the specimen UFRGS PV0716T that the tooth replacement stopped in the adult stage (Bonaparte *et al.*, 2003) is only partially confirmed here. In the adult specimen described above (UFRGS PV0628T) most of the postcanines are strongly worn in a differential degree. However, the PC3 and PC8 are recently erupted, showing little wear. On the lower jaws the pc4 is almost unworn and the pc8 is just erupting. Both upper and lower unworn postcanines erupted after a significant time during which precedent postcanines were worn. The differential strong wear in upper postcanines 5 through 7 may be due to different times of eruption.

Lower jaw (Figures 4, 9, 10). In specimen UFRGS PV0628T the incomplete lower jaws were articulated to the skull. They have the horizontal ramus dorsoventrally low and laterally convex. In the symphysial area they are dorsoanteriorly directed as in *Prozostrodon* (Bonaparte and Barberena, 2001) and *Brasilitherium* (Bonaparte *et al.*, 2003). The symphysial

area is weaker than in the anterior portion of the horizontal ramus. The coronoid process is rather wide, with a well defined masseteric fossa extending on the horizontal ramus towards the level of the penultimate postcanine. The anterodorsal border is thick, with a lateral projection. The articular process appears to surpass posteriorly the articular area of the postdentary bones. It is transversely wide; however, there are no clear indications of a real condyle present.

The Meckelian groove does not reach the lower border of the dentary. In the anterior portion of the groove, near the symphysis, there is an expansion, possibly for an indeterminate ganglion. The Meckelian groove continues anteriorly above the plane of the symphysis except in the more anterior portion. The symphysis is unfused, with a rough surface for ligaments.

Lower dentition (Figures 4, 8, 9, 10). Incomplete lower dentitions are preserved in specimens UFRGS PV0628T and UFRGS PV0765T. Only one incisor is preserved in the left dentary of specimen UFRGS PV0628T. It is probably i3. It is small, transversely flat, and dorsally directed. The number of lower incisors is three (Figure 10). There is no diastema between the incisors and canine.

The canine is transversely narrow and of considerable size. The number of lower postcanines is seven or eight in both dentaries of UFRGS PV0628T, and six or seven in UFRGS PV0765T. In the former only five postcanines are rather complete, preserved on the left dentary and only two postcanines on the right one. On the left tooth row pc1 preserves only the broken crown and is separated from the canine by a long diastema. The pc2 is fragmentary. In pc3 the main cusp is worn and cusps b and c are slightly

developed. Lingual cingular cusps are well defined on the anterior and posterior borders. The pc4 is recently erupted with the main cusp almost complete, as well as the small cusps b and c, and the well pronounced anterior and posterior lingual cingular cusps. The pc5 shows strong wear up to near the lingual cingular cusps. The pc6 is even more worn than the previous one, bearing a posterolingual cingulum with three cuspules. The pc7 only preserves its alveolus. Incipient bifurcation of the root is seen in pc3 through pc6.

On the right tooth row, pc1 only preserves the root and pc2 is strongly worn with the occlusal plane anteriorly inclined. Pc3 to 7 are broken at the alveolar level. The pc8 is in the process of eruption, showing that cusp a is strongly developed and slightly posteriorly directed. Cusp b is possibly not developed, and cusp c is small. The root shows incipient bifurcation.

In UFRGS PV0765T only incomplete lower dentition is preserved in both jaws. In the left lower jaw pc1 is broken at the alveolar level. The pc2 through 7 are in different stages of replacement.

The pc3 is just erupting, and pc5 is in a more advanced eruption. In all the postcanines the remarkable character is the big proportional size of the central cusp a, and the small buccal cusps b and c, both strongly affected by wear. Cusps b and c are much smaller than a and symmetrically distributed on a mesodistal plane. In the two erupting postcanines cusp a (without wear) is very large and prominent.

In the pc4 and pc6 there is a small cusp posteriorly adhered to cusp a. The lingual accessory cusps, present on the anterior and posterior section of the lingual side of the postcanines are well defined. Two of them are in the anterolingual side, and one on the posterior lingual side, separated by a small lingual depression.

Postcanine replacement and tooth morphology

The holotype skull of *B. quadrangularis* shows a homogeneous sequence of postcanines (Bonaparte *et al.*, 2003), without evident wear. It suggests that the individual was subadult, and that the tooth replacement had not yet started. The referred maxilla (Bonaparte *et al.*, 2003, fig. 8C) with all the five preserved postcanines heavily worn suggests that the postcanine replacement stopped in the adult
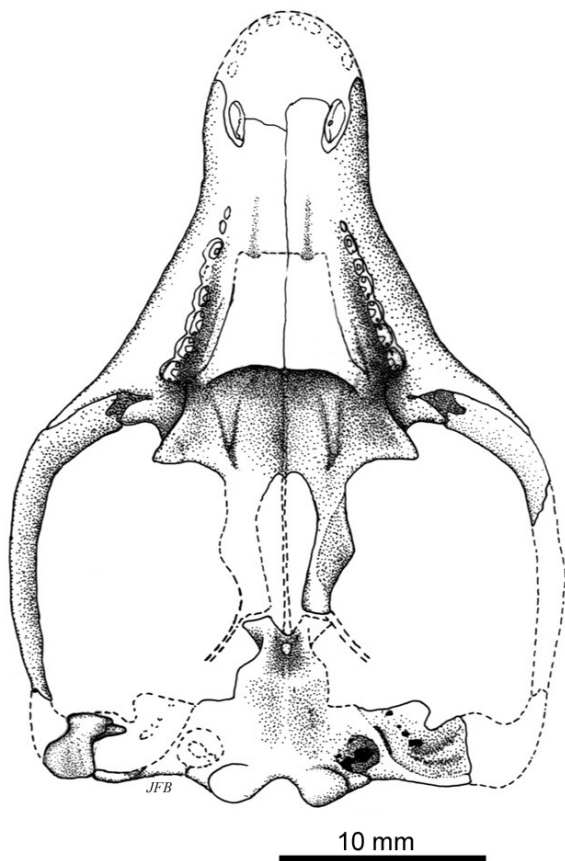

Figure 5. Reconstruction in ventral view of the skull of *Brasilodon quadrangularis* based mainly on UFRGS PV0628T.
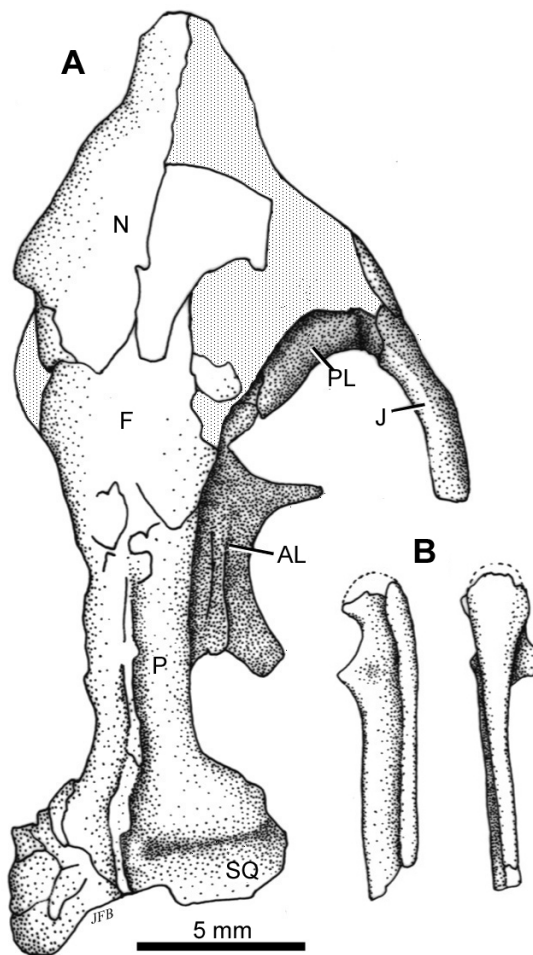

Figure 6. *Brasilodon quadrangularis*. UFRGS PV0765T, A, skull in dorsal view, and B, ulna in posterior and lateral views. **Abbreviations: AL,** alisphenoid; **F,** frontal; **J,** jugal; **N,** nasal; **P,** parietal; **PL,** palatine; **SQ,** squamosal.
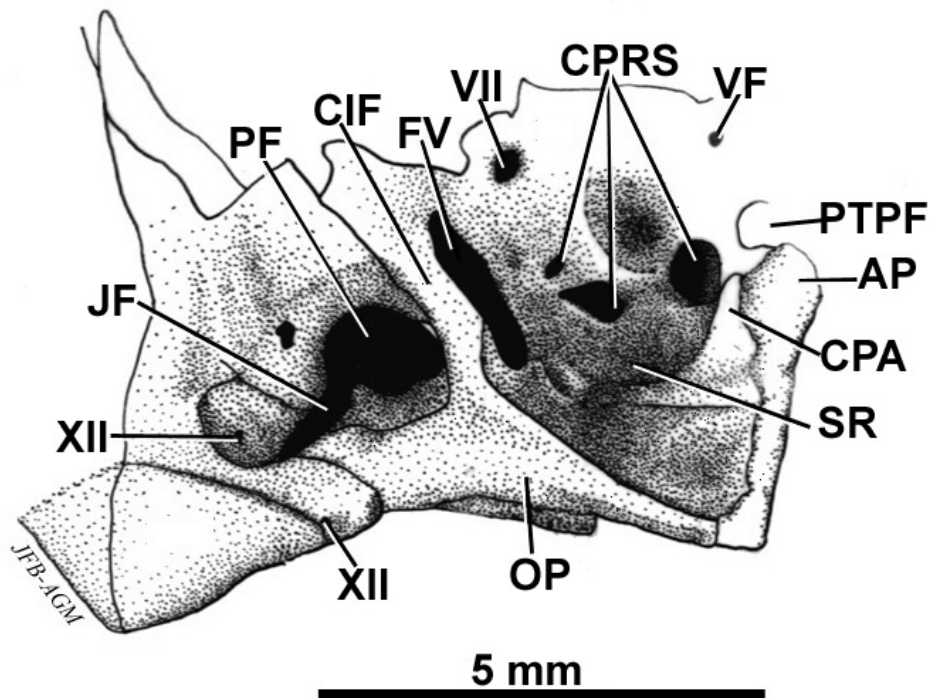
Figure 7. *Brasilodon quadrangularis*. UFRGS PV0628T**,** detail of the left basicranial region in ventral view. **Abbreviations: AP,** anterior process of the opisthotic **CIF,** interfenestralis crest; **CPA,** crista parotica; **CPRS,** canal prootic sinus vein; **EXO,** exoccipital; **PF,** perilymphatic foramen; **FV,** fenestra vestibuli; **JF,** jugular foramen; **OP,** opisthotic; **PR,** prootic; **PTPF,** pterygoparoccipital foramen; **"SR",** "stapedial recess"; **VF,** vascular foramen; **VII,** foramen for the secondary exit of the facial nerve; **XII,** hypoglossal foramen.

individuals of *B. quadrangularis*. But, the new specimens described here, which appear to be adult individuals, show that the replacement did not stop. A delayed and limited replacement of some upper and lower postcanines occurred in *B. quadrangularis*. The lower jaws of UFRGS PV0765T show a more active replacement.

There is poor evidence in *B. quadrangularis* of fusing tissues between alveoli and the teeth, except on both sides of PC6 (UFRGS PV0628T). Most of the teeth are separated from the wall of the alveoli suggesting the presence of some thickness of ligaments permitting some mobility of each tooth to perform an adjusted occlusion (Crompton, 1972; Rowe, 1993).

Upper and lower postcanines of *B. quadrangularis* show several derived characters discussed above. In *Morganucodon* (Kermack *et al.*, 1981) the basic morphology of the lower dentition is not very different from that of *Thrinaxodon* (Osborn & Crompton, 1973), with the main cusp present on the anterior half of the crown. In *Brasilodon* the morphology of the upper and lower postcanines is different from and morphologically more derived than in *Morganucodon*. Their morphology suggests some kind of affinities or parallel development with the "symmetrodont type" of tooth present in *Kuehneotherium* (Kermack *et al.*, 1968) at least in the incipient triangulation of the cusps and the similarities of the lower postcanines:
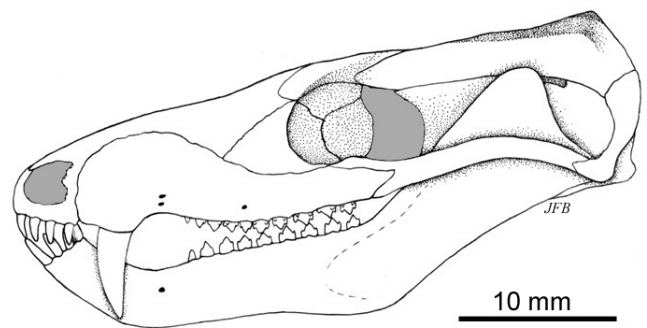

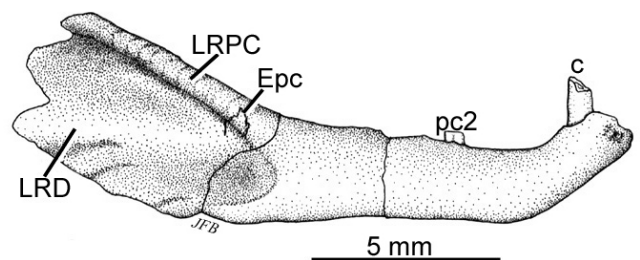**Figure 8.** Reconstruction in lateral view of the skull and lower jaw of *Brasilodon quadrangularis*.

Figure 9. *Brasilodon quadrangularis*. UFRGS PV0628T, right lower jaw in lateral view. **Abbreviations: c,** lower canine; **EPC,** erupting postcanine; **LRCP,** lateral relief of the coronoid process; **LRD,** lateral ridge of the dentary; **pc2,** lower second postcanine.
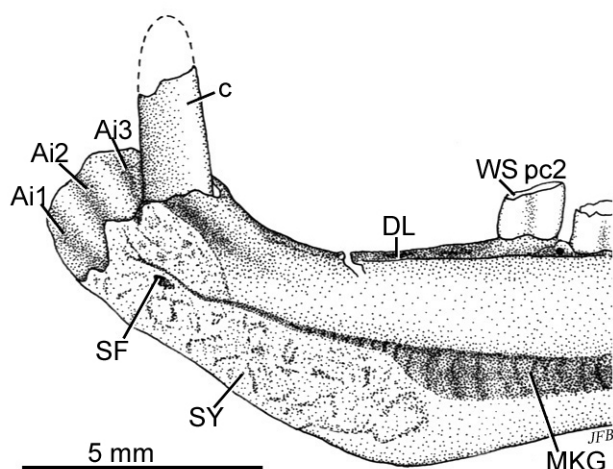
Figure 10. *Brasilodon quadrangularis.* UFRGS PV0628T, anterior portion of the right lower jaw in medial view. **Abbreviations: Ai1, Ai2, Ai3,** alveolus for first**,** second and third incisors; **c,** lower canine; **DL,** groove for the dental lamina; **MKG,** meckelian groove; **pc2,** lower second postcanine; **SF,** symphysial foramen; **SY,** symphysis; **WS,** worn surface.

1. Usually the main cusps (A and a) of the *Brasilodon* upper and lower postcanines are located in the center of the mesio-distal plane, and they are much larger than cusps B, b and C, c. In the *Kuehneotherium* molariforms (Kermack *et al.*, 1968) the position and proportions of the main cusp are basically of this kind.
2. Cusps B, b and C, c in the postcanines of *Brasilodon* are of similar size.
3. In *Kuehneotherium* the main cusp of the upper molariforms is widely exposed on the lingual side, different from *Brasilodon*, while the lower molariformes the main cusp occupies a large proportion of the buccal side. So, in *Brasilodon* there are no reversed triangles on the upper and lower postcanines.
4. The lingual side of the upper and lower postcanines of *Brasilodon* is concave, while in *Kuehneotherium* the buccal side of the uppers and the lingual side of the lowers is concave.
5. The mesial and distal borders of the upper and lower postcanines of *Brasilodon* are rather wide with a buccal and a lingual cusp. In *Kuehneotherium* only the mesial border of the upper and lower molariforms is rather wide, bearing a buccal and a lingual cuspule.
6. A very large angle is present in some upper and lower postcanines of *Brasilodon*, (UFRGS PV0628T) formed by cusps A,a, B,b, and C,c. In the upper and lower molariforms of *Kuehneotherium* the angle is more pronounced.
7. A talonid-like structure is present in some lower postcanines of *Brasilodon* (left and right postcanines in specimen UFRGS PV0765T). A similar character was

recognized by Kermack *et al.* (1968) in lower molariforms of *Kuehneotherium* (*i.e.* M 19155).
8. In the upper postcanines of *Brasilodon* there is a small buccal cingulum with a cusp, and in the lower postcanines there is a lingual cingulum with one or more cusps. In *Kuehneotherium* the cingulum of the upper and lower molariforms is on the lingual side (Kermack *et al.*, 1968, figs.1, 3).

Brasilodon and *Kuehneotherium* show a common basic plan in the postcanines with small differences which may be the result of phylogenetic relationships or parallel evolution. The unique morphology of the postcanines of *Brasilodon*, and the unusually type of tooth replacement allows us to propose *Brasilodon* as the type genus of a new family of probainognathian cynodonts: Brasilodontidae nov.

Brasilitherium riograndensis Bonaparte, Martinelli, Schultz & Rubert, 2003

Emended diagnosis. Small brasilodontid cynodont with the following combination of features: Upper postcanines with a large central cusp, a small anterior and a small posterior cusp arranged in line on the lingual side as in *Brasilodon*. Lower postcanines different from those of *Brasilodon*, with the main cusp a on the mesial half of the crown, followed by cusps c and d on the distal half. Incipient embrasure between posterior lower postcanines, absent in *Brasilodon* and similar to *Megazostrodon*. Perilymphatic and jugular foramina separated, different from *Brasilodon* in which they are partially confluent; more developed promontorium than in *Brasilodon* but less inflated than in *Morganucodon*. The prootic and opisthotic fused. The premaxilla is far forward from the anterior border of dentary. Numerous incisiforms on the anterior portion of the snout; and small upper postcanines. Central portion of the pterygoid with a medially and ventrally projected process; rostrum of the parasphenoid transversely laminar and dorsoventrally high. The frontal fused to neighboring bones. Pronounced lateral ridge and medial ridge of the postdentary trough of the lower jaw; the articular process of dentary with incipient condyle reaching a more posterior position than the surangular and almost touching the squamosal just above the quadrate. Small ventral lamina of the angular between articular and the stem of the surangular. Skull length of about 27 mm.

Description

The original description (Bonaparte *et al.*, 2003) is based on an incomplete skull and jaws of the type specimen and on some fragmentary specimens providing some information on the upper and lower postcanines, but with meager information on several important regions of the skull. Here we provide further anatomical information on the skull and dentition, based on recently collected specimens: UFRGS PV0760T, an incomplete skull with articulated lower jaws, incomplete
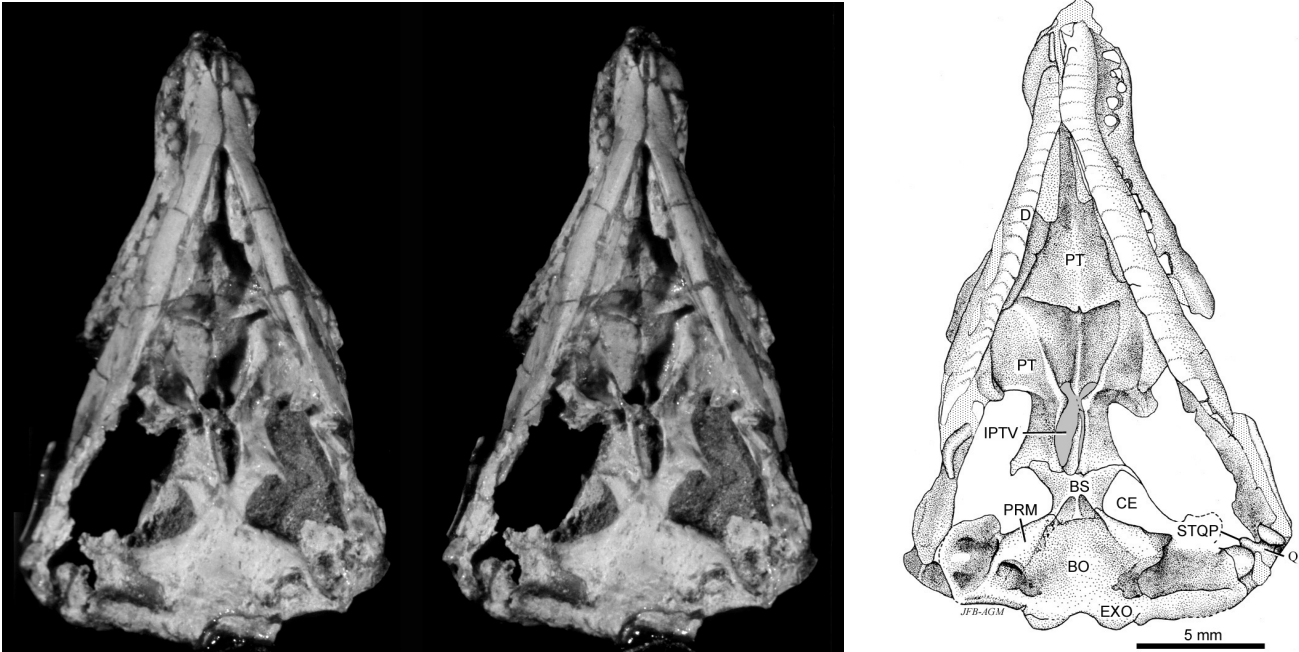
Figure 11. *Brasilitherium riograndensis*. UFRGS PV0929T**,** stereophotograph of the skull and lower jaws in ventral view**,** and drawing of the same. **Abbreviations: BO,** basioccipital; **BS,** basisphenoid; **CE,** cavum epiptericum; **D,** dentary; **EXO,** exoccipital; **IPTV,** interpterygoid vacuity; **PL,** palatine; **PRM,** promontorium; **PT,** pterygoid; **Q,** quadrate; **STPQ,** stapedial process of the quadrate.

pectoral girdle and humerus; UFRGS PV0804T, an incomplete skull with a fragment of right lower jaw (Figures 14, 15 and 16); and UFRGS PV0929T, an incomplete skull articulated with the lower jaws, and some postcranial remains (Figures 11, 12, 13 and 17).

Maxilla. The lateral view of the maxilla shows the highest dorsal point at the maximum constriction of the snout, and from there an evenly declining upper border directed backwards, which is longer than the anterior border reaching the premaxilla. The long maxilla makes the muzzle longer than in *Brasilodon, Pachygenelus* (Hopson, pers. com.), *Morganucodon* (Kermack *et al.*, 1981), and *Sinoconodon* (Crompton & Sun, 1985; Luo, 1994). The posterior, ventral portion of the maxilla covers laterally and ventrally the jugal, forming a step between the zygomatic portion and the alveolar area. The anterior area of the maxilla has a rather high and vertical contact with the premaxilla. One maxillary foramen is present near the lacrimal, and two or three in the area of maximum constriction, showing variation in the number and position of them in different specimens. The right septomaxilla, with dubious borders, is present in UFRGS PV0929T.

The maxilla participates extensively in the osseous secondary palate. Its contacts with the premaxilla is not clear on the available specimens. The posterior area of the maxilla has a deep furrow medially to the last five postcanines to accommodate the lower postcanines.

Palatine. Palatines are well preserved (UFRGS PV0929T). They extend backwards past the level of the last postcanine (Figure 11). The palatine-maxilla contact is not clearly observed. The orbital projection of the palatine is large, contacting the lacrimal anterolaterally and dorsally; there is a dubious contact with the frontal. Posterior to the palatine orbital process, there is an ossification that may correspond to the orbitosphenoid.

Lacrimal. The lacrimal is triangular in lateral view, large as in *Morganucodon* with a pronounced anterior projection between nasal and maxilla (Figures 12 and 13). The dorsoposterior area of the lacrimal appears to be closely attached to the frontal or possibly fused to it. The posterior border forms the anterior concavity of the orbit, showing a superficial canal extending out from the orbit, directed anterodorsally. A single lacrimal foramen is present, surrounded by a large depression. The lateral exposure of the lacrimal within the orbit is more reduced than in *Morganucodon* (Kermack *et al.*, 1981) because in *Brasilitherium* it is partially covered by the long orbital process of the frontal. In *Pachygenelus*, according to the unpublished reconstruction (Hopson pers. com.) the lacrimal resembles that of *Brasilitherium*.

Frontal. The frontals appear to be fused with the dorsoposterior area of the lacrimals and with the nasals. In specimen UFRGS PV0760T the suture between frontals is strongly ossified. These have a rather large foramen on the dorsolateral surface, near the medial border of the orbit and anteriorly directed. Possibly these foramina are related with a branch of the opththalmic nerve (V1) or artery as is present
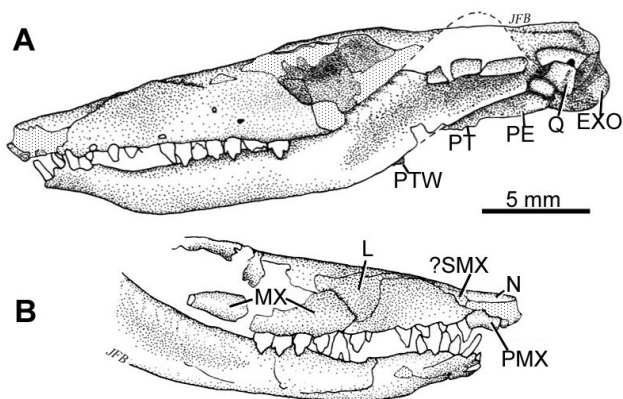
Figure 12. *Brasilitherium riograndensis*. UFRGS PV0929T, **A,** skull and lower jaw in left lateral view; and **B,** rostrum in right lateral view. **Abbreviations: EXO,** exoccipital; **L,** lacrimal; **MX,** maxilla; **N,** nasal; **PMX,** premaxilla; **PE,** petrosal; **PT,** pterygoid; **PTW,** pterygoid wing; **Q,** quadrate; **?SMX,** ?septomaxilla.

in some modern mammals. The orbital projection of the frontal is rather large, contacting the lacrimal and the orbital process of the palatine (Figure 14).

Interorbital wall. This area, although not perfectly preserved, preserves the ethmoidal and sphenopalatine foramina (UFRGS PV0804T). The ethmoidal foramen is anteriorly and dorsally bordered by the ventral projection of the frontal. Possibly the orbitosphenoid participates in the ventral delimitation of it. The relative position of this foramen is more posterior than in *Morganucodon* (Kermack *et al.*, 1981) perhaps because of a more posterior ossification of the interorbital wall in *Brasilitherium*.

The sphenopalatine foramen is longer dorsoventrally than transversely and it is open posteriorly. Its medial side is bordered by the palatine which here is medially twisted, unfortunately incomplete ventroposteriorly. The lateral side of the foramen is bordered, eventually, by part of the medial

projection of the lacrimal. Sutures are not seen here. The unossified area behind the orbitosphenoid is large (Figure 14), showing a considerable distance to the anterior border of the alisphenoid, larger than in *Morganucodon* (Kermack *et al.*, 1981, fig. 99), and very different to the closed area in *Kayentatherium* and *Sinoconodon* (Sues, 1986; Luo, 1994). *Brasilitherium* is primitive in this character.

Basicranium. The main feature of this area is the presence of fused prootic and opisthotic, forming the petrosal that bears a well defined promontorium. The promontorium is developed to the similar extent as the promontorium of *Adelobasileus* (Lucas and Luo, 1993; Luo *et al.*, 1995) although it is less developed than in *Sinoconodon*, *Morganucodon*, *Haldanodon*, and *Hadrocodium* (*e.g.* Luo *et al.*, 2001). It is elongate and slightly convex transversely (Figures 11, 15). On the ventral face of the promontorium there is a rounded crest anteromedially projected along its longest axis (UFRGS PV0804T). On the lateroposterior surface of the promontorium, the fenestra vestibuli opens with a ventral rounded border. Anterolaterally to this fenestra there is a foramen that we interpret as the facial foramen (nerve VII; Rougier *et al.*, 1992). The morphology and position of the lateral flange of the petrosal and the foramen is very similar to the condition in *Probainognathus* (Rougier *et al.*, 1992, fig. 7B). The lateral flange of the petrosal is less developed than in *Adelobasileus* (Lucas & Luo, 1993) and *Morganucodon* (Kermack *et al.*, 1981), but more than in *Pachygenelus* (Hopson, pers. com.), and *Yunnanodon* (Luo, 2001). The anterior paroccipital process of the petrosal is bulbous and larger than the posterior one which is only a weak posterolateral projection.

The incomplete pterygoparoccipital foramen is bordered by the petrosal, and seems to be open, but the lateral and posterior projections are broken.

The cavum epentericum is large, with a medial expansion bordered anteriorly by the basipterygoid process of the basisphenoid and posteriorly by the lateral projection of the petrosal occupied by the promontorium. Laterally the cavum

Figure 13. *Brasilitherium riograndensis*. UFRGS PV0929T, photograph of the skull and lower jaw in left lateral view.

is bordered by the alisphenoid and the quadrate ramus of the pterygoid, which does not reach the quadrate area, and appears to be fused to the inner side of the alisphenoid. The lateral flange of the petrosal borders the posterior area of the cavum (Figure 15). The large size of the cavum epiptericum, suggests a primitive character.

The perilymphatic and jugular foramina are well separated by an osseous process (Figure 15), different from *Brasilodon* in which they are incompletely divided (Figure 7). The suture of the exoccipital with the petrosal is very clear. There are two hypoglossal foramina (nerve XII) separated from the jugular foramen, and located within the jugular fossa. The occipital condyles are rather small and oval, with an anteriorly deep indentation between them, accommodating for the odontoid process of the axis. The convexity of the condyles is ventrally, posteriorly and laterally exposed.

On the lateral side of the braincase, a suture is clearly seen between the anterior lamina of the prootic and the alisphenoid (Figure 16). This is different from the *Morganucodon*'s condition (Kermack *et al.*, 1981) in which these bones are not in contact.

The alisphenoid is large, superimposed over the parietal by a long anteroposterior contact (Figure 14). Its anterior border is not clearly defined in specimen UFRGS PV0804T. In specimen UFRGS PV0929T the anterior border is dorsoventrally concave, with a pronounced anterodorsal projection, similar to *Morganucodon* (Kermack *et al.*, 1981) and *Sinoconodon* (Luo, 1994). The ventral area of the alisphenoid borders the cavum, and the quadrate ramus of the pterygoid is medially attached or fused to it in specimen UFRGS PV0804T.

The large foramen for the trigeminal nerve opens entirely on the anterior lamina on the right side of the braincase (Figure 14), but on the left side (Figure 16) lies at the union between the anterior lamina and the alisphenoid illustrating a variable position for this character. Two small foramina, well defined on the left side, are located above and behind it, possibly for the rami of the V nerve. A crest on the lateral lamina runs mediodorsally from the anterior border of the pterygoparoccipital foramen. The ascending groove for the "proximal stapedial artery" (Rougier *et al.*, 1992) begins at the medial edge of the pterygoparoccipital foramen (in the left side of UFRGS PV0804T). Dorsally it is covered by the petrosal and the squamosal. In the upper section of this groove, before the dorsal closure, the posttemporal foramen of the arteria diploetica magna is present (*vide* Rougier *et al.*, 1992). Anterior to the dorsal closure of the groove there is a foramen, not present in *Morganucodon*, which may correspond to the ramus temporalis of the cited artery.

The zygomatic portion of the squamosal is quite small, with only a very short and weak anterior projection that contacts the long and weak jugal. A depression on the posterolateral corner of the squamosal, directed ventroanteriorly and following on the lateral side of the small quadratojugal

may correspond to the external auditory meatus. The medial process of the squamosal is anteroposteriorly short and transversely concave in dorsal view. It continues dorsally contributing to the braincase in a rather narrow but elongated area, more extended than in *Pachygenelus* (Hopson, pers. com.), and *Morganucodon* (Kermack *et al.*, 1981) forming the anterior side of the lambdoid crest.

Suspensory bones. Postdentary bones of *Brasilitherium* were described and figured for the type specimen (UFRGS PV0594T). The following additional information is reported from the specimens UFRGS PV0929T, showing the quadrate a little displaced from its original position; and from UFRGS PV0760T with both lower jaws articulated to the skull.

The thickening of the head of the articular process of the dentary is a precursor condition to the dentary condyle (UFRGS PV0760T). The right lower jaw shows the articular process of the dentary accommodated in an anterior concavity made by the dorsal process of the squamosal, or near the quadratojugal, attached to the anterior side of the squamosal and occupying a defined lateral position. Cracks on this area debar a more precise identification. The quadrate, exposed in posterior and ventral views is rather large. In short, the secondary articulation, if any, was between the squamosal (and possibly also the quadratojugal) and dentary, a feature not recorded in other cynodonts. In the left side of this specimen, the more lateral area of the squamosal and the quadratojugal are not preserved. The posterior section of the articular process of the dentary is preserved, extending posteriorly beyond the articular.

The left quadrate of specimen UFRGS PV0929T is almost complete (Figure 11). Its condyle for articulation with the articular is well defined, with a pronounced neck in most of its outline. It is very convex anteroposteriorly, forming almost a hemi-circumference. The stapedial process is well developed as in *Morganucodon* (Luo & Crompton, 1994). The expanded proximal area is not easy to interpret because is attached to the anterior paroccipital process and is partly covered by the squamosal. However, the overall morphology resembles very much that of *Morganucodon* (Luo & Crompton, 1994).

Primary palate and interpterygoid vacuities. The interpterygoid vacuities are well preserved in specimen UFRGS PV0929T, with some lateral displacement of the parasphenoid septum which intersect the vacuities all along their length (Figure 11). The size of the vacuities is rather small, representing only 1/8 of the skull length, different from the estimation of 1/6 for *Brasilodon*. The lateral side of the vacuities is made by the strongly developed pterygoids which posteriorly contact the basipterygoid process of the basisphenoid through a transverse and elongate suture. From this contact, the pterygoid continues forwards transversely wide, up to the base of the pterygoid wing. The lateral border is concave up to the end of the quadrate process which does not reach the quadrate. The medial border of the pterygoid bordering

the vacuity is in a lower position than the lateral one, and makes a ventral knob near the anterior border of the vacuities. This small ventral process projects ventrally and medially. From this process, here called "medio ventral process of pterygoid" a pronounced ridge is anteriorly formed which borders laterally a deep cavity medially separated by a low crest (Figures 11, 17). Such a ridge is present in *Probainognathus* (Romer, 1970) and in most of the Eucynodontia (Kemp, 1982). It continues forwards making a medial septum separating the two internal nasal openings as in *Brasilodon*. Sutures are not seen, but probably most of the anterior ridge is made by the pterygoids. Lateral to the anterior ridge the pronounced edges of the pterygoid wings form medially a concave surface. As interpreted by Barghusen (1986), this area of the primary palate was probably occupied by the nasopharyngeal organs and the Eustachian tubes.

Upper and lower dentition. The upper and lower postcanines of *Brasilitherium riograndensis* were described and figured by Bonaparte *et al.* (2003). The new available specimens do not afford additional information. We have no information on the upper incisors. We confirmed the alternated replacement of the postcanines in *Brasilitherium* and the replacement appears to be more frequent than in *Brasilodon*.

In specimen UFRGS PV0929T, the small upper canine can be recognized because of the diastema separating it from the PC1. Forward from the canine and on the maxilla there are 2 incisiforms and 1 alveolus, indicating the presence of three conical incisiform teeth plus the canine. The latter is slightly larger than the two more anterior teeth (Figures 12-13). Therefore, the total number of "incisors" is approximately 7, with 4 true incisors on the premaxilla and 3 incisiforms on the maxilla.
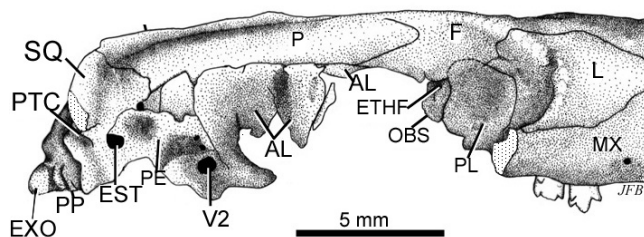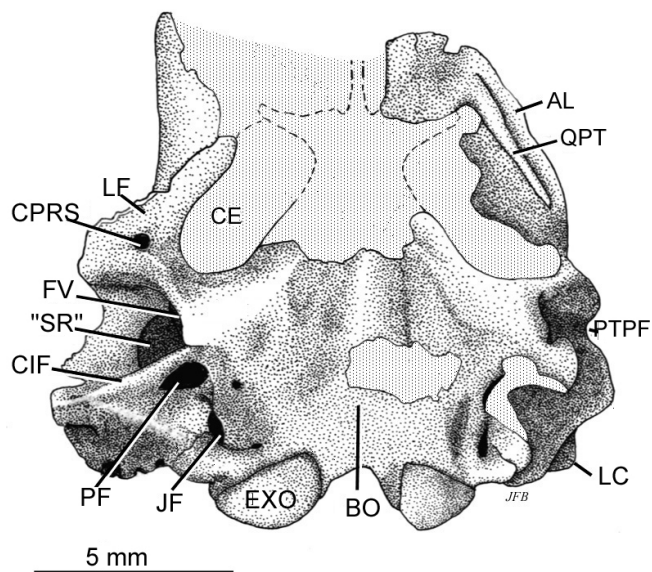

Figure 15. *Brasilitherium riograndensis*. UFRGS PV0804T**,** detail of basicranial area. **Abbreviations: AL,** alisphenoid; **BO,** basioccipital; **CE,** cavum epiptericum; **CIF,** interfenestralis crest; **CPRS,** canal pro- otic sinus vein; **EXO,** exoccipital; **FV,** fenestra vestibuli; **JF,** jugular fo- ramen; **LC,** lambdoid crest; **LF,** lateral flange; **PF,** perilymphatic fora- men; **PRM,** promontorium; **PTPF,** pterygoparoccipital foramen; **QPT,** quadrate process of the pterygoid; **"SR",** "stapedial recess".

Figure 14. *Brasilitherium riograndensis*. UFRGS PV0804T**,** detail of the posterior haft of the skull in lateral view. **Abbreviations: AL,** alisphenoid; **ETHF,** ethmoidal foramen; **EXO,** exoccipital; **F,** frontal; **FST,** foramen for the stapedial artery; **L,** lacrimal; **MX,** maxilla; **OBS,** orbitosphenoid; **P,** parietal; **PC,** parietal crest; **PL,** palatine; **PE,** petrosal; **PP,** posterior pro- cess of the petrosal; **PTC,** posttemporal canal; **SQ,** squamosal; **V2,** fora- men for the maxillary branch of the trigeminal nerve.
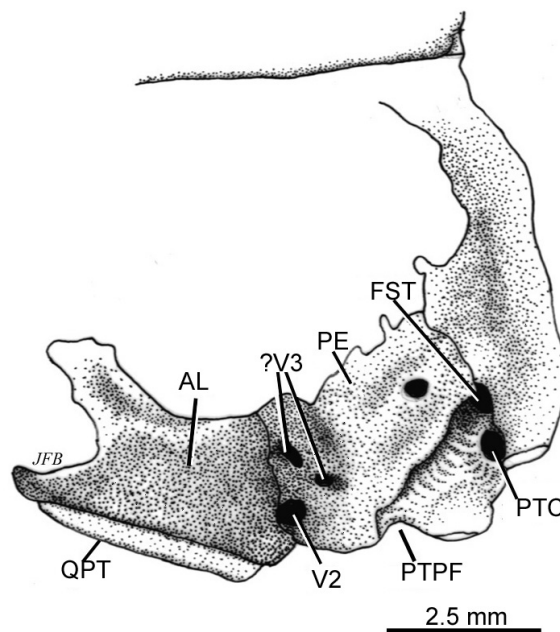

Figure 16. *Brasilitherium riograndensis*. UFRGS PV0804T**,** detail of lateral wall of the skull. **Abbreviations: AL,** alisphenoid; **FST,** fora- men for the stapedial artery; **PC,** parietal crest; **PE,** petrosal; **PTC,** posttemporal canal; **PTPF,** pterygoparoccipital foramen; **QPT,** qua- drate process of the pterygoid; **V2,** foramen for the maxillary branch of the trigeminal nerve; **?V3,** ?foramen for the mandibular branch of the trigeminal nerve.

DISCUSSION

From the new anatomical information provided by recently collected specimens of *Brasilodon* and *Brasilitherium* we have a better picture on the lower dentition of the former, and the tooth replacement, the interpterygoid vacuity, the craneo-mandibular articulation, and in the basicranial region, including the promontorium, "stapedial recess" and jugular fossa, in both genera.

The study of *Brasilodon* and *Brasilitherium* suggests that a significant radiation of advanced cynodonts with mammalian characters occurred, in species still retaining many primitive features. It is possible that the evolutionary situation we see in *Brasilodon* and *Brasilitherium* occurred in most of the species of probainognathians (Hopson & Kitching, 2001), known and unknown, providing us with a very diversified evolutionary picture of advanced cynodonts progressing towards the mammalian condition. Here it is important to admit that such radiation was not a limited process developed only in South America, but a very complex one which also developed on larger areas of Pangea, and probably radiated throughout all Pangea.

Tooth replacement. The few specimens available did not permit detailed comparison between the sequence of tooth replacement in *Brasilodon* and those fine observations made by Osborn & Crompton (1973). However, it is clear that postcanine replacement in *Brasilodon* was slow enough to permit an extremely strong wear in them, in some cases consuming more than half the height of the crown. The presence of some special abrading component in the diet is not confirmed by the postcanines of the synchronous *Brasilitherium*, supposedly living in the same environment as *Brasilodon* as both were found in the same beds. According to the tooth morphology both may have consumed a similar diet, but *Brasilitherium* possesed postcanines without notable wear suggesting an alternate replacement. Obviously the reason for such differences appears to be the different frequency of tooth replacement in each genus.

The evidence of delayed postcanine replacement in *Brasilodon* is a major difference from any probainognathian cynodont. Here it is interesting to note that the published postcanine dentitions of *Morganucodon* (Kermack *et al.*, 1973, 1981; Parrington, 1978; Mills, 1971; Crompton, 1974; Crompton, & Luo, 1993) show occlusal wear facets, but not so intensive wear as is present in *Brasilodon*. This condition gives room for estimating a non abrading diet in *Morganucodon* or eventually a not so delayed replacement as in *Brasilodon*.

The postcanine replacement in *Brasilodon* is here interpreted in evolutionary terms suggesting a condition nearer to the supposed diphyodonty of early mammals than to that recorded in other carnivorous cynodonts. In *Brasilitherium* the postcanine replacement is, in general terms, not very different to the condition seen in *Thrinaxodon* (Osborn & Crompton, 1973), although a detailed study of it may reveal a more complex derived condition.

Postcanine morphology. It seems evident that the morphology of the upper and lower postcanines of *Brasilodon* shows a partial convergence to the morphology of the *Kuehneotherium* molariforms with a voluminous main cusp in the center of the crown and a symmetrical distribution of the secondary cusps. At the same time it seems clear that they are morphologically more derived than those of *Morganucodon*. Not withstanding this fact, in *Brasilodon* the reversed triangle is not developed yet and neither are the precise wear facets. In addition, the continuous lingual and buccal cingula in the upper and lower molariforms (respectively) recorded in *Kuehneotherium* are not developed in *Brasilodon*. The morphological features discussed above of the *Brasilodon* postcanines, represent a related stage (not properly understood by now) to the molariforms of *Kuehneotherium*, possibly more significant than the poorly documented relationships of dental morphology between *Morganucodon* and *Kuehneotherium* currently accepted (Crompton, 1974).
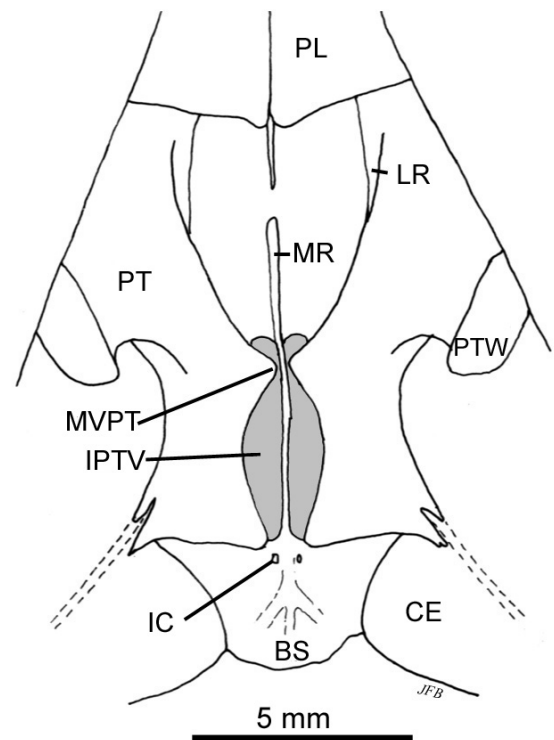

Figure 17. Reconstruction of the primary palate in *Brasilitherium rio-grandensis* based on UFRGS PV0929T. **Abbreviations: BS,** basisphenoid; **CE,** cavum epiptericum; **IC,** internal carotid foramen; **IPTV,** interpterygoid vacuity; **LR,** lateral ridge; **MR,** medial ridge of the pterygoid; **MVPT,** medial ventral process of pterygoid; **PL,** palatine; **PT,** pterygoid; **PTW,** pterygoid wing.
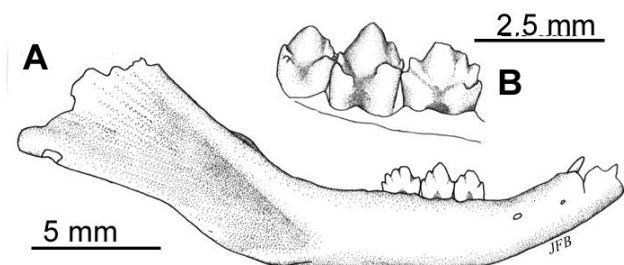
Figure 18. *Brasilitherium riograndensis*. A, right lower jaw in lateral view; and B, detail of postcanines in lingual view.

The presence of frequent replacements in *Brasilitherium* and of delayed replacements in *Brasilodon* along with a tooth morphology more derived than in *Morganucodon* suggest that tooth replacement and postcanine morphology had independent evolutionary trends. In addition, the large, imprecise wear facets in the postcanines of *Brasilodon* suggest that precise occlusion may be not necessarily correlated with postcanine morphology.

Interpterygoid vacuity. The ventrally wide portion of the pterygoid bordering the interpterygoid vacuities appears to be a derived character when we compare this area of the bone with that present in *Thrinaxodon* (Estes, 1961); *Ecteninion* (Martinez *et al.*, 1996); *Probainognathus* (Romer, 1970); *Chiniquodon* (Huene, 1935-42; Romer, 1969) and most of the Eucynodontia. In these cynodonts the pterygoid is transversely narrow and appressed to the cultriform process of the parasphenoid, except in some specimens of *Thrinaxodon* in which there is a small separation making an incipient vacuity, as well as in *Probelesodon lewisi* specimen MCZ 3777, and *Lumkuia* (Hopson & Kitching, 2001).

The ventrolateral wing of the pterygoid is pronounced in brasilodontids, basically of the same proportion and morphology present in the above cited carnivorous cynodonts, and in *Hadrocodium* (IVPP 8275) and different from the reduced condition seen in *Morganucodon* (Kermack *et al.*, 1981).

The interpterygoid vacuity present in the Late Permian *Procynosuchus* (Kemp, 1979) was interpreted as a plesiomorphic character present in more primitive therapsids. He interpreted the interpterygoid openings as remnant of a kinetism present in more primitive forms, "subsequently locked in the line leading to cynodonts" (Kemp, 1979: 101). Crompton (1958: 207-209) considered the vacuities recorded in the skull of *Diarthrognathus* as a primitive character. Hopson & Barghusen (1986) pointed out that the closure of interpterygoid vacuity is a character present in "post-procynosuchid cynodonts", and that the primitive condition of the vacuity interpreted by Crompton is actually a juvenile character and doubtfully present. Rowe (1993) in his "Node 5" made no reference to the interpterygoid vacuity or separate pterygoids. Sues (1986:fig.6) showed the interpterygoid fenestrae in *Kayentatherium* but did not discuss it.

Here we consider that the separate pterygoids of brasilodontids may be a derived or reversed character, if we consider that these cynodonts were originated from some indeterminate group of Epicynodontia (Hopson & Kitching, 2001) in which the interpterygoid vacuities are reduced or absent. But, if we consider the possibility of origin of brasilodontids from Procynosuchidae then the vacuities are simply a plesiomorphic character. Eventually the vacuities in brasilodontids might have a different function to that suggested by Kemp (1979). They may be medially incomplete or continued by cartilage up to the medial contact with the parasphenoid. Vestiges of thin bone between both pterygoids have been observed in the skull UFRGS PV0596T of *Riograndia candelariensis* (Soares, 2004), indicating that the interpterygoid vacuity was closed by bone.

Functionally, this area of the palate may have been occupied by the nasopharyngeal organs, palatal musculature, respiratory passages, and by Eustachian tubes (Kielan-Jaworowska, 1970; Barghusen, 1986; Sues, 1986), in any case requiring hard structures for their placement. Probably separated pterygoids represent an initial stage of the condition present in *Morganucodon* (Kermack *et al.*, 1981), *Sinoconodon* (Crompton & Luo, 1993), and in the tritylodontid *Kayentatherium* (Sues, 1986), in which the pterygoid bones are transversely wide in ventral view and develop longitudinal crests. *Kayentatherium*, with comparatively small interpterygoid fenestrae, may represent an intermediate stage in the ossification of the area but acquired independently.

Cavum epiptericum. As far as we have observed in *Brasilitherium* the cavum remains widely open, without much development of its floor. This ventral opening is larger (therefore more primitive) than in *Adelobasileus* (Lucas & Luo, 1993), but possibly smaller (therefore more derived) than in *Probainognathus*.

Basicranium. In the basicranium the most outstanding features are the presence of a well differentiated promontorium in *Brasilitherium*, and the complex morphology of the "stapedial recess" in *Brasilodon*. The promontorium is less bulbous than in *Morganucodon* (Kermack *et al.*, 1981) but definitely more developed than in any other Middle or Late Triassic cynodont. Obviously it represents a further specialization for hearing, not far from the level of *Morganucodon*. The well developed stapedial process of the quadrate in both *Brasilodon* and *Brasilitherium* is another indication of the degree of derivation of the middle ear in brasilodontids.

The different degree of derivation of the union between prootic and opisthotic in *Brasilodon* (plesiomorphic condition) and *Brasilitherium* (apomorphic condition), as well as in the relationships between perilymphatic and jugular foramina in *Brasilodon* (plesiomorphy) and *Brasilitherium* (apomorphy) suggest that *Brasilitherium* is more derived. However, the presence of several foramina on the "stapedial recess" of *Brasilodon* suggests that it is more derived. Possibly the

several differences in the state of some characters in both genera are the result of an active evolutionary process that was developing differentially in the brasilodontids during early Coloradian times (Bonaparte, 1973).

Cranio-mandibular articulation. The quadrate-articular joint is fully developed and functional, with a secondary and incipiently developed joint between dentary and squamosal in specimen UFRGS PV0760T. In the evolution of the quadrate (Luo & Crompton, 1994, fig 14) it seems clear that the condition present in *Morganucodon* is very similar to that present in *Brasilodon* and *Brasilitherium*, characterized by a well defined neck around the distal condyle and with a long stapedial process. This character state of the quadrate fits well with derived characters of the articular process of the dentary.

Bifurcation of the postcanine root. The incipient bifurcation of the postcanine root in *Therioherpeton* and *Prozostrodon* (Bonaparte & Barberena, 1975, 2001), in *Pachygenelus* (Shubin *et al.*, 1991), and in *Riograndia* (Bonaparte *et al.*, 2001), is a derived character which appears convergent in "ictidosaurs", therioherpetids and brasilodontids, associated with very different morphology of the crown. In some postcanines of *Brasilitherium* it has been observed that the bifurcation of the nutritious canal occurred before the bifurcation of the root.

Interorbital wall. Only in *Brasilitherium* it is possible to observe the interorbital wall but not in complete detail because of the incompleteness and poor preservation. However, its morphology indicates a derived condition, in agreement with the Node 5 of Rowe (1993).

Comments on some small Late Triassic cynodonts

An interesting group of fairly derived cinodonty are poorly known from the Late Triassic (mainly Norian) rocks from Europe and North America, most of them showing partial similarities with the Brazilian cynodonts here discussed.

These taxa are *Dromatherium* (Emmons, 1857; Osborn, 1886) and *Microconodon* (Osborn, 1886) from North America; *Tricuspes* (Huene, 1933) recorded in Germany, Switzerland and France (Hahn *et al.*, 1994); *Pseudotriconodon* (Hahn *et al.*, 1984) from Luxemburg; *Meurthodon* (Sigogneau-Russell & Hahn, 1994) from Central Europe; *Lepagia* and *Gaumia* (Hahn *et al.*, 1987) from Belgium; and *Tikitherium* from India (Datta *et al.*, 2004). Except for *Microconodon* and *Dromatherium* that are known from fragmentary jaws (*e.g.* Emmons, 1857; Sues, 2001), all the remaining taxa are known only from isolated postcanines bearing three or four cusps in line, without cingula. Without doubt that the knowledge on these genera is very poor indeed because of the absence of information on the postcanine sequence and on the skull in order to have additional anatomical references for their systematic interpretation, concept widely recognized by Sigogneu-Russell & Hahn (1994).

The presence in the Late Triassic of Southern Brazil of *Therioherpeton*, *Prozostrodon*, *Brasilitherium*, and *Brasilodon* (all represented by skull and postcranial materials), demonstrate the variety of taxa of small and derived cynodonts recorded in that region of South America. Probably, such diversity was not limited to South America. Many other regions of Pangea were also inhabited by small and derived cynodonts as those recorded in Europe and North America producing a complex assemblage of these cynodonts. The attempt to recognize relationships of those small cynodonts diagnosed on isolated teeth appears to be only tentative, and as such we consider the proposal of Hahn *et al.* (1994) to include several taxa within the family Dromatheriidae. The interpretations on these small cynodonts representing the sister group of mammals (Hahn *et al.*, 1994), although poorly justified (Sues, 2001; Luo *et al.*, 2002) is a reasonable proposal.

One example of the weak systematic information provided by isolated postcanines is seen in the lower dentition of *Brasilitherium*, which shows outstanding similarities in the pc3 and pc4 with those of *Megazostrodon* (Crompton, 1974), while pc5 and pc6 are very different (Bonaparte *et al.,* 2003:figs. 13-15).

The presence of Late Triassic mammals in Europe is widely documented through the discoveries of *Morganucodon* and *Kuehneotherium*. These taxa are known from good cranial and mandibular remains or diagnostic sequence of postcanines. In addition, the Haramiyidae are known from many isolated teeth, as well as lower jaws and fragment of maxilla with teeth. Their relationships with the multituberculate group of mammals have been interpreted as doubtful (Jenkins *et al.*, 1997).

Other Late Triassic mammals based on isolated teeth such as *Brachyzostrodon*, *Helvetiodon*, *Hallautherium*, and *Woutersia* may be related to small and derived cynodonts of the *Brasilodon* and *Brasilitherium* type. We do not deny that they might be mammals, but the very mammalian morphology of the postcanines of these Brazilian cynodonts forces us to consider the referral of these taxa to the Mammalia (*sensu* Crompton & Jenkins, 1979) as only tentatively. It seems clear that the appearance of postcanines of mammalian morphology was previous to the mammalian tooth replacement, to the precise occlusion, to the dentary-squamosal articulation, to the reduction of the pterygoid wings, and to the well developed promontorium.

Comments on *Hadrocodium*

During a visit to the Carnegie Museum of Natural History, we had opportunity to examine the type specimen of *Hadrocodium wui* (IVPP 8275) and compare it with both *Brasilodon* and *Brasilitherium*. The tooth morphology of *Hadrocodium* is basically of the same type as is present in *Brasilitherium*, with the rather symmetrical upper postcanines bearing a large central cusp and one small cusp on both the mesial and distal side of it. The lower postcanines are less symmetrical, with the largest cusp slightly
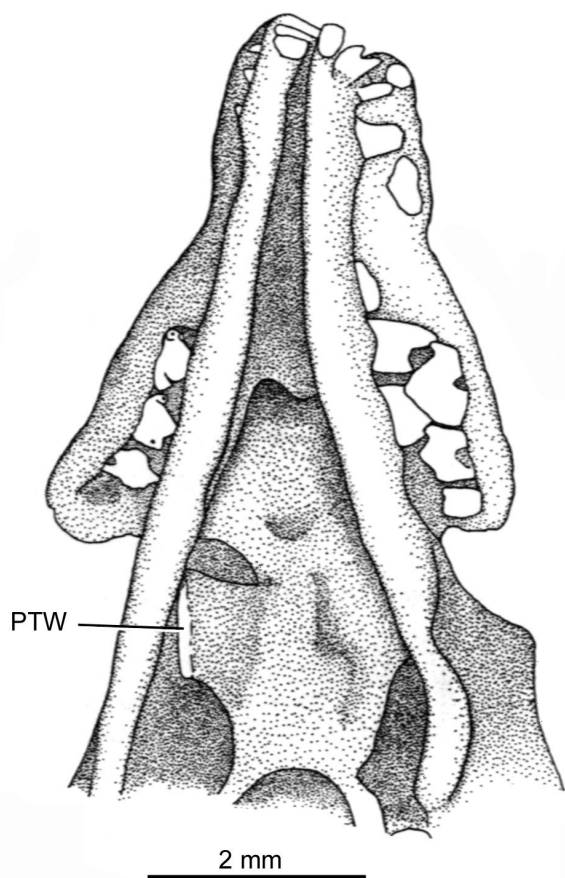
& Crompton (1994), Luo (1994), and Hopson & Kitching (2001); nevertheless, most of them were modified for the analysis here presented. Furthermore, more ingroup taxa were selected for the analysis. All characters were treated as unordered and of the same weight. The data matrix (Appendix 2) was analyzed in NONA program (Goloboff, 1993). A heuristic search strategy was used (Multiple TBR branch swapping; mult1000*, hold/30) producing a single most parsimonious tree with L: 193, CI: 0.59, RI: 0.76 (Figure 20; see Appendix 3 for characters of nodes). *Brasilodon* and *Brasilitherium* are postulated to be the sister group of *Adelobasileus* plus Mammaliaformes. More material is needed to confirm the phylogenetic location of *Adelobasileus* given the incompleteness of the available data for this taxon and the homoplasic of several basicranial features among eucynodonts. Our results, as that preliminary reported in Bonaparte *et al.* (2003), hold the hypothesis that *Brasilodon* and *Brasilitherium* are more closely related to mammaliaforms than are the Tritheledontidae, different from previous phylogenetic inferences (*e.g.* Hopson & Barghusen, 1986; Shubin *et al.*, 1991; Crompton & Luo, 1993; Luo & Crompton, 1994; Luo, 1994; Hopson & Kitching, 2001).

ACKNOWLEDGMENTS

Figure 19. *Hadrocodium wui,* holotype*,* IVPP 8275, camera lucida sketch drawing of the palatine view of the type specimen as preserved showing the wing of the pterygoid.

displaced anteriorly. Cusps b and a are on the mesial area of the crown, and cusps c and d are on the slightly larger distal area of the crown. However, the wear surfaces indicated by Luo *et al.* (2001:fig. 1D) for both upper and lower postcanines of *Hadrocodium* are not recorded in *Brasilitherium*.

The pterygoid wing of both brasilodontid genera is well developed and of the same morphology as that present on the right side of the *Hadrocodium* palate (Figure 19), wrongly described and figured by Luo *et al.* (2001:fig. 1B) as "hamulus" of pterygoid. In addition, it is important to note here that the *Hadrocodium* skull has suffered a strong dorso-ventral deformation, making the braincase secondarily wider both laterally and posteriorly.

Phylogenetic Analysis.

This analysis is a complement to the first one presented in Bonaparte *et al.* (2003). New cranial characters were introduced and in most cases character-states were modified from that of Bonaparte *et al.* (2003). Most of the characters were taken from previous studies of Hopson & Barghusen (1986), Luo

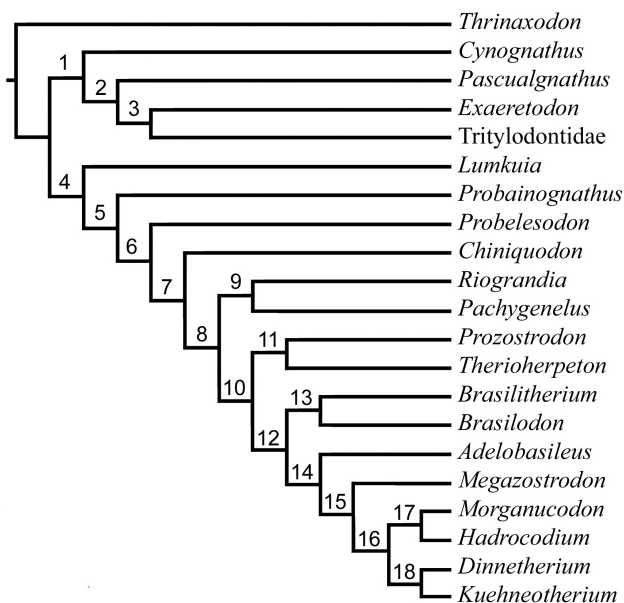**Figure 20.** Cladogram showing the phylogenetic relationships of the Brazilian species among cynodonts (see Appendixes 1, 2, and 3).

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APPENDIX 1. Character list**.**

1. Mode of occlusion: (0) bilateral; (1) unilateral.
2. Direction of mandibular movement during occlusion: (0) orthal; (1) posterodorsal; (2) dorsomedial.
3. Upper incisor number: (0) 5 or more; (1) 4; (2) 3; (3) 2; (4) 1.
4. Lower incisor number: (0) 4 or more; (1) 3; (2) 2; (3) 1.
5. Some incisor hypertrophied: (0) absent; (1) present.
6. Roots of postcanines: (0) single; (1) constricted root; (2) complete separation of roots; (3) multiple roots.
7. Upper postcanines buccal cingulum: (0) absent; (1) distinctive cingulum, straight; (2) cingulum crenulated with distinctive and even-sized multiple cuspules.
8. Upper postcanines lingual cingulum: (0) absent; (1) narrow; (2) lingually expanded.
9. Cuspule e on the lingualmesial side of the lower postcanines: (0) absent; (1) present.
10. Cuspule g on the lingual side of the lower postcanines: (0) absent; (1) present.
11. Cuspule f on the buccodistal side of lower postcanines: (0) absent; (1) present.
12. Mesial and distal buccal accessory cusps symmetrically arranged on upper postcanines: (0) absent; (1) present.
13. Alignment of main cusp of the posterior lower postcanines: (0) simple longitudinal row; (1) obtuse angle (>95); (2) multiple longitudinal multicuspate rows.
14. Posterior portion of the maxillary tooth row extends medial to the temporal fossa: (0) absent; (1) present.
15. Posterior portion of the maxillary tooth row inset from the lateral margin of the maxilla (cheek well developed): (0) absent; (1) present.
16. Axis of posterior part of maxillary tooth row: (0) directed lateral to temporal fossa; (1) directed toward center fossa; (2) directed toward medial rim.
17. Tooth row: (0) divergent posteriorly; (1) parallel to subparallel from the axial plane of the cranium.
18. Interlocking of adjacent lower postcanines: (0) absent; (1) distal cuspule d of anterior molar fits into embayment between cuspule e and cusp b of the succeeding molar; (2) distal cuspule d of anterior molar fits into embayment between cuspules e and f of the succeeding molar.
19. Functional development of wear facets on molar: (0) absent; (1) absent at eruption but developed later by wear; (2) wear facet present at eruption.
20. Relationships of wear facets to main cusps: (0) wear facet absent; (1) simple longitudinal facet that extends entire length of crown; (2) principal cusp bear two longitudinal wear facets; (3) single facet supported by two cusps; (4) multiple cusps, with each cusp bearing one or two transverse facets.
21. Symphysis: (0) fused; (1) unfused.
22. Groove for the replacement dental lamina: (0) present; (1) absent.
23. Angular process of the dentary: (0) absent or weakly developed; (1) present.
24. Horizontal ramus of the dentary: (0) relatively short and thick; (1) long and slender.
25. Meckelian groove: (0) does not reach the ventral edge of the horizontal ramus; (1) reaches the ventral edge of the horizontal ramus.
26. Dentary: (0) does not participates in the temporomandibular joint; (1) contacting squamosal by posterior enlargement of the lateral ridge; (2) presence of slender and dorsoventrally compressed condyle; (3) presence of bulbous condyle.
27. Premaxilla forms posterior border incisive foramen: (0) absent; (1) present.
28. Anterolateral projection of the frontal contacting medially the nasal: (0) absent; (1) present.
29. Posterolateral end of maxilla: (0) passes obliquely posterodorsally into suborbital bar; (1) forms right angle ventral to jugal contact.
30. Prefrontal: (0) present; (1) absent.
31. Postorbital: (0) present; (1) absent.
32. Postorbital bar: (0) present; (1) absent.
33. Parietals: (0) fused; (1) unfused.
34. Parietal foramen: (0) present; (1) absent.
35. Interpterygoid vacuity in adult between pterygoid: (0) absent; (1) present.
36. Length secondary palate relative to tooth row: (0) shorter; (1) about equal; (2) longer.
37. Squamosal glenoid that articulates with mandibule: (0) absent; (1) formed by small and medially facing facet; (2) formed by broad and anteroventrally facing glenoid; (3) glenoid buttressed by postglenoid ridge; (4) glenoid facing ventrally and separated from the cranial moiety by a neck.
38. Length secondary palate relative to anterior border of orbit: (0) shorter; (1) about equal; (2) longer.
39. Ventral surface of basisphenoid depressed below occipital condyles: (0) less than ¼ occipital height; (1) less than ¼ occipital height.
40. Zygomatic arch dorsoventral height: (0) slender; (1) moderately deep; (2) very deep.
41. Zygomatic arch dorsal extent: (0) below middle of orbit; (1) above middle of the orbit.
42. Greatest width of zigomatic arches: (0) near middle of arch; (1) at posterior end of arch.
43. Jugal depth in zygomathic arch relative to exposed squamosal depth: (0) less than twice; (1) greater than twice.
44. Jugal suborbital process: (0) absent; (1) present.
45. Squamosal groove for external auditory meatus: (0) moderately deep; (1) very deep; (2) shallow.
46. Frontal-palatine contact in the orbit: (0) absent; (1) present.

47. Descending flange of squamosal lateral to quadratojugal: (0) present not contacting surangular; (1) present contacting surangular; (2) absent.
48. Internal carotid foramina in basisphenoid: (0) present; (1) absent.
49. Complete ossification of the orbital floor: (0) absent; (1) present.
50. Groove on prootic extending from pterygoparoccipital foramen to trigeminal foramen: (0) open; (1) enclosed as a canal.
51. Mandibular brach (V3) of the trigeminal nerve exit via foramen: (0) between prootic and epipterygoid (alisphenoid ascending process); (1) V3 foramen placed within the prootic (or anterior lamina of the petrosal); (2) two V3 foramina within the prootic (or anterior lamina of the petrosal).
52. Quadrate ramus of pterygoid: (0) present; (1) absent.
53. Length of palatine relative to maxilla in secondary palate: (0) shorter; (1) about equal; (2) longer.
54. Parietal crest: (0) prominently developed; (1) weakly developed.
55. V-shaped notch separating lambdoid crest from zygomatic arch: (0) absent; (1) present.
56. Prootic and ophistotic: (0) separated; (1) fused.
57. Petrosal promontorium: (0) absent; (1) incipiently developed; (2) fully developed with longitudinal crest and flat medial facet; (3) fully rounded.
58. Foramen and passage of prootic sinus: (0) absent; (1) present.
59. Fenestra vestibulis with thickened ring: (0) present; (1) absent.
60. Perilymphatic foramen separation from jugular foramen: (0) confluent; (1) partially separated by fingerlike projection from posterolateral wall of jugular foramen; (2) completely separated.
61. Stapedial muscle fossa: (0) absent; (1) present.
62. Pterygoparoccipital foramen: (0) enclosed by lateral flange of petrosal and/or rami of pterygoid and epipterygoid; (1) squamosal contributes to enclosure of the foramen; (2) open.
63. Relationship of the petrosal lateral flange to the crista parotica (or the anterior paroccipital process that bears the crista): (0) widely separated; (1) narrow separated.
64. Morphology of the internal acoustic meatus: (0) the region for the VII and VIII nerves is poorly ossified and no clearly developed internal auditory meatus is present; (1) the floor is ossified and the meatus is a deep tube; (2) present as a shallow depression.
65. Hypoglossal foramen: (0) indistinct, either confluent with the jugular foramen or sharing a depression with the jugular foramen; (1) separated from the jugular foramen.
66. Bifurcation of paroccipital process: (0) absent; (1) present.
67. Presence of a quadrate-incus neck (separation of the dorsal plate and the trochlea): (0) absent; (1) present.
68. Scapular elongation between acromion and glenoid: (0) present; (1) absent.
69. Scapular constriction below acromion: (0) absent; (1) present.
70. Acromion process: (0) absent; (1) present.
71. Procoracoid in glenoid: (0) present; (1) barely present or absent.
72. Procoracoid contact with scapula: (0) greater than coracoid contact; (1) equal to or less than coracoid contact.
73. Humerus ectepicondilar foramen: (0) present; (1) absent.
74. Length of anterior process of ilium anterior to acetabulum (relative to diameter of acetabulum): (0) between 1.0-1.5; (1) greater than 1.5.
75. Dorsal profile of ilium: (0) strongly convex; (1) flat to concave.
76. Greater trochanter separated from the femoral head by distinct notch: (0) absent; (1) present.
77. Lesser trochanter position: (0) on the ventromedial surface of femoral shaft; (1) on medial surface of femoral shaft.
78. Vertebral centra: (0) amphicoelous; (1) platycoelous.
79. Greater trochanter location at the level of the femoral head: (0) absent; (1) present.
80. Lesser trochanter location near the level of the femoral head: (0) absent; (1) present.

Appendix 2. Matrix with character-states for the 80 characters enunciated above. Coding for character-states: 0, primitive; 1 to 4, derived; A, 0+1; B, 1+2; C, 2+3; ?, missing or uncertain data.

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Thrinaxodon      0011000011010000A000000000?00000000001000000000000000000000000?00?0000000000000
Cynognathus      0111000000000000001?0000000?00001000000211011011000100000000000?00?0010000000000
Pascualgnathus   ?11100020000?01210??100000?00000100001021111011011100100000?0?000011?000100000
Exaeretodon      012100020000?11210240010000011000112110110110111001001000010?0000111001100000
Tritylodontidae  014C13?20000211210241100011011111A00212111011011111001100021201010011111?1????
Lumkuia          0011000000000000000000000?0000011001010000001000010010000000000?00?0?110????????
Probelesodon     0011000000000000000010001?100001010200000011000110100001000?00?0111001100000
Chiniquodon      00110002000000000000010000??10000102020100000110001201000?000000?0111001100001
Probainognathus  00110001000000010000001000??00000101110100000011000010010010100?000011??01100000
Prozostrodon     1200010100000001001110011011??11????2?1?????0?1??0??1?????????????????????0????0??
Therioherpeton   ?2???1000000?0010011???????1011101011?1?00000?1??????11???????????????????1101011
Riograndia       1221110000000001001110100111011?112?2?0000021?0????20???????????????????????????
Pachygenelus     12321121000001021011101001??0111011222000000021200001201100020200?0011111101111111
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Brasilitherium   1211010011010001011210011?101110111?200000021?0002001111102??0?001?????1????????
Brasilodon   12??01001101000101121 00111?101110112?200000021?000?001100101?0??A?1?????????????
Adelobasileus   ??????????0?????????????????????????????????????1?2??1?11?12011?10?????????????
Megazostrodon   11110221110000011112100112??011101?24100???2????1?1??1?121121?12111?????????????
Morganucodon   12100221110000011112101112010111010242000000021201121011131121212111111111?111111
Hadrocodium   1200022?1??0000111121?1123?10111010232?00000212?1?11?1?1311213??10?????????????
Dinnetherium   11?0022?1?100????212110112?2????????4??????????????1????1311?121?11?????????????
Kuehneotherium   11???21?10101????2131101?2??

Appendix 3. The following characters of nodes are based on the most parsimonious tree (Figure 20). Asterisks (*) indicate equivocal characters.

Node 1:   (Cynognathia): 2(1), 33(1), 40(2), 41(1), 42(1), 44(1), 45(1), 48(1)
Node 2:   8(2)*, 15(1), 16(2)*, 17(1)*, 50(1)*, 51(1)*
Node 3:   14(1)*, 34(1)*, 39(1), 74(1)*
Node 4:   (Probainognathia): 34(1)*
Node 5:   23(1)*, 27(1)*, 36(1)*, 46(1)*, 60(1)*
Node 6:   38(2)*
Node 7:   36(2), 80(1)
Node 8:   1(1), 2(2), 6(1), 16(1)*, 19(1)*, 20(1), 21(1)*, 30(1)*, 31(1)*, 32(1)*, 40(0), 45(2), 47(2), 56(1)*, 68(1), 72(1)*, 77(1), 79(1)
Node 9:   (Tritheledontidae): 5(1)*, 35(1)*
Node 10: 23(0)*, 24(1), 25(1), 54(1)
Node 11: 38(1)*
Node 12: 9(1)*, 10(1)*, 18(1), 20(2), 73(1)*
Node 13: (Brasilodontidae): 12(1)*, 35(1)*, 52(0)*
Node 14: 49(1)*, 59(1), 63(1), 65(1)
Node 15: (Mammaliaformes): 51(1)*, 61(1)*, 66(1)*
Node 16: 4(0)*
Node 17: 23(1)*
Node 18: 11(1), 18(2), 22(1)*