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A new tritheledontid (Therapsida, Eucynodontia) from the Late Triassic of Rio Grande do Sul (Brazil) and its phylogenetic relationships among carnivorous non-mammalian eucynodonts

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Abstract. A new tritheledontid, *Irajatherium hernandezi* gen. et sp. nov., from the Late Triassic Caturrita Formation of Brazil is described. The specimen consists of a left maxilla bearing the canine, five postcanines, and the alveolus of another one, two fragments of lower jaw, a humerus, and a femur. The association of the following features is unique for this taxon: 1) anterior upper postcanines transversely narrow bearing a higher cusp A and smaller cusp C; 2) last upper postcanines with higher, bulbous cusp A and smaller lingual cusps B and C, differing from *Pachygenelus* in lacking a buccal cingulum; 3) middle lower postcanines bearing a higher anterior cusp and three consecutively smaller posterior cusps, differing from *Pachygenelus* in lacking a lingual cingulum; 4) lower postcanines with sharp wear facets; 5) humerus with two thick osseous processes for the teres major muscle; and 6) femur with the greater trochanter at the head level and the lesser trochanter on the medial surface of the shaft. Our phylogenetic analysis placed *I. hernandezi* together with *Riograndia guaibensis* Bonaparte *et al.* , *Chaliminia musteloides* Bonaparte, *Pachygenelus monus* Watson and *Diarthrognathus broomi* Crompton. These taxa represent the family Tritheledontidae. The presence of two kinds of upper postcanines in different replacement waves in *Irajatherium* could be a useful feature for inference of possible mechanism of dental differentiation among non-mammalian cynodonts. Possible fossorial adaptations are documented in the humerus of *Irajatherium* .

Resumen. Un nuevo Tritheledóntido (Therapsida, Eucynodontia) del Triásico Tardío de Río Grande do Sul, (Brasil) y su posición filogenénetica entre eucinodontes carnívoros no mamalianos. Se describe un nuevo tritheledóntido, *Irajatherium hernandezi* gen. et sp. nov., de la Formación Caturrita del Triásico Tardío de Brasil. El especimen consiste en un maxillar izquierdo con el canino, cinco postcaninos y el alvéolo para uno más, dos fragmentos de mandíbula, un húmero y un fémur. La asociación de los siguientes caracteres es única para este taxón: 1) postcaninos superiores anteriores transversalmente angostos, con la cúspide A prominente y la cúspide C de pequeño tamaño; 2) último postcanino con la cúspide A prominente y bulbosa, y las cúspides B y C pequeñas desplazadas lingualmente, diferente a *Pachygenelus* por la ausencia de un cíngulo bucal; 3) dientes inferiores medios con una cúspide anterior alta y tres cúspides consecutivamente menores, diferentes de *Pachygenelus* por la ausencia de un cíngulo lingual; 4) facetas de desgaste en los postcaninos inferiores; 5) húmero con dos robustas tuberosidades para el músculo teres major; y 6) fémur con el trocánter mayor ubicado al nivel de la cabeza y trocánter menor proyectado medialmente. Nuestro análisis filogenético ubica a *I. hernandezi* junto con *Riograndia guaibensis* Bonaparte *et al.* , *Chaliminia musteloides* Bonaparte, *Pachygenelus monus* Watson, and *Diarthrognathus broomi* Crompton. Estos taxones representan la familia Tritheledontidae. La presencia de dos tipos distintos de morfologías de postcaninos superiores involucrados en el recambio dentario de *Irajatherium* podría ser un rasgo importante para inferir sobre posibles mecanismos de diferenciación dentaria entre cinodontes. Se documentan posibles adaptaciones fosoriales en el húmero de *Irajatherium*

Key words. Eucynodontia. Tritheledontidae. *Irajatherium hernandezi* . Late Triassic. Brazil.

Palabras clave. Eucynodontia. Tritheledontidae. *Irajatherium hernandezi* . Triásico Tardío. Brasil.

Introduction

The family Tritheledontidae was established by Broom (1912) to include an extremely rare cynodont, *Trithelodon riconoi* Broom, from the Lower Jurassic Red Beds Stormberg Series of South Africa, based on some cranial and dental elements. Later, Watson (1913) described a new species, *Pachygenelus monus* , based on a fragment of a lower jaw from the same region. In 1929, Broom published two new specimens of cynodonts, one based on an almost complete skull (Ictidosaurian A) and the other based on a partial skull and fairly complete postcranial remains (Ictidosaurian B). All these taxa were included together in the Suborder Ictidosauria (Broom, 1929). Furthermore, Crompton (1958) studied the Ictidosaurian B, named it *Diarthrognathus broomi* , and proposed the family Diarthrognathidae for this taxon principally because of its peculiar temporomandibular joint formed by the articularquadrate and dentary-squamosal articulations. In a more recent review of the group, Hopson and Kitching (1972) proposed to abandon the infraordinal rank Ictidosauria to include the ictidosaurian species within the infraorder Cynodontia. They used the familiar rank Tritheledontidae to include *Trithelodon* and *Pachygenelus* . Furthermore, they considered Diarthrognatidae and *Diarthrognathus* as a synonym of the family Tritheledontidae and the genus *Pachygenelus* respectively because the only known specimen of the genus *Diarthrognathus* was referred as a juvenile. Nevertheless, based on several new remains, Gow (1980) made an extensive description of the dentition of the Tritheledontidae and showed sufficient differences to merit separation of the three genera. In 1980, Bonaparte described the first South American "ictidosaur", *Chaliminia musteloides* , from the Upper Triassic Los Colorados Formation of Argentina.

He proposed the family Pachygenelidae to include the new taxon and *Pachygenelus* , and at the same time, he referred *Diarthrognathus* and *Trithelodon* to the Tritheledontidae based on their specialized dental morphology (Bonaparte, 1980). Recently, another "ictidosaur", *Riograndia guaibensis* from the Upper Triassic of southern Brazil, was described and assigned to the new family Riograndidae (Bonaparte *et al.* , 2001).

The knowledge about the tritheledontids has improved in recent years (*e.g* . Shubin *et al.* , 1991; Gow, 1994). This family was considered a group of small advanced non-mammalian cynodonts implicated in the origin of the early mammaliaforms (*e.g* . Hopson and Barghusen, 1986; Shubin *et al.* , 1991; Crompton and Luo, 1993; Luo and Crompton, 1994; Luo, 1994; Sidor and Hopson, 1998; Hopson and Kitching, 2001; Luo *et al.* , 2001, 2002; however see Bonaparte and Barberena, 1975, 2001; Bonaparte *et al.* , 2003). Nevertheless, the phylogenetic relationships among the taxa within tritheledontids are not clear.

Thus, the aim of this paper is to describe a new tritheledontid cynodont discovered in 2000 during fieldworks organized by the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Argentina) and the Universidade Federal of Rio Grande do Sul (Brazil) in outcrops of the Upper Triassic Caturrita Formation (*sensu* Andreis *et al.* , 1980; Montardo, 1982) in southern Brazil. Morover, a cladistic analysis was conducted to clarify the relationships of tritheledontids among eucynodonts.

Abbreviation. Institutional abbreviations used in this paper are as follows: MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Buenos Aires) (N, Colección Neuquén; PV, Paleontología de Vertebrados); MCN: Museu de Ciências Naturais, Fundação Zoobotânica (Porto Alegre); MCZ: Museum of Comparative Zoology, Harvard University (Massachusetts); PVL: Instituto Miguel Lillo, Universidad Nacional de Tucumán (Tucumán), Vertebrate Paleontology Collection; SAM: South African Museum (Cape Town); UFRGS: Universidade Federal do Rio Grande do Sul (Porto Alegre) (PV, Vertebrate Paleontology; T, Triassic collection).

Geological setting

The Upper Triassic Caturrita Formation (Andreis *et al.* , 1980) consists of a coarsening-upward succession that transitionally replaces the transgressive mudstones of the upper layers of the Santa Maria Formation. The faunal content of the Caturrita Formation, dominated by rhynchosaurs (mainly *Hyperodapedon*), indicates a Carnian to Norian age. This Formation constitutes the highstand systems tract of the Santa Maria two-third-order sequence (Zerfass *et al.* , 2003).

The Caturrita Formation contains isolated, smallscale trough cross-bedded sandstone lenses (St facies *sensu* Miall, 1996) that are interpreted as ribbon fluvial channels. Rhytmites and sigmoidal, massive to climbing cross-laminated sandstone bodies are also present. This facies association is interpreted as a lacustrine- deltaic depositional system. Upwards, the mudstone content decreases and the sandstone amalgamation increases. Sandstones occur as narrow, massive or stratified (horizontal and trough cross bedding) lenses (Sm, Sh and St facies *sensu* Miall, 1996) interpreted as amalgamated sandstone bodies related to high width/depth ratio channels. The described succession reveals a progressive reduction of accommodation space, shallowing of the lacustrine basin and its progressive replacement by a fluvial system. In the outcrop where *Irajatherium hernandezi* was A new tritheledontid from the Late Triassic of Brazil 193 collected (figure 1) the massive sandstones (Sm facies *sensu* Miall, 1996) are predominant (figure 2). The fossil-bearing sandstones occupy the basal portion of the outcroup. Towards the top of the sequence occur tabular and intercalated layers of siltstone and fine sandstone (Fl facies *sensu* Miall, 1996).

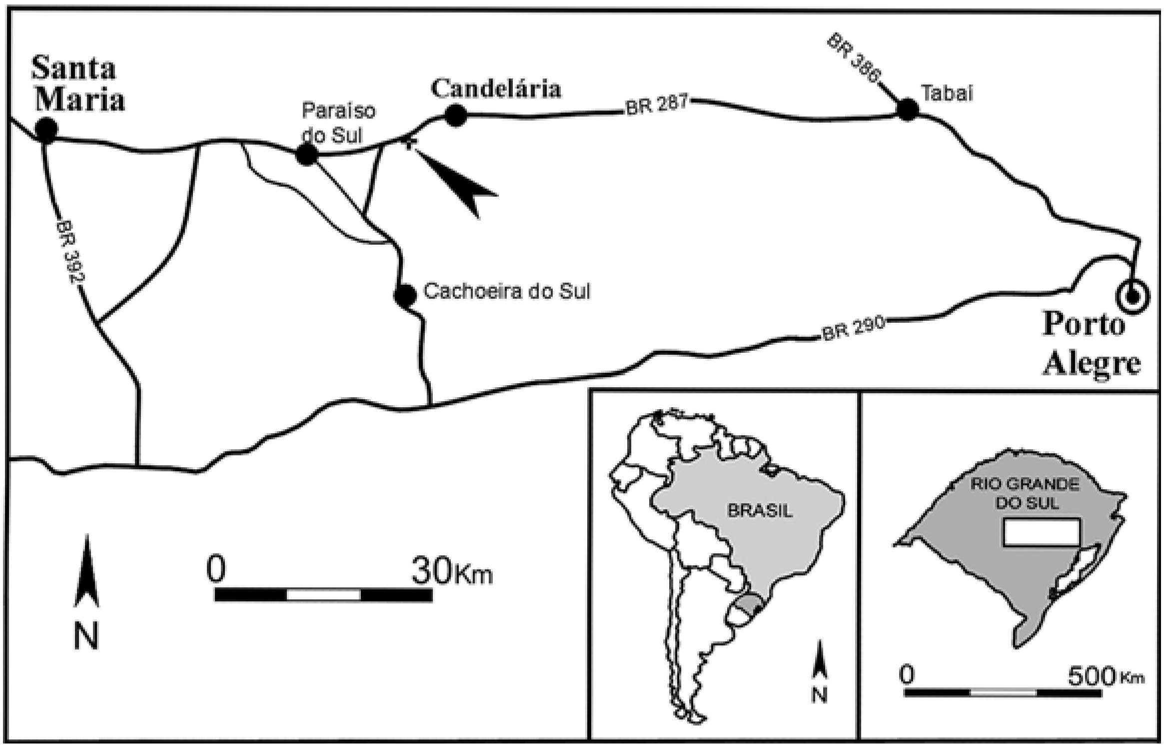
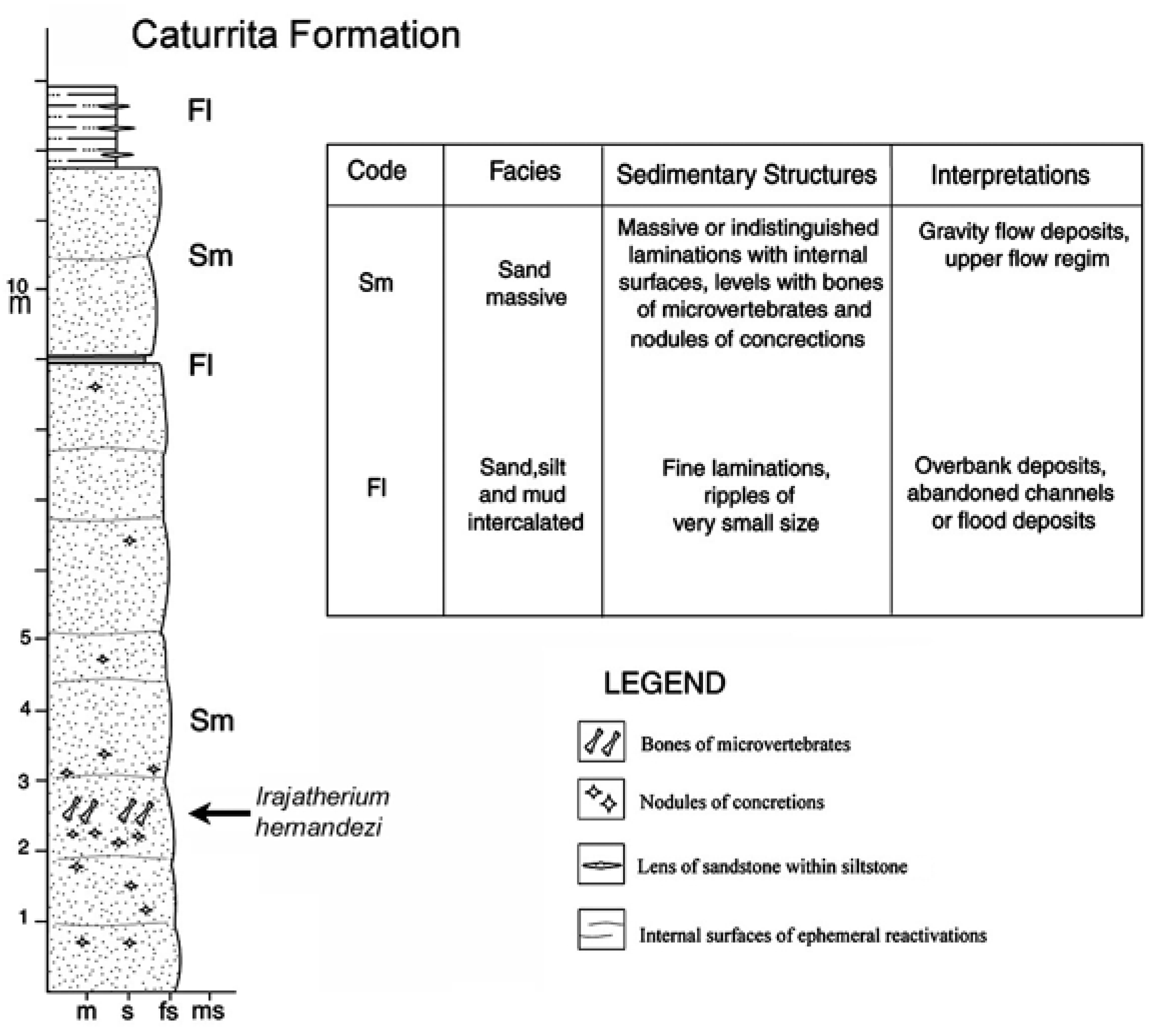


Figure 1. Location map of Candelaria, State of Rio Grande do Sul, Brazil. The arrow indicates the type fossil locality of *Irajatherium hernandezi* . / *Mapa de ubicación de Candelaria, Estado de Río Grande do Sul, Brasil. La flecha indica la localidad tipo de* Irajatherium hernandezi.



Code	Facies	Sedimentary Structures	Interpretations
Sm	Sand massive	Massive or indistinguished laminations with internal surfaces, levels with bones of microvertebrates and nodules of concrections	Gravity flow deposits, upper flow regim
Fl	Sand,silt and mud intercalated	Fine laminations, ripples of very small size	Overbank deposits, abandoned channels or flood deposits

Figure 2. Stratigraphical section of the middle-upper portion of the Caturrita Formation, near Candelaria, Rio Grande do Sul. / *Perfil estratigráfico de la porción media-superior de la Formación Caturrita, cerca de Candelaria, Río Grande do Sul.*

This succession is considered to represent the middle-upper portion of the Caturrita Formation. Equivalent levels in other localities have yielded a rich vertebrate assemblage composed by the probainognathians *Riograndia guaibensis* (Bonaparte *et al.* , 2001), *Brasilodon quadrangularis* (Bonaparte *et al.* , 2003) and *Brasilitherium riograndensis* (Bonaparte *et al.* , 2003); a primitive dinosaur, *Guaibasaurus candelariensis* (Bonaparte *et al.* , 1999); a leptopleuronin procolophonid, *Soturnia caliodon* (Cisneros and Schultz, 2003); a tuskless dicynodont, *Jachaleria candelariensis* (Araújo and Gonzaga, 1980); an indeterminated phytosaur (Kischlat and Lucas, 2003); and an unnamed sphenodont (Ferigolo, 2000).

The vertebrate association of the middle-upper portion of the Caturrita Formation suggests an early Coloradian age (*sensu* Bonaparte, 1973, approximately Early Norian, Late Triassic).

Systematic paleontology

Therapsida Broom, 1905

Cynodontia Owen, 1861

Epicynodontia Hopson and Kitching, 2001

Eucynodontia Kemp, 1982

Probainognathia Hopson, 1990

Tritheledontidae Broom, 1912

Definition. The clade including the more recent common ancestor of *Riograndia* and *Pachygenelus* , and all its decendents.

Irajatherium gen. nov.

Type and only know species. *Irajatherium hernandezi* sp. nov.

Diagnosis. Small tritheledontid with anterior upper postcanines transversely narrow bearing a high cusp A and a small cusp C; posterior upper postcanines with high bulbous cusp A, and small lingual cusps B and C, differing from *Pachygenelus* in lacking a buccal cingulum; middle lower postcanines bearing a high anterior cusp and three consecutively smaller posterior cusps, with mesial accessory cusps in posteriormost postcanines, differing from *Pachygenelus* in a lacking lingual cingulum. *Irajatherium* differs from most eucynodonts with lower sectorial teeth in having sharp wear facets on the buccal side that indicates unilateral occlusion. The humerus has a deep and narrow biccipital groove in the proximal area and two thick osseous processes on the medial side below the lesser tuberosity, near the half of the humeral length. The femur is similar to that of *Therioherpeton* with the greater trochanter located at the level of the head and the lesser trochanter placed on the medial surface of the femoral shaft. This femur differs from that of *Pachygenelus* and *Morganucodon* in lacking the notch between the head and the greater trochanter.

Etymology. In honor to Professor Irajá Damiani Pintos, outstanding invertebrate paleontologist of the Universidade Federal do Rio Grande do Sul, Brazil.

Irajatherium hernandezi sp. nov.

Figures 3-6, 8, 10

Holotype. UFRGS-PV 0599T, incomplete left maxilla bearing the canine, five postcanines, and the alveolus of another one, both canine and the last postcanine are erupting (figure 3); natural cast of the incomplete left dentary bearing an anterior postcanine (figure 4), and a fragment of the left lower jaw with two postcanines (figure 5); left humerus (figure 8); left femur (figure 10); and other indeterminated fragments.

Diagnosis. As for genus.

Etymology. Named after the technician Daniel Henández (Museo Municipal "Carmen Funes", Neuquén, Argentina) who discovered the type specimen.

Locality and horizon. From an outcrop of the Caturrita Formation located 8 kilometers west of Candelaria, in a roadcut on the route (BR 287) to Santa Maria, Rio Grande do Sul State, Brazil (figure 1), possibly of Early Coloradian age (*sensu* Bonaparte, 1973) (approximately Early Norian, Late Triassic).

Description and comparisons

Maxilla (figure 3)

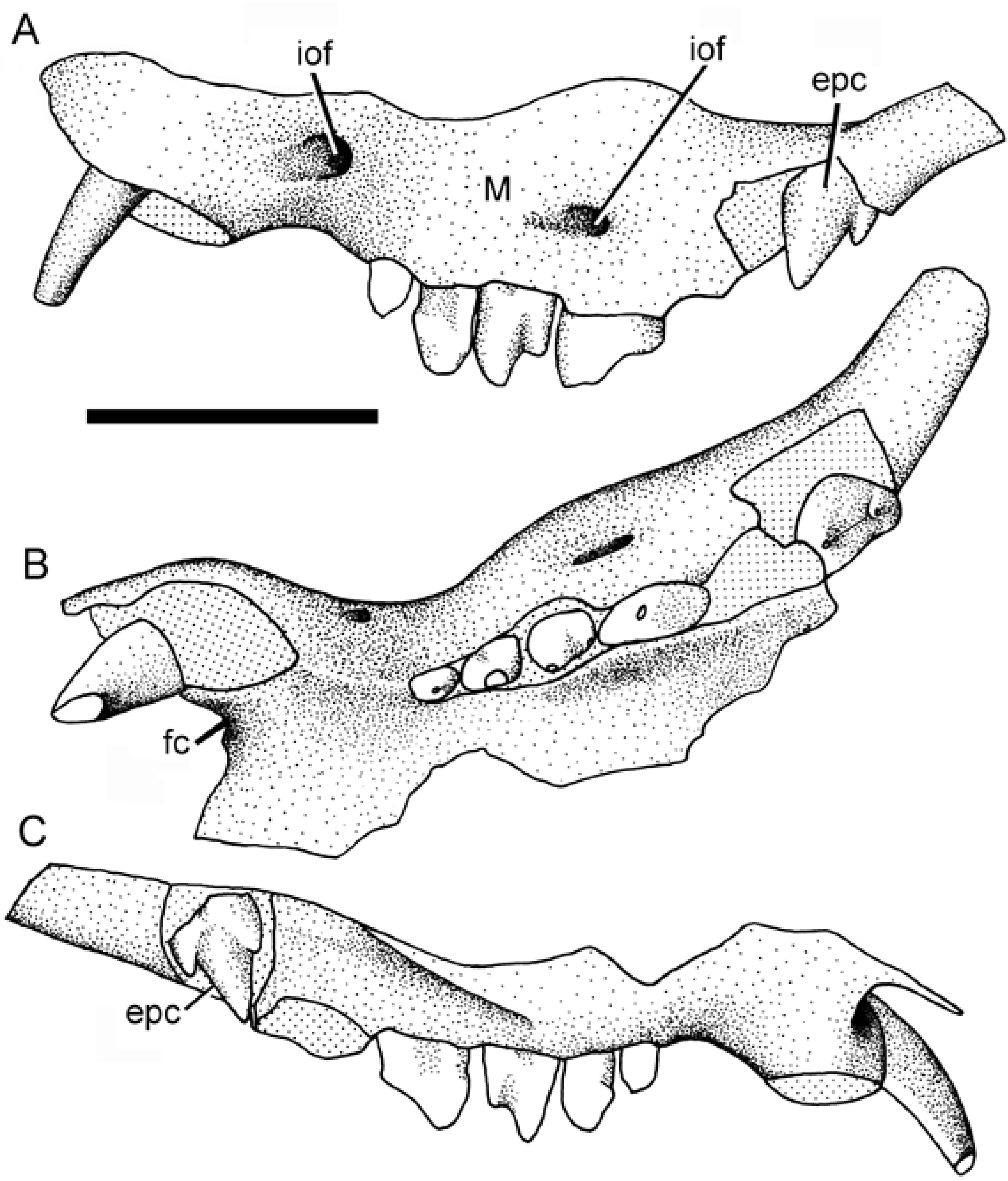


Figure 3. Left maxilla of *Irajatherium hernandezi* (UFRGS-PV 599T holotype) in lateral (A), ventral (B) and medial (C) views. Scale bar equals 5 mm. Abbreviations in Appendix 3 / *Maxilar izquierdo de* Irajatherium hernandezi *en vista lateral (A), ventral (B) y medial (C). La escala representa 5 mm. Abreviaturas en Apéndice 3.*

The only cranial material available is a fairly complete left maxilla with a canine, five postcanines and the alveolus of another tooth. The lateral aspect of the maxilla shows two antero-posteriorly concave regions, one above the postcanine diastema and the second near the beginning of the zygomatic arch. The lateral wall of the canine alveolus is convex and bears small pits. There are two large infraorbital foramina for the maxillary branch of the trigeminal nerve (V2), one placed behind the thick alveolar process of the canine and the other above the fourth postcanine. The latter is smaller and both face anteriorly. In the posterior portion, the maxilla forms part of the root of the zygomatic arch. The contacts with the jugal and other bones are not preserved.

In ventral view, the anteriormost medial edge of the maxilla projects ventrally, possibly due to deformation. The posterior border of the paracanine fossa reaches the level of the canine alveolus. Medially and backwards from the third postcanine there is a deep narrow groove which accommodate the lower sectorial postcanines (figure 3.B).

Comparison. The distribution of the maxillary branch of the trigeminal nerve in the snout is similar to that found in *Pachygenelus* , *Diarthrognathus* , and *Morganucodon* (Kermack *et al.* , 1981) in which the anteriormost opening is located behind the canine root and the middle opening above the tooth row (Kemp, 1982). The posterior foramen near or in the contact between the lachrymal and the maxilla is not preserved in *Irajatherium* . In *Lumkuia* , *Ecteninion* , *Probainognathus* , *Probelesodon* , *Chiniquodon* , *Therioherpeton* , and *Prozostrodon* these foramina are smaller, lack a regular distribution, and their number is variable (Romer, 1969a, 1969b, 1970; Teixeira, 1982; Martinez and Forster, 1996; Martinez *et al.* , 1996; Hopson and Kitching, 2001; Bonaparte and Barberena, 2001).

As in cynognathians (*Cynognathus* plus Gomphodonthia) (Hopson and Kitching, 2001), basal probainognathians and some mammaliaforms (*e.g* . *Sinoconodon* ; Crompton and Luo, 1993) there is a fossa for the lower canine. Gow (1980) observed that in tritheledontids the fossa was not present due to the reduction of the lower canine. The deep groove parallel to the posterior half of the tooth row is a feature also present in carnivorous non-mammalian probainognathians and also in *Cynognathus* (*e.g* . Abdala, 1996).

Lower jaw (figures 4 and 5)

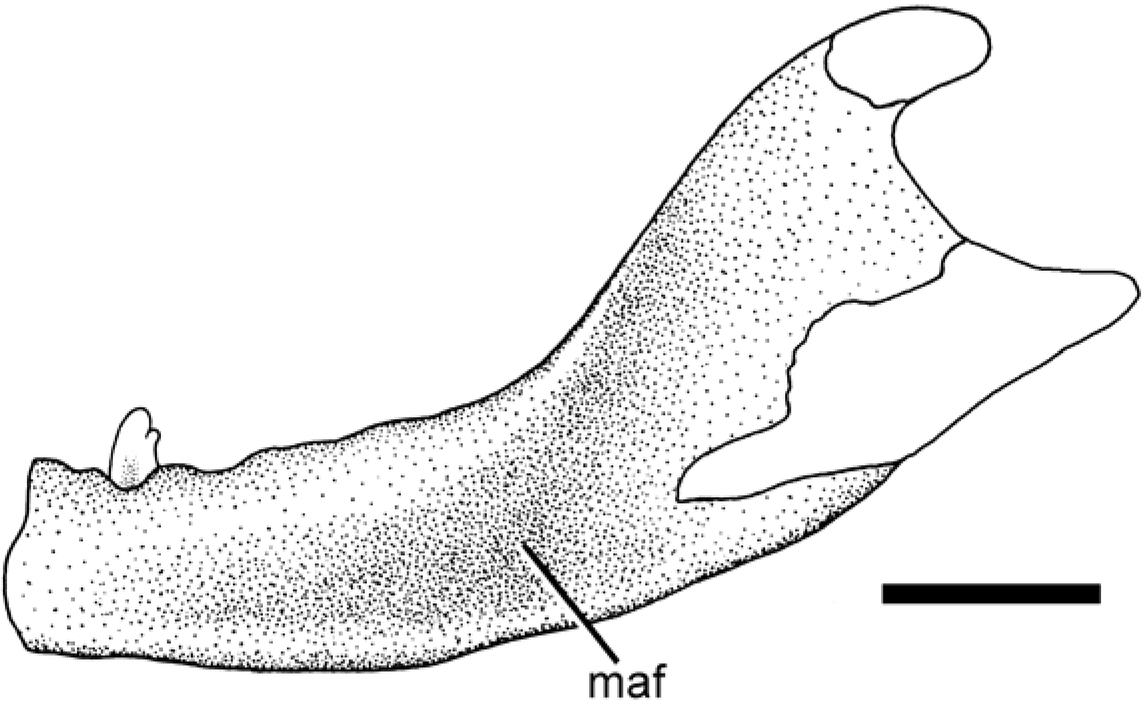


Figure 4. Cast of the left lower jaw of *Irajatherium hernandezi* (UFRGS-PV599T holotype) in lateral view. Tooth and white regions correspond to original bone. Scale bar equals 5 mm. Abbreviations in Appendix 3 / *Molde de la mandíbula izquierda de* Irajatherium hernandezi *en vista lateral. El diente y las regiones blancas corresponden a hueso original. La escala representa 5 mm. Abreviaturas en Apéndice 3.*

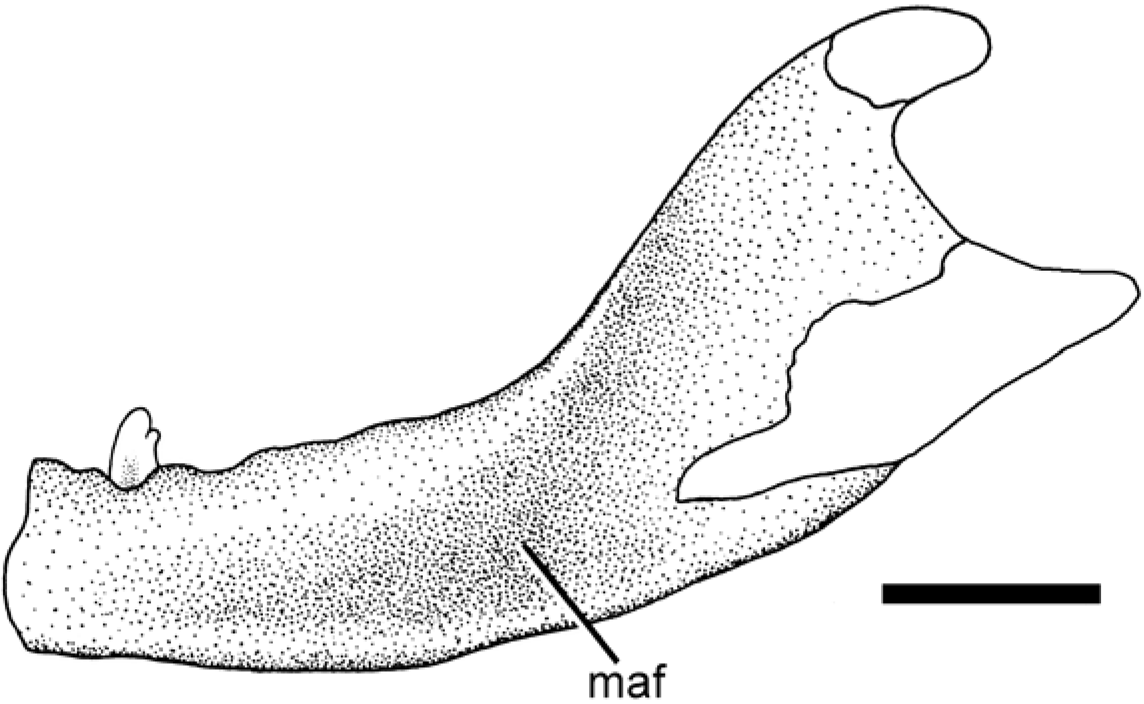


Figure 5. Fragment of left lower jaw with middle postcanines of *Irajatherium hernandezi* (UFRGS-PV599T holotype) in lateral (A) and medial (B) views. Schematic position of this fragment in the cast of the jaw in lateral view (C). Scale bar equals 5 mm. Abbreviations in Appendix 3 / *Fragmento de la mandíbula izquierda con los postcaninos medios de* Irajatherium hernandez *i en vistas lateral (A) y medial (B). Posición esquemática del fragmento en el molde de la mandíbula en vista lateral (C). La escala representa 5 mm. Abreviaturas en Apéndice 3.*

A natural cast of the lateral side of a portion of the left dentary is preserved. The coronoid process is high and bears a thick anterior edge. The masseteric fossa extends anteriorly in the horizontal ramus of the jaw near the level of the last preserved postcanine alveolus. The craniomandibular joint was probably located above the tooth row level as in *Diarthrognathus* and *Pachygenelus* (Crompton, 1958, 1963a; Luo, 1994).

In medial view, the dentary medial ridge of the postdentary trough is preserved. This ridge is a prominent crest and below it there is a broad and deep groove for the postdentary bones. The angular process of the dentary is not preserved.
In a fragment of the dentary cast bearing two teeth, part of the Meckelian groove is observed (figure 5.B). This groove is parallel and close to the ventral edge of the horizontal ramus of the dentary.

Furthermore, the groove for the dental lamina (Crompton, 1963b) is evident near the alveolar border.

Comparison. The postdentary trough and the medial ridge are similar to that of most eucynodonts and *Morganucodon* (Kermark *et al.* , 1973; Luo, 1994) while the arrangement of the Meckelian groove is comparable to that of most non-mammalian cynodonts and *Sinoconodon* (Luo, 1994). Luo (1994) considered that a Meckelian groove parallel to the lower border of the horizontal ramus of the dentary is a plesiomorphic feature because it is present in most basal eucynodonts. In the probainognathian *Prozostrodon braziliensis* (Bonaparte and Barberena, 2001) this groove reaches the lower border of the dentary behind the symphysis at the level of the first postcanine. Among Mammaliaformes the arrangement of the Meckelian groove is variable. In docodonts (*e.g* . *Haldonodon* and *Docodon*) and in some triconodonts (*e.g* . *Priacodon* , *Triconodon* and *Triorachodon*) the Meckelian groove does not reach the inferior border while in morganucodontids (*e.g* . *Morganucodon* and *Megazostrodon*), *Amphilestes* , *Amphiodon* , *Gobiconodon, Amphitherium* and spalacotheriids, it does (*e.g* . Rougier *et al.* , 2001).

The shape of the lower jaw cast resembles the jaw of tritheledontids (Crompton, 1963a) in which the horizontal ramus is high and the coronoid process has a deep masseteric fossa with a well-defined anterior edge. However, these features are also observed in some cynognathians (*e.g* . *Exaeretodon* ; Bonaparte, 1962).

Upper dentition (figures 3 and 6).

The left maxilla bears the erupting canine and six postcanines of which the fifth is lost and the sixth is erupting. The upper postcanines increase their size posteriorly and a small diastema is present among them. The erupting canine is conical with a distal cutting edge; the size of the alveolus suggests it should be large. The postcanines are separated from the canine by a large diastema. The postcanines are transversely narrow and lack a lingual or buccal cingulum. The PC 1 is the smallest and has only one cusp. This postcanine is probably not fully erupted. The PC 2 has one low cusp with the crown thickened at the base. This tooth possibly was being replaced because its root is in a high position. The PC 3 bears two cusps. The mesial one is the biggest and slightly curved, while the distal cusp is smaller and located in a higher position. The main cusp has the mesial edge more convex than the distal one. Both cusps are in line and separated by a shallow furrow. On the buccal side the root is slightly constricted bucco-lingually as in the PC 4 . The PC 4 is badly preserved but seems to be similar in morphology than the PC 3 . Behind the PC 4 there is an empty alveolus and then the last postcanine, PC 6 . This erupting tooth bears a high bulbous central cusp A with the tip in a buccal position, and two smaller cusps, one on the mesiolingual edge (cusp B) and the other on the disto-lingual edge (cusp C), slightly tricker than cusp B (figure 6). The cusp A has mesial and distal cutting edges where the enamel is observed. There is no buccal cingulum. The root is not preserved but the beginning of a dividing groove is present on the lingual aspect on the base of the crown. The outline in occlusal view is almost triangular, being as wide as long, while the remaining postcanines are narrow transversely.

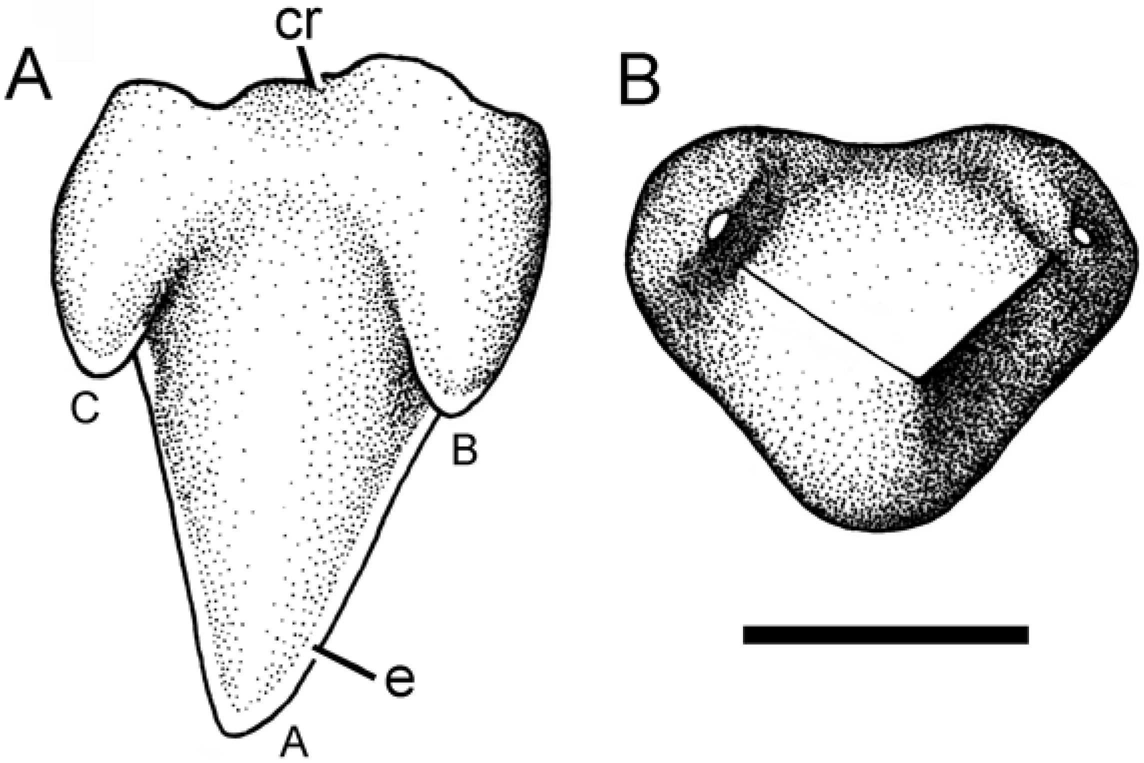


Figure 6. Sixth upper left postcanine of *Irajatherium hernandezi* (UFRGS-PV599T holotype) in lingual and occlusal views. Scale bar equal 1 mm. Abbreviations in Appendix 3 / *Sexto postcanino superior izquierdo de* Irajatherium hernandezi *en vistas lingual y oclusal. La escala representa 1 mm. Abreviaturas en Apéndice 3.*

Comparison (figure 7). In *Irajatherium* the four anterior upper postcanines, despite being not well preserved, are different from the last erupting tooth, lacking the mesial cusp B and being transversely narrow. In *Pachygenelus* and *Diarthrognathus* the tooth row shows an unique model, being the teeth more complex backwards where the buccal cingulum is thick and in some cases crenulate (Gow, 1980). The anterior upper postcanines of *Irajatherium* resemble those of *Probelesodon lewisi* (Romer, 1969b) and *Chiniquodon theotonicus* (Romer, 1969a), although in them the main cusp is curved backwards and they lack a constricted root.

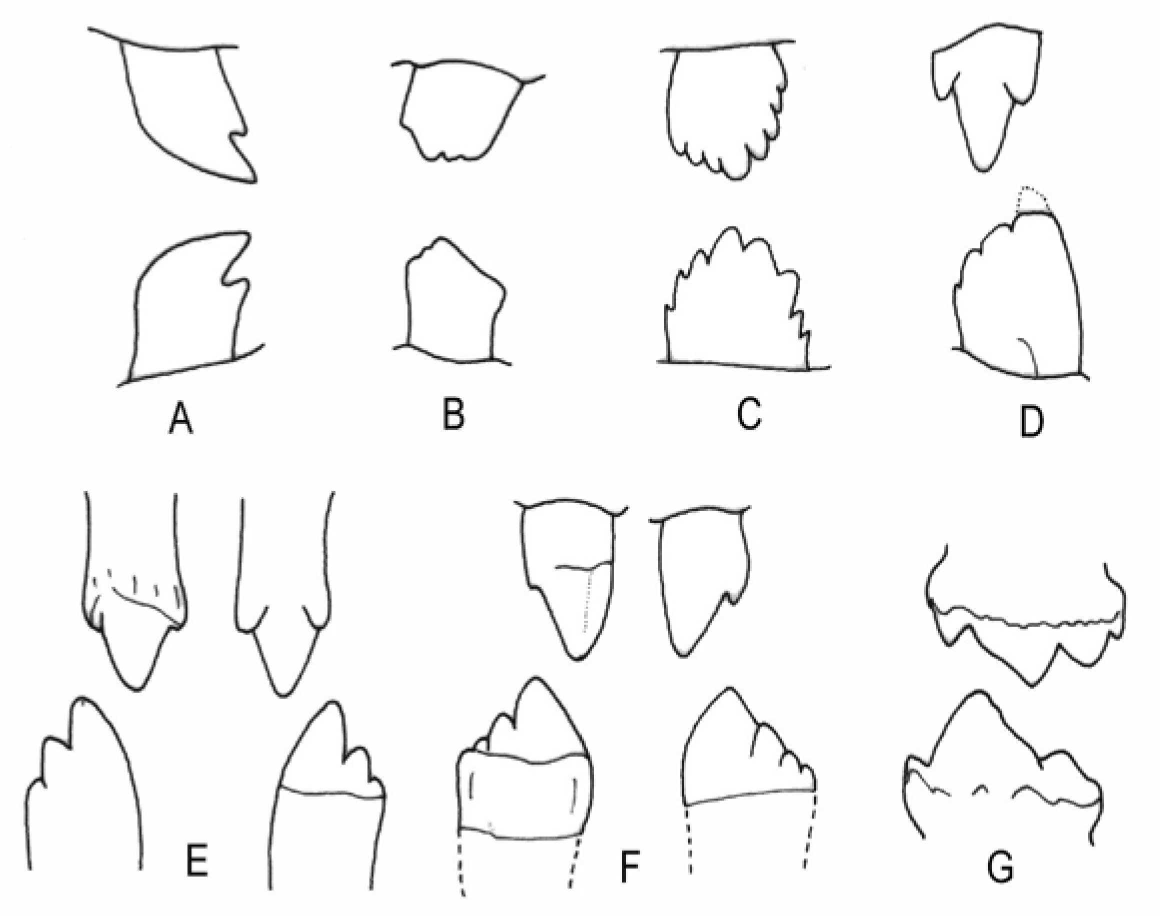


Figure 7. Comparison of upper and lower postcanines among probainognathian cynodonts. **A,** left teeth in buccal view of *Probelesodon* (after Romer, 1969b); **B,** left teeth in buccal view of *Probainognathus* (after Romer, 1970); **C,** left teeth in buccal view of *Riograndia* (after Bonaparte *et al.* , 2001); **D,** left teeth in lingual view of *Irajatherium* ; **E,** right teeth in buccal and lingual views of *Pachygenelus* (after Gow, 1980); **F,** left teeth in lingual and buccal views of *Diarthrognathus* (after Gow, 1980); and **G,** right teeth in lingual view of *Morganucodon* (after Crompton and Jenkins, 1968). Not to scale / *Comparación de los postcaninos superiores e inferiores entre cinodontes probainognatios.* **A,** *dientes izquierdos en vista bucal de* Probelesodon *(modificado de Romer, 1969b);* **B,** *dientes izquierdos en vista bucal de* Probainognathus *(modificado de Romer, 1970);* **C,** *dientes izquierdos en vista bucal de* Riograndia *(modificado de Bonaparte* et al., *2001);* **D,** *diente izquierdo en vista lingual de* Irajatherium; **E,** *dientes derechos en vistas lingual y bucal de* Pachygenelus *(modificado de Gow, 1980);* **F,** *dientes izquierdos en vista lingual y bucal de* Diarthrognathus *(modificado de Gow, 1980);* and **G,** *dientes derechos en vista lingual de* Morganucodon *(modificado de Crompton and Jenkins, 1968). No están a escala.*

The last erupting upper tooth is similar to the cheek teeth of *Pachygenelus* and this condition is one of the main features to consider *Irajatherium* as a Tritheledontidae. However, a buccal cingulum is absent in this postcanine such as in *Chaliminia* , *Riograndia* and most cynodonts, but is it well developed in *Pachygenelus* (Gow, 1980). The buccal cingulum is interpreted a derived character (*e.g* . Crompton and Jenkins, 1968; Hopson and Kitching, 2001), also present in the postcanines of young individuals of *Thrinaxodon* (Crompton and Jenkins, 1968) and in morganucodontids (*e.g* . Crompton, 1963b, 1974; Parrington, 1973). There are strong differences with *Diarthrognathus* in which the postcanines are closely packed, bulbous, bearing a prominent main cusp, and a posterior accessory cusp. The anterior cusp is lost and a mesial cingulum is present in this African genus (Gow, 1980). The available upper postcanines of *Chaliminia* are not well preserved (Bonaparte, 1980), but share with *Irajatherium* the shape of the main cusp and the plesiomorphic condition of the lack of a cingulum. *Riograndia* (Bonaparte *et al.* , 2001) differs from *Irajatherium* because the former has narrower upper postcanines with numerous smaller cusps aligned mesiodistally (figure 7).

Lower dentition (figures 4 and 5)

The number of lower postcanines is unknown due to the fragmentary condition of the dentary; only three postcanines are preserved in the holotype of *Irajatherium* . The first postcanine is in a natural cast of the left dentary (figure 4), and the following two (second and third postcanines) are implanted in a fragment of the dentary bone that fits well to this mold (figure 5.C). The first preserved postcanine (figure 4) is small and bears two cusps. The mesial cusp is high and the distal is very low, both curving backwards. The outline in lateral view of both cusps is rounded. The remaining two teeth are transversely narrow with a well-defined wearing facet on the buccal side (figure 5). The second postcanine (figure 5) is smaller and has four cusps in line that decrease in size backwards; the cusps are separated by shallow furrows. The anterior and posterior edges of the tooth are convex and concave respectively. The third postcanine has the upper edge of the crown broken but the bases of the four cusps are observed. This tooth also has two tiny cingular cusps in line at the base of the mesiolingual edge. Both postcanines show incipient bifurcation of the root on the lingual side.

Comparison (figure 7). The lower postcanine crowns are similar to those of *Pachygenelus* (Gow, 1980). Nevertheless, on the lingual side, *Pachygenelus* has a pronounced cingulum (SAM K 1350) sometimes slightly crenulated (Gow, 1980; in figure 2 of Gow's paper the references are inverted) that becomes better developed on the posterior postcanines. This feature is absent in *Irajatherium* , however two tiny cingular cusps are present on the mesiolingual edge of the base of the crown in the last preserved lower postcanine. In buccal aspect, *Diarthrognathus* is similar to *Pachygenelus* and *Irajatherium* , except for the presence of a deep groove between the anterior high cusp and the remaining smaller cusps. Differing from *Irajatherium* , in *Diarthrognathus* the postcanines are as wide as long in occlusal view, the cusps are mesio-lingual to disto-buccal aligned, and the lingual cingulum is crenulated (Gow, 1980, 1994).

The lower teeth of *Irajatherium* resemble *Chaliminia* (Bonaparte, 1980) in having transversely narrow postcanines, with the same distribution of the cusps and without a fully developed lingual cingulum. In *Riograndia* , the lower postcanines have, as the upper ones, minuscule cusps in line (Bonaparte *et al.* , 2001).

In *Probelesodon* , the lower postcanines have more than three cusps, with the main central cusp strongly curved backwards (Romer, 1969b; PVL 4444). *Probainognathus* bears a prominent central cusp and accessory small cusps mesial and distally located (Romer, 1970; PVL 4445 and 4446).

These morphologic patterns are different to that of *Irajatherium* .

The only lower postcanine preserved of *Therioherpeton cargnini* (Bonaparte and Barberena, 1975, 2001) and those of *Charruodon tetracuspidatus* (Abdala and Ribeiro, 2000) have the four cusps in line; the two central cusps are taller than the mesial and distal cusps. This pattern differs from that of *Irajatherium* , but it is closely similar to that of *Probainognathus* , however the latter taxon has until five cusps in line being the tallest the central one.

Humerus (figure 8)

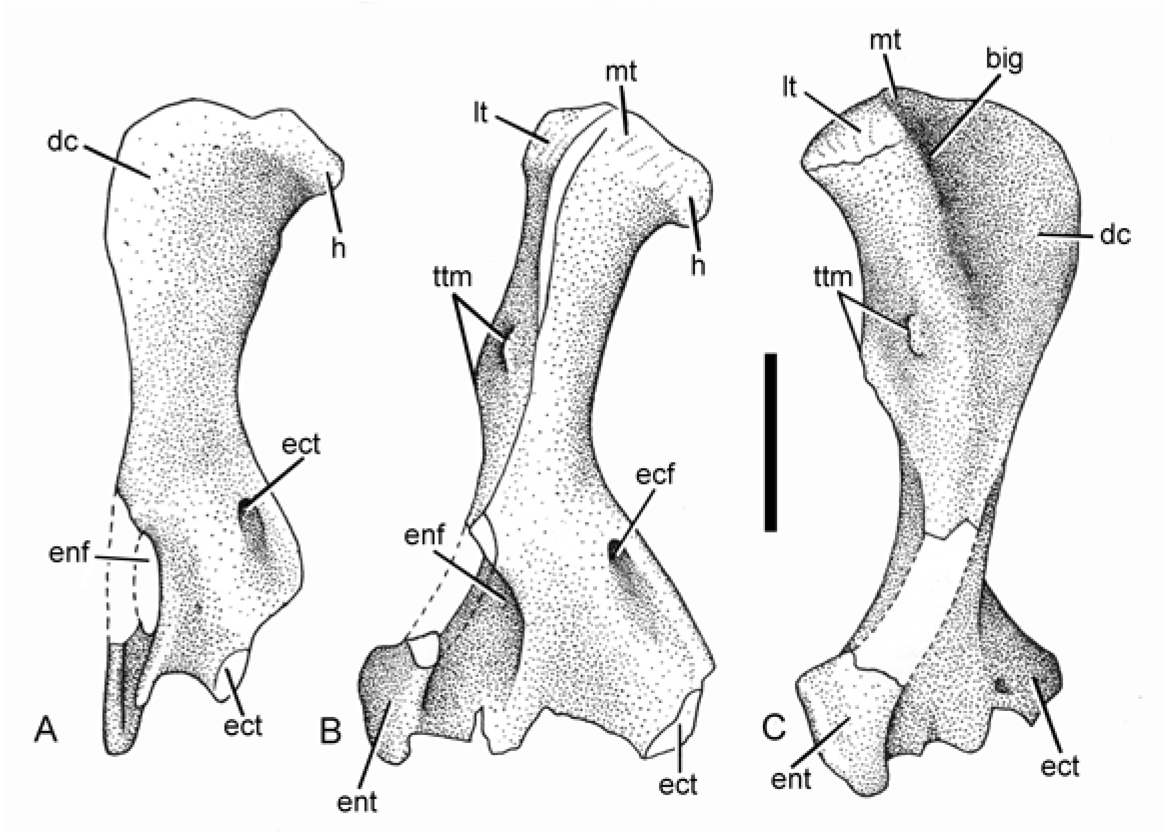


Figure 8. Left humerus of *Irajatherium hernandezi* (UFRGS-PV599T holotype) in lateral (**A),** ventral, (**B)** and medial (**C)** views. Scale bar equals 5 mm. Abbreviations in Appendix 3. / *Húmero izquierdo de* Irajatherium hernandezi *en vistas lateral (* **A)** *; ventral* (**B)** *y medial* ***(* C)** *. La escala representa 5 mm. Abreviaturas en Apéndice 3.*

An almost complete left humerus is preserved; the entepicondylar bridge, the capitulum, and the ulnar condyle are missing. The proximal and principally distal ends are expanded and twisted relative to one another.

The head is well defined and is mediodorsally projected. Proximally, the deltopectoral crest is prominent and it extends by more than half of the shaft length. Distally, the deltopectoral crest connects with the base preserved of the entepicondylar bridge. The proximal edge of the deltopectoral crest is at the level of the humeral head. The position of the deltopectoral crest is almost perpendicular to the main axis of the distal end. The angle between the plane of the head and the lesser tuberosity and the plane of the deltopectoral crest is approximately 90 degrees. The lesser tuberosity stands apart from the head as a medial projected prominence. It is bulbous and well developed medially bearing a striated medial surface possibly for insertion of the subcoracoscapularis muscle (Jenkins, 1971). The major tuberosity is low and almost continuous with the humeral head. The biccipital groove is wide, becoming deeper on the laterodistal side of the lesser tuberosity.

Medioventrally, in the proximal half of the humerus and near the mid portion of the bone there are two well-defined osseous processes (figures 8.B and C), possibly for the insertion of the teres major shoulder muscle (Jenkins, 1971; see also Discussion).

The distal width of the humerus is more than onehalf of the proximo-distal length. The ectepicondyle is dorsoventrally thin. The olecranon fossa is slightly concave; and the capitulum is not preserved. The ectepicondylar foramen is small and opens distally.

The entepicondyle is prominent, separated by a groove from the olecranon fossa. The entepicondyle is flat and lacks a medioproximal projection as in *Thrinaxodon* , ? *Cynognathus* , *Pascualgnathus* , *Luangwa* , and *Probelesodon* (Jenkins, 1971; Bonaparte, 1966a, 1966b; Kemp, 1980; Romer and Lewis, 1973). The ulnar condyle is not preserved. The entepicondylar foramen is large and oval, ventrally covered by the entepicondyle bridge which is partially broken.

Comparison (figure 9). The general aspect of the humerus of *Irajatherium* is comparable to that of several cynodonts and early mammals, which have expanded proximal and distal ends and a short shaft. The angle of the deltopectoral crest is similar to the small sized traversodontids *Pascualgnathus* , *Andescynodon* , and *Massetognathus* (Bonaparte, 1966b; Jenkins, 1970; Abdala, 1999).

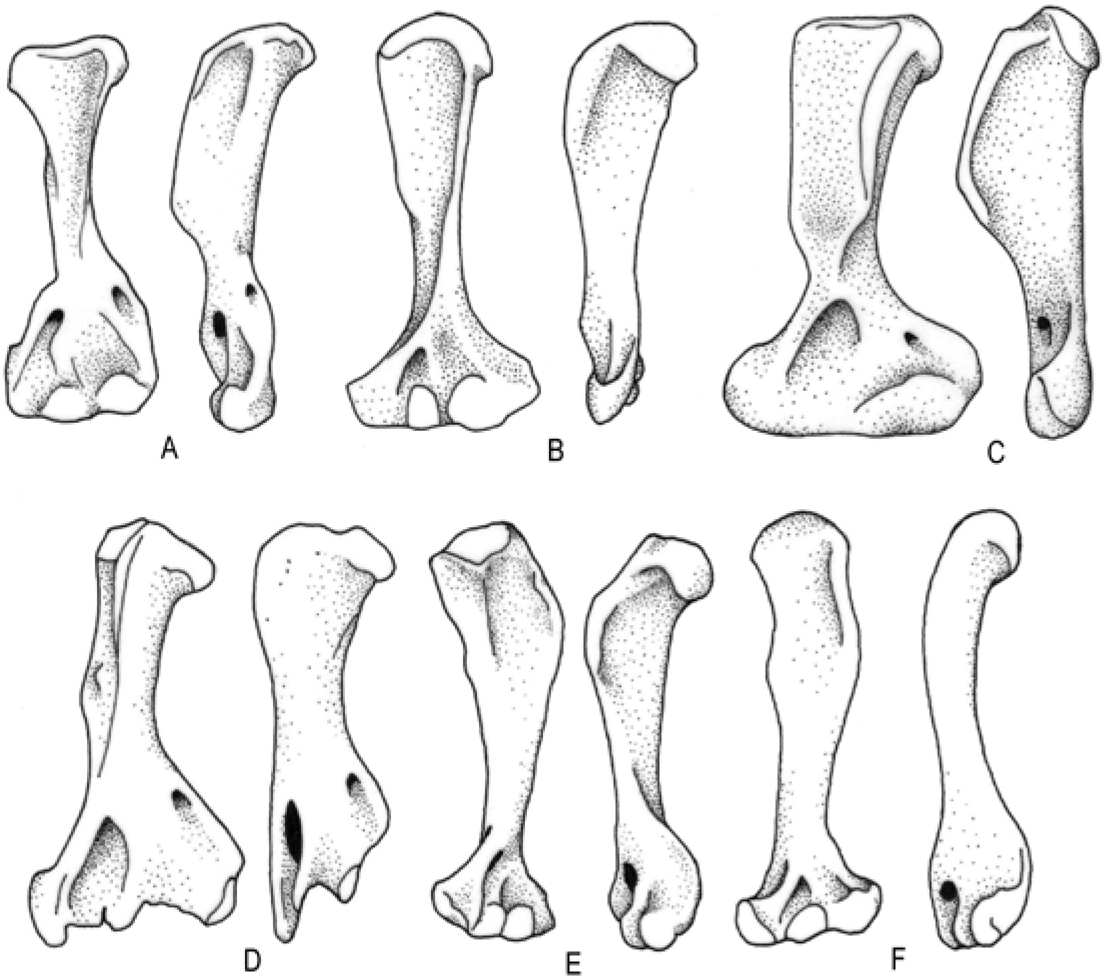


Figure 9. Comparison of the left humerus among eucynodont and mammaliaforms in lateral and ventral views. **A,** the traversodontid *Luangwa* (after Kemp, 1980); **B,** the tritylodontid *Oligokyphus* (after Kühne, 1956); **C,** the probainognathian *Probelesodon* (after Romer and Lewis, 1973); **D,** the tritheledontid *Irajatherium* ; **E,** the morganucodontid *Morganucodon* (after Jenkins and Parrington, 1976); and **F,** the cladotherian *Vincelestes* (after Rougier, 1993). Not to scale / *Comparación del húmero izquierdo entre eucinodontes y mamaliaformes en vistas lateral y ventral.* **A,** *el traversodóntido* Luangwa *(modificado de Kemp, 1980);* **B,** *el tritilodóntido* Oligokyphus *(modificado de Kühne, 1956);* **C,** *el probainognatia* Probelesodon *(modificado de Romer and Lewis, 1973);* **D,** *el triteledóntido* Irajatherium; **E,** *el morganucodóntido* Morganucodon *(modificado de Jenkins and Parrington, 1976); y* **F,** *el cladoterio* Vincelestes *(modificado de Rougier, 1993). No están a escala.*

The shape of the lesser tuberosity as well as the biccipital groove of *Irajatherium* is similar to that of most cynodonts, morganucodontids (Jenkins and Parrington, 1976), and monotremes (Murray, 1978; Gambaryan and Kielan-Jaworowska, 1997). Nevertheless, *Irajatherium* has the biccipital groove deeper proximally as in the digging multituberculate ? *Lambdopsalis bulla* (Kielan-Jaworowska and Qi, 1990) and some fossorial therians (*e.g* . Gambaryan and Kielan- Jaworowska, 1997).

In *Irajatherium* , the two processes for the teres major muscle are here considered a derived feature. *Pascualgnathus polanski* (Bonaparte, 1966b), *Massetognathus pascuali* (Jenkins, 1970), ? *Cynognathus* (Jenkins, 1971), *Luangwa drysdalli* (Kemp, 1980), and *Morganucodon* (Jenkins and Parrington, 1976) have a groove and a crest in the same position, which were considered to attach the teres major or the latissimus dorsi muscles (*e.g* . Jenkins, 1971). This structure in *Pascualgnathus* was interpreted for the attachment of the triceps muscle (Bonaparte, 1966b), but probably this crest refers to the teres major or the latissimus dorsi muscles. The presence of an area for the attachment of the teres major muscle is a feature observed in most mammals. Thus, in the metatherians *Didelphis* (personal observation) and *Mayulestes ferox* (Muizon, 1998) there is a weak tuberosity located on the medial side below the lesser tuberosity for the teres major muscle, while in other recent mammals such as edentates (personal observation) there is a well-marked crest for both teres major and latissimus dorsi muscles.

The humerus of *Irajatherium* differs from that of *Pachygenelus* (Hopson, personal communication; Gow, 2001) and *Morganucodon* (Jenkins and Parrington, 1976) because the deltopectoral crest is not reduced, the shaft is thicker and more robust, and the entepicondyle is relatively flat (i.e. not strongly projected to the mediodistal side). Despite the similarities among the humerus of *Pachygenelus* , tritylodonts, *Morganucodon* , and *Vincelestes* , the three latter taxa lack an ectepicondylar foramen. Absence of this foramen in tritylodonts is probably convergent with mammaliaforms (*e.g* . Hopson and Kitching, 2001).

Femur (figure 10)

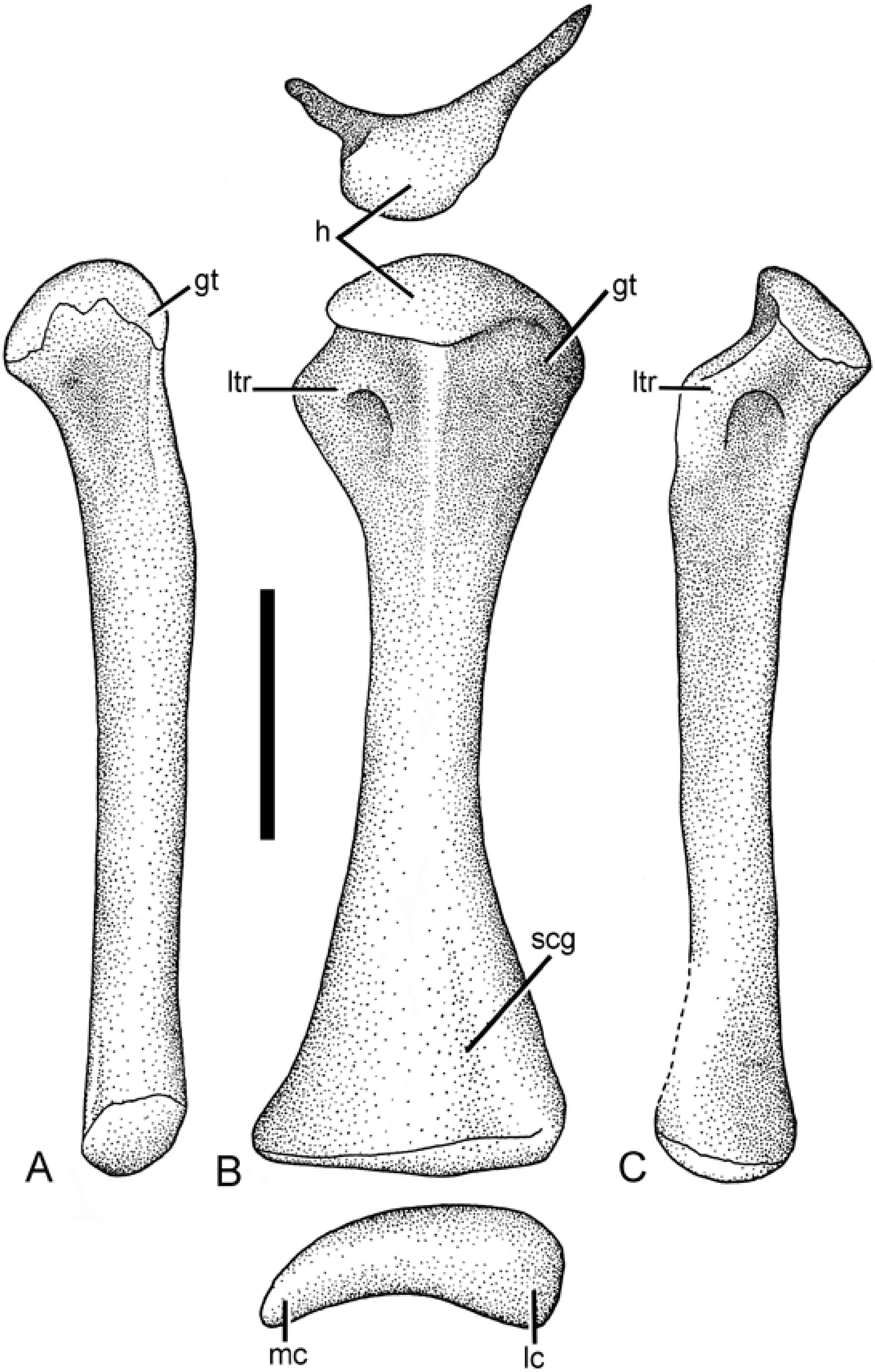


Figure 10. Left femur of *Irajatherium hernandezi* (UFRGS-PV599T holotype) in lateral **(A)** , dorsal **(B)** and medial **(C)** views. Scale bar equal 5 mm. Abbreviations in Appendix 3 / *Fémur izquierdo de* Irajatherium hernandezi *en vistas lateral* **(A)** *, dorsal* **(B)** *y medial* **(C)** *. La escala representa 5 mm. Abreviaturas en Apéndice 3.*

Only the left femur of *Irajatherium* is preserved. The femoral head is convex, dorsomedially projected, and without a well defined neck. Distally to the femoral head, there is a smooth ridge defining a shallow lateral and a deep medial concave area, for the attachment of the pubio-ischio-femoralis internus muscle (Jenkins, 1971).

The greater trochanter is laterally projected at the same level of the femoral head, and is continuous with the latter. This trochanter is thin and less developed than in *Exaeretodon* (Bonaparte, 1963), *Massetognathus* (Jenkins, 1970), ? *Cynognathus* (Jenkins, 1971), and *Luangwa* (Kemp, 1980). The lesser trochanter has a more proximal position than in most eucynodonts (*e. g. Exaeretodon* , *Massetognathus* and *Probelesodon* ; Bonaparte, 1963; Jenkins, 1970; Romer and Lewis, 1973).

This trochanter is medially projected and separated from the femoral head. The femoral shaft is thin, cylindrical in cross section, with the lateral border more concave than the medial one. The distal half is wider than the proximal. The lateral condyle is more prominent than the medial one, but the latter is more laterally projected. The supracondylar groove is shallow reaching the lateral condyle.

Comparison (figure 11). The femur of *Irajatherium* , as in *Therioherpeton* , has more derived features than that of *Probelesodon* , but it clearly presents more plesiomorphic traits than that of *Pachygenelus* , *Oligokyphus* and *Morganucodon* .

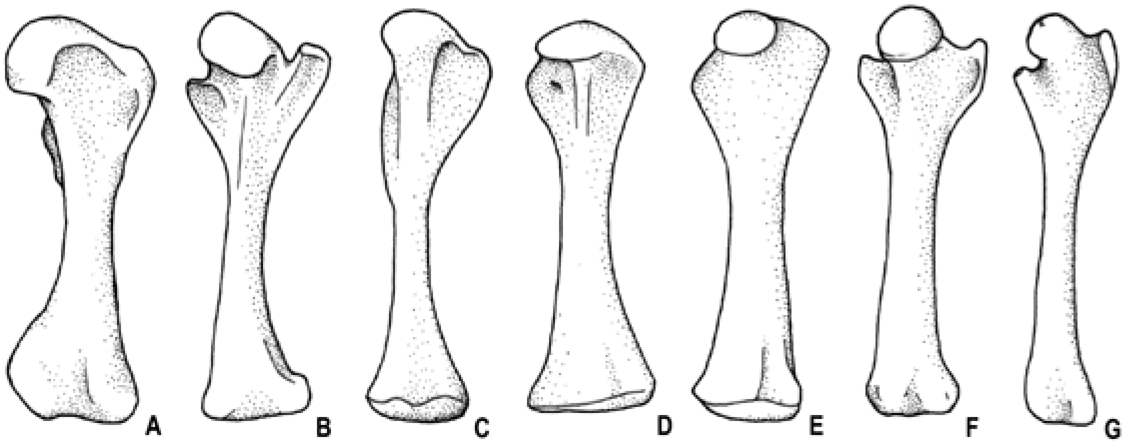


Figure 11. Comparison of the left femur among eucynodont and mammaliaforms in dorsal view. **A,** the traversodontid *Exaeretodon* (after Bonaparte, 1963); **B,** the tritylodont *Oligokyphus* (after Kühne, 1956); **C,** the probainognathian *Probelesodon* (after Romer and Lewis, 1973); **D,** the tritheledontid *Irajatherium* ; **E,** the probainognathian *Therioherpeton* (after Bonaparte and Barberena, 2001); **F,** the morganucodontid *Morganucodon* (after Jenkins and Parrington, 1976); and **G,** the cladotherian *Vincelestes* (after Rougier, 1993). Not to scale. / *Comparación del fémur izquierdo entre eucinodontes y mamaliaformes en vista dorsal.* **A,** *el traversodóntido* Exaeretodon *(modificado de Bonaparte, 1963);* **B,** *el tritilodóntido* Oligokyphus *(modificado de Kühne, 1956);* **C,** *el probainognatia* Probelesodon *(modificado de Romer y Lewis, 1973);* **D,** *el triteledóntido* Irajatherium; **E,** *el probainognatia* Therioherpeton *(modificado de Bonaparte and Barberena, 2001);* **F,** *el morganucodóntido* Morganucodon *(modificado de Jenkins y Parrington, 1976); y* **G,** *el cladoterio* Vincelestes *(modificado de Rougier, 1993). No están a escala.*

The projection of the head is similar to *Therioherpeton* , *Pachygenelus* , and *Morganucodon* (Bonaparte and Barberena, 2001; Jenkins and Parrington, 1976; Garbaryan and Averianov, 2001), while it is more medially projected in most cynodonts. The head of the femur of *Irajatherium* is bulbous as in *Exaeretodon* , *Massetognathus* , ? *Cynognathus* , and *Luangwa* (Bonaparte, 1963; Jenkins 1970, 1971; Kemp, 1980). In most non-mammalian cynodonts (*e.g* . *Probelesodon* ; Romer and Lewis, 1973) the greater trochanter is more distally located than in *Irajatherium* . The location and projection of the lesser trochanter is similar to *Therioherpeton* (Bonaparte and Barberena, 2001), *Pachygenelus* , tritylodontids (Kühne, 1956; Sues, 1983) and *Morganucodon* (Jenkins and Parrington, 1976). The medial projection of the lesser trochanter in *Therioherpeton* was interpreted

(Bonaparte and Barberena, 2001) as a local deformation, however its position on the medial surface of the femur is a derived feature and possibly related to the enlargement of the ventral fossa for the insertion of the adductor musculature and the pubo-ischio-femoralis internus muscle (Jenkins, 1971).

The proximal portion of the femur of *Irajatherium* is very similar to that of *Therioherpeton* , but the latter seems to have the head less developed. In *Pachygenelus* , tritylodontids, *Morganucodon* , and *Vincelestes* there is a distinctive notch between the head and the greater trochanter. In addition, the femoral head of *Morganucodon* and *Vincelestes* is globular with a fovea capitis, and a well defined femoral neck.

In *Irajatherium* the relative size and projection of both condyles seem to be similar to that of *Morganucodon* (Jenkins and Parrington, 1976); but in the latter the condyles are more convex. Jenkins and Parrington (1976) noted that when the supracondylar groove ends on the lateral condyle, the fibula participate in the knee joint, while when this groove ends between both distal condyles (condition present in most eutherians mammals), there is not articulation of the fibula with the femur. A lateral facet for articulation of the fibula is not observed in *Irajatherium* , nevertheless and according to Jenkins and Parrington (1976) it is most probable that the fibula contacted with the femur due to the lateral position of the supracondylar groove.

Discussion

Phylogenetic relationships of *Irajatherium hernandezi* . In the last years, the tritheledontids were considered to be the sister group of mammaliaforms (*e.g* . Hopson and Barghusen, 1986; Shubin *et al.* , 1991; Crompton and Luo, 1993; Luo and Crompton, 1994; Luo, 1994; Luo *et al.* , 2002; Hopson and Kitching, 2001). *Pachygenelus* , the best known tritheledontid, shares with Mammaliaformes a large number of synapomorphies specially in basicranial and palatal regions, upper and lower dentitions, and postcranium as well (*e.g* . Allin and Hopson, 1992; Hopson and Barghusen, 1986; Shubin *et al.* , 1991; Crompton and Luo, 1993; Luo, 1994; Luo and Crompton, 1994; Gow, 2001; Hopson and Kitching, 2001).

In most studies (*e.g* . Hopson and Barghusen, 1986; Rowe, 1988; Sidor and Hopson, 1998; Crompton and Luo, 1993), the Tritheledontidae is treated as a natural group, but the phylogenetic relationships among their members are not clear. Bonaparte (1980) proposed the family Pachygenelidae to include *Chaliminia musteloides* and *Pachygenelus monus* , and Tritheledontidae to include *Trithelodon riconoi* and *Diartrognathus broomi* . Later authors did not follow this proposal. More recently, a new family Riograndidae was erected for the only species *Riograndia guaibensis* (Bonaparte *et al.* , 2001), based on the particular morphology of its dentition. In the phylogenetic analysis of Hopson and Barghusen (1986), the diagnostic characters of tritheledontids were: three upper incisors, first lower incisor enlarged, upper postcanine teeth with lateral surface of the main cusp bulging laterally, and an extremely long bony secondary palate. Later, Crompton and Luo (1993) diagnosed the Tritheledontidae by: reduced number of incisors, bulbous upper postcanines, and a large descending process of the frontal. *Irajatherium hernandezi* is here referred to the family Tritheledontidae due to the morphology of the upper last erupting postcanine and the lower postcanines which resemble those of *Pachygenelus monus* (Watson, 1913; Gow, 1980) and *Chaliminia musteloides* (Bonaparte, 1980). A cladistic analysis was performed here in to test the position and relationships of *Irajatherium hernandezi* among eucynodonts. The taxa analyzed included 14 non-mammalian cynodonts and two mammaliaforms. *Thrinaxodon* was used as outgroup taxon and to root the tree. Ingroup taxa are represented by *Cynognathus* , *Exaeretodon* , *Lumkuia* , *Chiniquodon* , *Probelesodon* , *Probainognathus* , *Prozostrodon* , *Therioherpeton* , *Riograndia* , *Chaliminia* , *Irajatherium* , *Pachygenelus* , *Diarthrognathus* , and the early mammaliaforms *Sinoconodon* and *Morganucodon* .

Tritylodontidae is excluded of this analysis because they have many derived features (*e.g* . Kemp, 1982, 1983; Wible, 1991; Luo, 1994, 2001) possibly acquired in parallel to the Probainognathia clade (*e.g* . Sues, 1985; Hopson and Barghusen, 1986; Hopson and Kitching, 2001). The ingroup taxa were selected following previous analyses (*e.g* . Hopson and Barghusen, 1986; Crompton and Luo, 1993; Rowe, 1988; Luo and Crompton, 1994; Luo, 1994; Martinez *et al.* , 1996; Luo *et al.* , 2001, 2002; Hopson and Kitching, 2001).

The matrix (Apendix 1) is composed of 63 characters (character list in Appendix 2), most of which were taken from previously published studies, especially the analysis of Hopson and Kitching (2001) and Luo (1994). Modifications in some character-states and scored data were made and also new characters were added. All characters have the same weight and the multi-state characters were treated as unordered. The data matrix was analyzed under program NONA version 2.0 (Gologoff, 1993) using a heuristic search and edited with Winclada (Nixon, 1999). In the analysis, four most parsimonious trees of 129 steps, a consistency index of 0.65 and a retention index of 0.73 were obtained. The strict con *sensu* s of these trees is shown in figure 12.

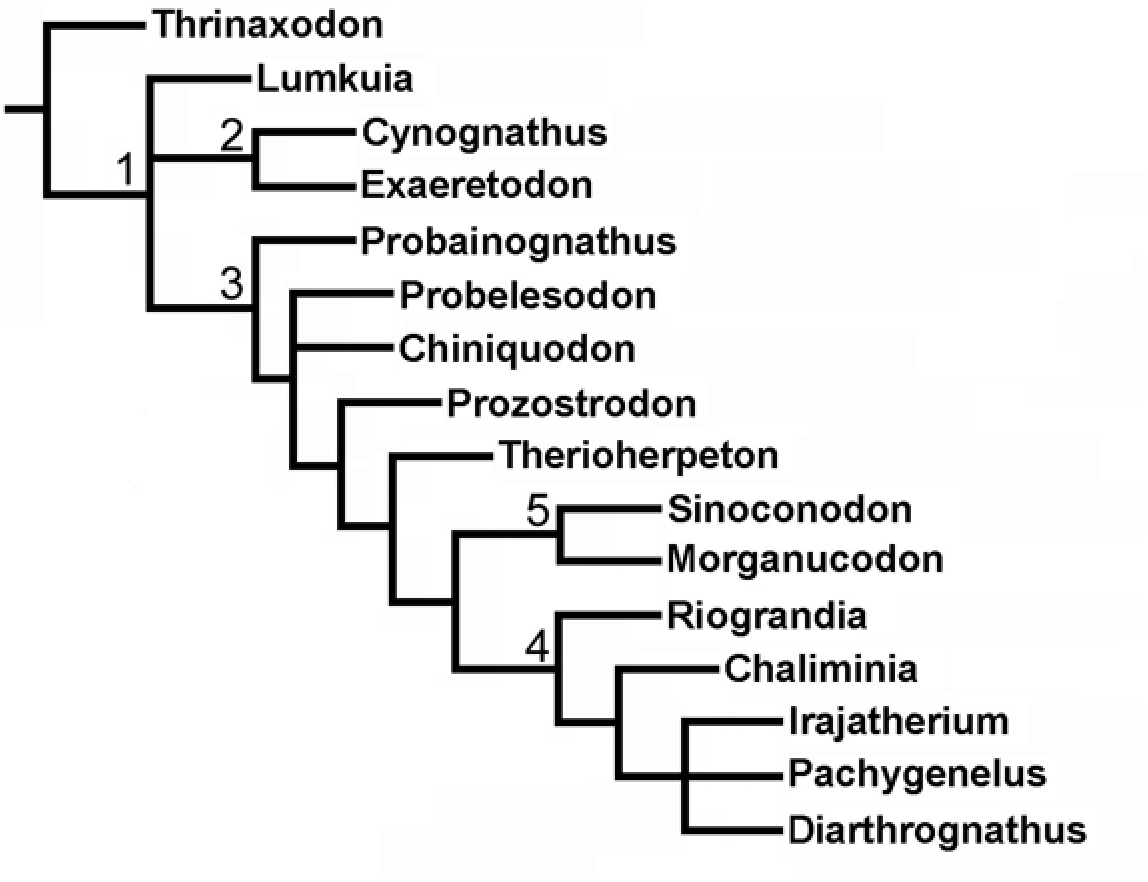


Figure 12. Strict consensus of the four most parsimonious trees obtained under NONA program and edited with Winclada. Clades: 1, Eucynodontia; 2, Cynognathia; 3, Probainognathia; 4, Tritheledontidae; 5, Mammaliaformes. / *Consenso estricto de los cuatro árboles más parsimoniosos obtenido por el programa NONA y editados con Winclada.*

In all the trees *Cynognathus* and *Exaeretodon* , representing the Cynognathia clade (Hopson and Barghusen, 1986), share the presence of posterodorsal mandibular movement during the occlusion (Ch. 2); sequential addition posteriorly of postcanine replacement (Ch. 8); unfused parietals (Ch. 27); zygomatic arch dorsally extended above the middle of the orbit (Ch. 34); presence of jugal suborbital process (Ch. 36); very deep squamosal groove for the external auditory meatus (Ch. 37); absence of the internal carotid foramina in the basisphenoid (Ch. 40); and greatest width of the zygomatic arch at the posterior end (Ch. 44). *Lumkuia fuzzi* , the most plesiomorphic taxon of the

Probainognathia clade (*sensu* Hopson and Kitching, 2001), is unresolved in this analysis, forming a trichotomy with Cynognathia and Probainognathia (figure 12). The clade Probainognathia is supported by two unequivocal and one equivocal synapomorphies: the premaxilla forms the posterior border of the incisive foramen (Ch. 24); the frontal contacts the palatine in the orbit (Ch. 38); and the fenestra rotunda and jugular foramen are partially separated by a fingerlike projection from the posterolateral wall of the jugular foramen (Ch. 47). *Probelesodon* and *Chiniquodon* are sister taxa of *Prozostrodon* and the most inclusive clade. Both chiniquodontid genera are not resolved in this analysis. The clade including *Prozostrodon* , *Therioherpeton* , Tritheledontidae, and Mammaliaformes is supported by five unequivocal and one equivocal synapomorphies: unilateral occlusion (Ch. 1); dorsomedial mandibular movement during occlusion (Ch. 2); presence of constricted root on the postcanines (Ch. 9); presence of wear facets on the postcanines (Ch. 18, absent in *Sinoconodon*) (Ch. 19); and presence of an unfused symphysis (Ch. 21). The postorbital bone was described in *Prozostrodon* (Bonaparte and Barberena, 2001), but it possibly corresponds to the anterolateral projection of the parietal, similar to *Therioherpeton* (Bonaparte and Barberena, 1975, 2001). *Therioherpeton* , Tritheledontidae, and Mammaliaformes share the absence of prefrontal (Ch. 32) and postorbital bones (Ch. 33). In addition, the sutures of the prefrontal bone, if present, are not clear in the holotype of *Prozostrodon* . However, until new studies of this material are done, we will follow the interpretation of Bonaparte and Barberena (2001). *Sinoconodon* and *Morganucodon* share two unequivocal features: squamosal glenoid cavity facing ventrally and separated from the cranial moiety by a neck (Ch. 22), and the presence of the stapedial muscle fossa (Ch. 48). In addition, they share four equivocal synapomorphies: characters 11(1); 24(0); 41(1) and 42(2). The tritheledontid group is supported by one unequivocal and two equivocal synapomorphies: presence of three upper incisors (Ch. 3); some incisor enlarged (unequivocal, Ch. 5); and the presence of an interpterygoid vacuity (Ch. 29). *Riograndia* is considered the most plesiomorphic taxon within the Tritheledontidae. *Chaliminia* , *Irajatherium* , *Pachygenelus* , and *Diarthrognathus* share one unequivocal and three equivocal synapomorphies: presence of middle and posterior lower postcanines with four cusps aligned that decreasing in size backward (unequivocal, Ch. 14); posterior portion of the maxillary tooth row that extends medial to the temporal fossa (Ch.16); axis of the posterior part of the maxillary tooth row directed toward the medial rim of the temporal fossa (Ch. 17); and the tooth row oriented parallel or subparallel to the axial plane of the cranium (Ch. 20). *Irajatherium* , *Pachygenelus* , and *Diarthrognathus* form an unresolved trichotomy. These taxa share five unequivocal synapomorphies: two upper (Ch. 3) and two lower incisors (Ch. 4); presence of a dominant central bulbous main cusp on upper postcanines (Ch. 12); presence of lower teeth much larger than the uppers ones (Ch. 15); and the squamosal formed a broad and anteroventrally facing glenoid cavity (Ch. 22). The characters 3, 4 and 22 are unknown in *Irajatherium* . This analysis supports that Tritheledontidae are the sister taxon of Mammaliaformes without considering the two newly described *Brasilodon quadrangularis* and *Brasilitherium riograndensis* from Caturrita Formation (Rio Grande do Sul, Brazil). Nevertheless, these latter taxa are depicted as more closely related to Mammaliaformes than are the tritheledontids as can be seen in the analysis of Bonaparte *et al.* (2003). **Dental features.** Gow (1980) noted that *Pachygenelus* has the most generalized dentition among tritheledontids. However, *Riograndia* , *Chaliminia* , and *Irajatherium* are still more plesiomorphic, due to the lack of a cingulum in the upper and lower postcanines. Among these taxa *Riograndia* shows a plesiomorphic tooth morphology directly related with the more derived type of the tritheledontid's postcanines (Bonaparte *et al.* , 2001).

The strong wear facets present on the buccal side of the lower postcanines of *Irajatherium* indicated dorsomedial movements of the lower jaw during mastication, similar to *Pachygenelus* (Gow, 1980; Shubin *et al.* , 1991), *Diarthrognathus* (Gow, 1980), and *Riograndia* (Bonaparte *et al.* , 2001). Despite the sharp wear facets, no other precise pattern of occlusion between upper and lower postcanines were observed. Patterns of occlusion are present in mammaliaforms (*e.g* . *Morganucodon* and *Megazostrodon* ; Mills, 1971; Crompton, 1974; Gow, 1986), however in

Sinoconodon , despite having a well-developed mandibular condyle, wear facets are not observed (Crompton and Sun, 1985; Crompton and Luo, 1993). In *Irajatherium* , the mesiodistal length of the upper postcanines is almost one-half the length of the lower postcanines, similar to *Pachygenelus* and *Diarthrognathus* (Gow, 1980). This condition could represented a carnassial specialization in which the lower postcanines become narrower and elongated mesiodistally. The pattern of canine and postcanines replacement in *Irajatherium* is alternate as in most carnivorous non-mammalian cynodonts (*e.g* . Crompton, 1963b). This replacement is evidenced by the fact that the eruption of the first upper postcanine occurred long after the eruption of the second upper postcanine.

In *Irajatherium* there are at least two variants of crown morphology in the upper postcanines: one present in the anterior postcanines and the other in the last tooth, which resembles the postcanines of *Pachygenelus* . Possibly, the new generation of the posteriormost postcanines has a crown morphology more complex than the older teeth. However, this kind of replacement is not documented in the anteriormost postcanines because the erupting first tooth (a new generation) is similar to the second tooth that represents an older generation. *Pachygenelus* has also an alternate replacement, with different waves of replacement resulting in the same morphological type of tooth (Gow, 1980). In *Thrinaxodon* , the Early Triassic sister taxon of all Eucynodontia (*e.g* . Hopson and Kitching, 2001), an inverse replacement pattern has been noted (*e.g* . Crompton and Jenkins, 1968). The upper and lower postcanines of young individuals of *Thrinaxodon* have a crown morphology similar to that of *Morganucodon* that are replaced in older specimens with more simple postcanines (Parrington, 1936; Crompton, 1963b; Crompton and Jenkins, 1968). Gomphodont eucynodonts, which loose the anterior postcanines and add new larger postcanines at the end of the tooth row, also have different crown morphologies involved in the dental replacement (*e.g* . Fourie, 1963; Hopson, 1971; Crompton, 1972; Goñi, 1986). The Early-Middle Triassic gomphodont *Andescynodon mendozensis* (Bonaparte, 1969) shows in its juvenile stage posterior sectorial postcanines that are replaced by gomphodont teeth (Goñi, 1986; Goñi and Goin, 1987). In non-mammalian cynodonts the types of postcanines are classified following their morphology and placement on the dentary, but not according to their ontogenetic patterns as in mammals (the premolars are the only postcanine with replacement; *e.g* . Owen, 1845). In many mammals, the deciduous teeth are morphologically more complex than the permanent ones or quite similar (*e.g* . in *Morganucodon* the last deciduous premolar is molarized and in marsupials the only replacement, the dP3, is a molariform which is replaced by P 3 similar to the other premolars). The new posterior tooth of *Irajatherium* is more complex than the remaining postcanine as in gomphodonts but differing from *Thrinaxodon* and many mammals. This probably indicates that new types of teeth in a later stage of the ontogeny are a consequence of a different type of diet. In addition, the replacement waves of *Irajatherium* could be a useful reference to infer a possible mechanism of dental differentiation among non-mammalian cynodonts.

Irajatherium has a constricted root on the lingual side of the upper postcanines and on the buccal side of the lower ones. The incipient bifurcation of some roots on upper and lower teeth occurs in tritheledontids (except *Chaliminia* ; Bonaparte, 1980), *Therioherpeton* (Bonaparte and Barberena, 1975, 2001), and *Microconodon* (Sues, 2001). An incomplete separation of the roots occurs in some postcanines of *Sinoconodon* (Crompton and Luo, 1993; Luo, 1994). A fully division occurs in the ?chiniquodontid *Mitredon cromptoni* (Shapiro and Jenkins, 2001) and in Mammaliaformes. In *Morganucodon* this feature varies in the tooth row, some postcanine roots are completely separated whereas others are not. Shapiro and Jenkins (2001) claimed that tooth root bifurcation was developed more than once in the evolution of the nonmammalian cynodonts and early mammals, an interpretation that we follow here.

Postcranial features and adaptations. The knowledge of postcranial remains in tritheledontids was only based on *Pachygenelus* (Gow, 2001; Hopson and Kitching, 2001). The humerus and the femur of this taxon closely resemble that of *Morganucodon* (unpublished remains, Hopson, personal communication).

Some features observed in the humerus of *Irajatherium* might suggest burrowing adaptation. The presence of robust, short, heavily muscled, and large-clawed forelimbs represent a type of fossorial adaptations to digging (Dubost, 1968). These features are observed in the digging insectivorous moles Talpidae (Dubost, 1968) and the golden moles Chrysochloridae (Hickman, 1990), among others. Kielan-Jaworowska and Qi (1990) expressed that "it seems possible that adaptations for digging were more common among early mammals...". We think that this interpretation may also apply to several non-mammalian cynodonts (Sues, 1983). As the only forelimb bone preserved of *Irajatherium* is the humerus (figure 7), it is difficult to make unequivocal interpretations about functionality and behavior. Nevertheless, the combination of some features would indicate adaptations to dig or eventually to burrow: 1) the humerus of *Irajatherium* has a proximally deep biccipital groove as in the presumably digging multituberculate ? *Lambdopsalis bulla* (Kielan-Jaworowska y Qi, 1990) and some fossorial therians; 2) the lesser tuberosity is prominent representing a plesiomorphic feature among cynodonts, but may also indicate a burrow adaptation because a large lesser tuberosity is present in burrowing mammals with sprawling forelimbs increasing the function of the subscapularis and scapulohumerus muscles (homologous to subcoracoscapularis muscle of non-mammalian cynodonts; Jenkins, 1971) (Gambaryan and Kielan-Jaworowska, 1997); 3) the presence of well developed osseous processes for the teres major muscle is also evident in some non-mammalian cynodonts, early mammals, and in current fossorial mammals such as edentates (*e.g* . *Dasypus* , personal observation). The teres major muscle, jointly with other muscles, is a medial rotator and adductor of the humerus (Jenkins and Weijs, 1979; Argot, 2001). Based on the great development of the processes for the teres major in *Irajatherium* it is probable that in concordace this muscle was also well developed, increasing its functionality; 4) the deltopectoral crest is well developed in the humerus of *Irajatherium* . The position of this crest is similar to that of small traversodontids and some chiniquodontids, but the angle between the plane of the head and the lesser tuberosity and the plane of the deltopectoral crest is more reduced than in large sized nonmammalian cynodonts (Abdala, 1999). Finally, Groenewald *et al.* (2001) described burrow complexes in outcrops of the Early Triassic of South Africa in which the gomphodont cynodont *Trirachodon* was found inside. No functional studies were done in this taxon but probably it represents an example of fossorial behavior in cynodonts. However, further studies and new materials are needed to clarify these paleobiological inferences.

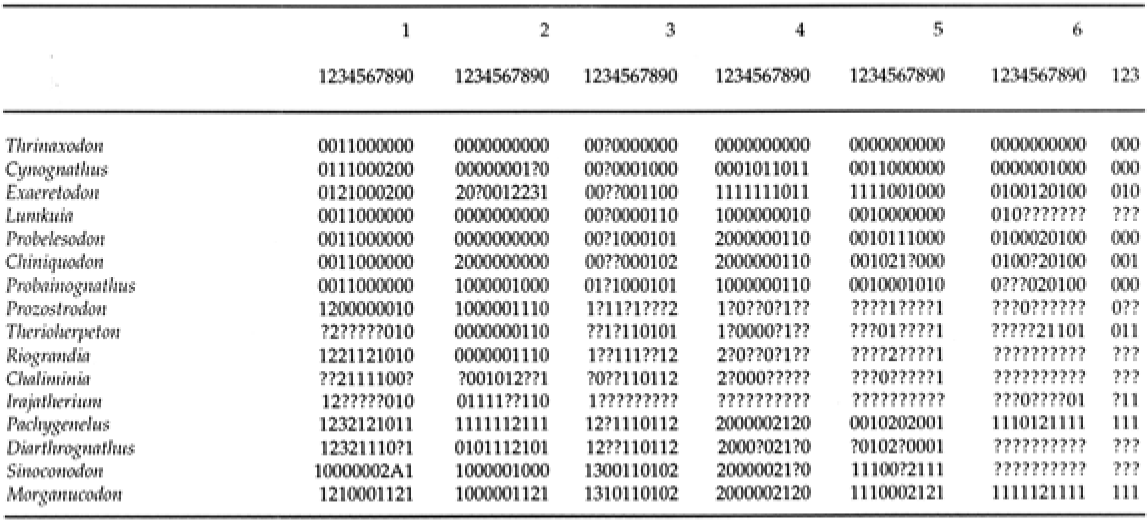
Conclusions

Irajatherium hernandezi is here considered a new tritheledontid closely related to the African and North American *Pachygenelus monus* and the African *Diarthrognathus broomi* . Five taxa, *Riograndia* , *Chaliminia* , *Irajatherium* , *Pachygenelus* , and *Diarthrognathus* , are included within the family Tritheledontidae.

The dentition of *Irajatherium* is clearly more complex than that of the South American *Riograndia* and *Chaliminia* , but less specialized than those of *Pachygenelus* and *Diarthrognathus* . The presence of two different kinds of upper postcanines in alternate replacement waves in *Irajatherium* could offer evidence for possible mechanism of dental differentiation among cynodonts taxa. However further studies and new specimens are needed to corroborate these inferences. Possible fossorial adaptations are documented in the humerus of *Irajatherium* ; and these features, related to digging or burrowing, might be common in several small-bodied non-mammalian cynodonts.

Appendix 1. Data matrix

Distribution of the character-states for the 63 characters listed in Appendix 2 among 15 ingroup taxa and 1 outgroup taxon considered in this analysis. Coding for character-states: 0, primitive; 1 to 3, derived; ?, missing information or uncertain character-states; A, polimorphic condition 1+2. We studied the following specimens for comparison and character scorings: *Exaeretodon frenguellii* : MACNPV 15175, MACN-PV 18114, MACN-PV 18125, PVL 2079 and PVL 2162; *Probainognathus jenseni* : MACN-PV 18916, PVL 3857, PVL 4445, PVL 4446, PVL 4678, PVL 5442 and MCZ 4015; *Probelesodon* sp.: PVL 4444; *Chaliminia musteloides* : PVL 3857; *Riograndia guaibensis* : MCNPV 2264; MCN-PV 2265, MCN-PV 2271; *Prozostrodon* brasiliensis: UFRGS-PV 0248 T; *Pachygenelus monus* : SAM K 1350; *Diarthrognathus broomi* : MCZ without number; *Vincelestes neuquenianus* : MACN-PV N 38 and MACN-PV N 39. Other anatomical information was taken from the literature.



	1	2	3	4	5	6	
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	123
Thrinaxodon	0011000000	0000000000	00?0000000	0000000000	0000000000	0000000000	000
Cynognathus	0111000200	00000001?0	00?0001000	0001011011	0011000000	0000001000	000
Exaeretodon	0121000200	20?0012231	00??001100	1111111011	1111001000	0100120100	010
Lumkuia	0011000000	0000000000	00?0000110	1000000010	0010000000	010???????	???
Probelesodon	0011000000	0000000000	00?1000101	2000000110	0010111000	0100020100	000
Chiniquodon	0011000000	2000000000	00??000102	2000000110	001021?000	0100?20100	001
Probainognathus	0011000000	1000001000	01?1000101	1000000110	0010001010	0???020100	000
Prozostrodon	1200000010	1000001110	1?11?1???2	1?0??0?1??	????1????1	???0??????	0??
Therioherpeton	?2?????010	0000000110	??1?110101	1?0000?1??	???01????1	?????21101	011
Riograndia	1221121010	0000001110	1??111??12	2?0??0?1??	????2????1	??????????	???
Chaliminia	??2111100?	?001012??1	?0??110112	2?000?????	???0?????1	??????????	???
Irajatherium	12?????010	01111??110	1?????????	??????????	??????????	???0????01	?11
Pachygenelus	1232121011	1111112111	12?1110112	2000002120	0010202001	1110121111	111
Diarthrognathus	12321110?1	0101112101	12??110112	2000?021?0	?0102?0001	??????????	???
Sinoconodon	10000002A1	1000001000	1300110102	20000021?0	11100?2111	??????????	???
Morganucodon	1210001121	1000001121	1310110102	2000002120	1110002121	1111121111	111

Appendix 2. Phylogenetic analysis

List of characters used in the phylogenetic analysis:

1. Mode of occlusion: bilateral (0) or unilateral (1) (Luo, 1994).
2. Direction of mandibular movement during occlusion: orthal (0), posterodorsal (1) or dorsomedial (2) (Luo, 1994).
3. Upper incisor number: 5 or more (0), 4 (1), 3 (2) or 2 (3) (modified from Hopson and Kitching, 2001).
4. Lower incisor number: 4 or more (0), 3 (1) or 2 (2) (modified from Hopson and Kitching, 2001).
5. Some incisor enlarged: absent (0) or present (1).
6. Upper incisor size: all small (0), incisor 1 enlarger and the others small (1) or incisor 2 enlarger and the others small (2).
7. Lower incisor size: all small (0) or incisor 1 enlarger and the others small (0).
8. Postcanine replacement: alternate (0), partial (1) or sequential addition posteriorly (2) (modified from Luo, 1994).
9. Roots of postcanines: single (0), contricted root (1), complete separation of roots (2) or multiple roots (3) (modified from Luo, 1994).
10. Upper postcanine buccal cingulum: absent (0) or present (1) (Hopson and Kitching, 2001).
11. Upper postcanine lingual cingulum: absent (0), narrow (1) or lingually expanded (2) (Hopson and Kitching, 2001).
12. A dominant central bulbous main cusp on upper postcanines: absent (0) or present (1).
13. Upper posterior postcanines with cusps B and C buccally displaced and bulbous, prominent cusp A: absent (0) or present (1).
14. Lower middle and posterior postcanines with four cusps aligned decresingin size backwards: absent (0) or present (1).
15. Lower teeth much larger than the uppers: absent (0) or present (1).
16. Posterior portion of the maxillary tooth row extends medial to the temporal fossa: absent (0) or present (1) (Hopson and Kitching, 2001).
17. Axis of posterior part of maxillary tooth row: directed lateral to temporal fossa (0), directed toward center fossa (1) or directed toward medial rim (2) (Hopson and Kitching, 2001).

18. Wear facets on postcanines: absent (0), absent at eruption but developed later by wear (1) or wear facets present at eruption (2) (Luo, 1994).

19. Relationships of wear facet to main cusps: absent (0), simple longitudinal in most of the length of crown (1), two distintive facets (2) or multiple cusp, with each cusp bearing one or two transverse facets (3) (modified from Luo, 1994).

20. Tooth row: divergent posteriorly (0) or parallel to subparallel from the axial plane of the cranium (1) (Martinez *et al.* , 1996).

21. Symphysis: fused (0) or unfused (1) (Luo, 1994).

22. Squamosal glenoid for the dentary: absent (0), formed by small and medially facing facet (1), formed by broad and anteroventrally facing glenoid (2) or glenoid facing ventrally and separated from cranial moiety by neck (3) (modified from Luo, 1994).

23. Anterolateral projection of the frontal contacting medially the nasal: absent (0) or present (1).

24. Premaxilla forms posterior border of the incisive foramen: absent (0) or present (1) (Hopson and Kitching, 2001).

25. Prefrontal: present (0) or absent (1) (Hopson and Kitching, 2001).

26. Postorbital: present (0) or absent (1) (Hopson and Kitching, 2001).

27. Parietals: fused (0) or unfused (1) (Martinez *et al.* , 1996).

28. Parietal foramen: present (0) or absent (1) (Hopson and Kitching, 2001).

29. Interpterygoid vacuity in adult between pterygoid flanges: absent (0) or present (1) (Hopson and Kitching, 2001).

30. Length secondary palate relative to toothrow: shorter (0), about equal (1) or longer (2) (Hopson and Kitching, 2001).

31. Length secondary palate relative to anterior border of orbit: shorter (0), about equal (1) or longer (2) (Hopson and Kitching, 2001).

32. Ventral surface of basisphenoid depressed below occipital condyles: less than 1/4 occipital height (0) or less than 1/4 occipital height (1) (Hopson and Kitching, 2001).

33. Zygomatic arch dorsoventral height: slender (0), moderaty deep (1) or very deep (2) (Hopson and Kitching, 2001).

34. Zygomatic arch dorsal extent: below middle of orbit (0) or above middle of the orbit (1) (Hopson and Kitching, 2001).

35. Jugal depth in zygomathic arch relative to exposed squamosal depth: less than twice (0) or greater than twice (1) (Hopson and Kitching, 2001).

36. Jugal suborbital process: absent (0) or present (1) (Hopson and Kitching, 2001).

37. Squamosal groove for external auditory meatus: moderately deep (0), very deep (1) or shallow (2) (modified from Hopson and Kitching, 2001).

38. Frontal-palatine contact in the orbit: absent (0) or present (1) (Hopson and Kitching, 2001).

39. Descending flange of squamosal lateral to quadratojugal: present not contacting surangular (0), present contacting surangular (1) or absent (2) (modified from Hopson and Kitching, 2001).

40. Internal carotid foramina in basisphenoid: present (0) or absent (1) (Hopson and Kitching, 2001).

41. Groove on prootic extending from pterygoparoccipital foramen to trigeminal foramen: open (0) or enclosed as a canal (1) (modified from Hopson and Kitching, 2001).

42. Trigeminal nerve exit via foramen: between prootic and epipterygoid (0) or via two foramina (1) (modified from Hopson and Kitching, 2001).

43. Quadrate ramus of pterygoid: present (0) or absent (1) (Hopson and Kitching, 2001).

44. Greatest width of zygomatic arches: near middle of arch (0) or at posterior end of arch (1) (Hopson and Kitching, 2001).

45. Length of palatine relative to maxilla in secondary palate: shorter (0), about equal (1) or longer (2) (Hopson and Kitching, 2001).

46. Posterolateral end of maxilla: passes obliquely posterodorsally into suborbital bar 0) or forms right angle ventral to jugal contact (1) (Hopson and Kitching, 2001).

47. Fenestra rotunda separation from jugular foramen: confluent (0), partially separed by fingerlike projection from posterolateral wall of jugular foramen (1) or completely separated (2) (Luo, 1994).

48. Stapedial muscle fossa: absent (0) or present (1) (Luo, 1994).

49. Foramen and passage of prootic sinus: separate tympanic foramen for prootic sinus absent from the lateral trough of petrosal (0), foramen present in lateral trough, but vessel passed through cavum epiptericum (1) or foramen present in lateral trough, but vessel passed through cavum epiptericum (2) (modified from Luo, 1994).

50. Postorbital bar: present (0) or absent (1) (Luo, 1994).

51. Scapular elongation between acromion and glenoid: present (0) or absent (1) (Hopson and Kitching, 2001).

52. Procoracoid in glenoid: present (0) or barely present or absent (1) (Hopson and Kitching, 2001).

53. Procoracoid contact with scapula: greater than coracoid contact (0) or smaller than coracoid contact (1) (Hopson and Kitching, 2001).

54. Humerus ectepicondilar foramen: present (0) or absent (1) (Hopson and Kitching, 2001).

55. Ulna olecranon process: absent (unossified) (0) or present (1) (Hopson and Kitching, 2001).

56. Length of anterior process of ilium anterior to acetabulum (relative to diameter of acetabulum): less than 1.0 (0), 1.0-1.5 (1) or 1.0- 1.5 (2) (Hopson and Kitching, 2001).

57. Length of posterior process of ilium posterior to acetabulum (relative to diameter of acetabulum): greater than 1.0 (0) or less than 0.5 (1) (Hopson and Kitching, 2001).
58. Dorsal profile of ilium: strongly convex (0) or flat to concave (1) (Hopson and Kitching, 2001).
59. Greater trochanter separated from the femoral head by distinct notch: absent (0) or present (1) (Hopson and Kitching, 2001).
60. Lesser trochanter position: on the ventromedial surface of femoral shaft (0) or on medial surface of femoral shaft (1) (Hopson and Kitching, 2001).
61. Vertebral centra: amphicoelous (0) or platycoelous (1) (Hopson and Kitching, 2001).
62. Greater trochanter location at the level of the femoral head: absent (0) or present (1).
63. Lesser trochanter location near the level of the femoral head: absent (0) or present (1).

Appendix 3

***List of abbreviations* :** big, biccipital groove; cr, constricted root; D, dentary; dc, deltopectoral crest; dl, dental lamina; e, enamel; ecf, ectepicondylar foramen; ect, ectepicondyle; enf, entepicondylar foramen; ent, entepicondyle; epc, erupting last postcanine; fc, fossa for lower canine; gt, greater trochanter; h, head; iof, infraorbital foramen; M, maxilla; maf, masseteric fossa; mc, medial condyle; meg, Meckelian groove; mt, major tuberosity; lc, lateral condyle; lt, lesser tuberosity; ltr, lesser trochanter; scg, supracondylar groove; ttm, tuberosities for insertion of the teres major muscle; wf, wear facet.

Lista de abreviaturas: *big, canal bicipital; cr, raiz constrictida; D, dentario; dc, cresta deltopectoral; dl, lamina dental; e, esmalte; ecf, foramen ectepicóndilar; ect, ectepicóndilo; enf, foramen entepicóndilar; ent, entepicóndilo; epc, último postcanino en erupción; fc, fosa para el canino inferior; gt, trocánter mayor; h, cabeza; iof, foramen infraorbital; M, maxilar; maf, fosa masetérica; mc, cóndilo medial; meg, canal Meckeliano; mt, tuberosidad mayor; lc, cóndilo lateral; lt, tuberosidad menor; ltr, trocánter menor; scg, surco supracondilar; ttm, tuberosidades para la inserción del músculo teres major; wf, faceta de desgaste.*

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References

1. Abdala, F. 1996. Redescripción del cráneo y reconsideración de la validez de *Cynognathus minor* (Eucynodontia-Cynodonthidae) del Triásico Inferior de Mendoza. *Ameghiniana* 33: 115-126. [Links]

2. Abdala, F. 1999. Elementos postcraneanos de *Cynognathus* (Synapsida- Cynodontia) del Triásico Inferior de la Provincia de Mendoza, Argentina. Consideraciones sobre la morfología del húmero en cinodontes. *Revista Española de Paleontología* 14: 13- 24. [Links]

3. Abdala, F. and Ribeiro, A.M. 2000. A new therioherpetid cynodont from the Santa Maria Formation (middle Late Triassic), sourthern Brazil. *Geodiversitas* 22: 589-596. [Links]

4. Allin, E.F. and Hopson, J.A. 1992. Evolution of the auditory system in Synapsida ("mammal-like reptiles" and primitive mammals) as seen in the fossil record. In: D.B. Webster, R.R. Fay and A.N. Popper (eds.), *The Evolutionary Biology of Hearing* , Springer-Verlag, New York, pp. 587-614. [Links]

5. Andreis, R.R., Bossi, G.E. and Montardo, D.K. 1980. O grupo Ros ário do Sul (Triássico) no Rio Grande do Sul. *31º Congreso Brazileiro de Geología* (Camboriú-SC) 2: 659-673. [Links]

6. Ara újo, D.C. and Gonzaga, T.D. 1980. Uma nova espécie de *Jachaleria* (Therapsida, Dicynodontia) do Triássico do Brasil. *2º Congreso Argentino de Paleontología y Bioestratigrafía y 1º Congreso Latinoamericano de Paleontología, Actas* 2: 159-174. [Links]

7. Argot, C. 2001. Functional-adaptative anatomy of the forelimb in the Didelphidae, and the paleobiology of the Paleocene marsupials *Mayulestes ferox* and *Pucadelphys andinus* . *Journal of Morphology* 247: 51-79. [Links]

8. Bonaparte, J.F. 1962. Descripci ón del cráneo y mandíbula de *Exaeretodon frenguellii* Cabrera, y su comparación con Diademodontidae, Tritylodontidae y los cinodontes sudamericanos. *Publicaciones del Museo Municipal de Ciencias Naturales y Tradicional de Mar del Plata* 1: 135-202. [Links]

9. Bonaparte, J.F. 1963. Descripci ón del esqueleto postcraneano de *Exaeretodon* (Cynodontia-Traversodontidae). *Acta Geológica Lilloana* 4: 5-54. [Links]

10. Bonaparte, J.F. 1966a. Sobre nuevos ter ápsidos triásicos hallados en el centro de la Provincia de Mendoza (Therapsida: Dicynodontia y Cynodontia). *Acta GeológicaLilloana* 7: 91-100. [Links]

11. Bonaparte, J.F. 1966b. Una nueva "fauna" Triásica de Argentina. (Therapsida: Cynodontia - Dicynodontia). Consideraciones filogenéticas y paleobiogeográficas. *Ameghiniana* 6: 243-296. [Links]

12. Bonaparte, J.F. 1969. Dos nuevas "faunas" de reptiles Triásicos de Argentina. *Actas 1º International Symposium on Gondwana* , Unesco, Paris 1: 283-302. [Links]

13. Bonaparte, J.F. 1973. Edades/Reptil para el Tri ásico de Argentina y Brazil. *5º Congreso Geológico Argentino, Actas* 3: 93-129. [Links]

14. Bonaparte, J.F. 1980. El primer Ictidosaurio (Reptilia-Therapsida) de Am érica del Sur, *Chaliminia musteloides* , del Triásico Superior de La Rioja, Argentina. *Actas 2º Congreso Argentino de Paleontología y Bioestratigrafía y 1º Congreso Latinoamericano de Paleontología* 1: 123-133. [Links]

15. Bonaparte, J.F. and Barberena, M.C. 1975. A possible mammalian ancestor from the Middle Triassic of Brazil (Therapsida- Cynodontia). *Journal of Paleontology* 49: 931-936. [Links]

16. Bonaparte, J.F. and Barberena, M.C. 2001. On two advanced carnivorous cynodonts from the Late Triassic of Southern Brazil. *Bulletin of the Museum of Comparative Zoology* 156: 59-80. [Links]

17. Bonaparte, J.F., Ferigolo, J. and Ribeiro, A.M. 1999. A new early Late Triassic saurischian dinosaur from the Rio Grande do Sul State, Brazil. *Proceedings of the Second Dinosaur Symposium. National Sciences Museum Monographs* (Tokyo) 15: 89-109. [Links]

18. Bonaparte, J.F., Ferigolo, J. and Ribeiro, A.M. 2001. A primitive Late Triassic ‘Ictidosaur' from Rio Grande do Sul, Brazil. *Palaeontology* 44: 623-635. [Links]

19. Bonaparte, J.F., Martinelli, A.G., Schultz, C.L. and Rubert, R. 2003. The sister group of mammals: small cynodonts from the Late Triassic of southern Brazil. *Revista Brasileira de Paleontologia* 5: 5-27. [Links]

20. Broom, R. 1912. On a new type of cynodont from the Stormberg. *Annals of the South African Museum* 7: 334-336. [Links]

21. Broom, R. 1929. On some new ligtht on the origin of mammals. *Proceedings of the Linnean Society* 54: 688-694. [Links]

22. Cisneros, J.C. and Schultz, C.L. 2003. *Soturnia caliodon* n. g. n. sp., a procolophonid reptile from the Upper Triassic of Southern Brazil. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 227: 365-380. [Links]

23. Crompton, A.W. 1958. The cranial morphology of a new genus and species of ictidosauran. *Proceedings of the Zoological Society of London* 130: 183-216. [Links]

24. Crompton, A.W. 1963a. On the lower jaw of *Diarthrognathus* and the origin of the mammalian lower jaw. *Proceedings of the Zoological Society of London* 140: 697-753. [Links]

25. Crompton, A.W. 1963b. Tooth replacement in the cynodont *Thrinaxodon liorhinus* Seeley. *Annals of the South African Museum* 46: 479-521. [Links]

26. Crompton, A.W. 1972. Postcanine occlusion in cynodonts and tritylodonts. *Bulletin of the British Museum (Natural History), Geology* 21: 29-71. [Links]

27. Crompton, A.W. 1974. The dentitions and relationships of the southern African Triassic mammals, *Erythrotherium parringtoni* and *Megazostrodon rudnerae* . *Bulletin of the British Museum (Natural History), Geology* 24: 397-437. [Links]

28. Crompton, A.W. and Jenkins F.A. 1968. Molar occlusion in Late Triassic mammals. *Biological Reviews* 43: 427-458. [Links]

29. Crompton, A.W. and Luo, Z.-X. 1993. Relationships of the Liassic mammals *Sinoconodon* , *Morganucodon oehleri* , and *Dinnetherium* . In: F.S. Szalay, M.J. Novacek and M.C. McKenna (eds.), *Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians and Marsupials*, New York: Springer- Verlang, pp. 30-44. [Links]

30. Crompton, A.W. and Sun, A. 1985. Cranial structure and relationships of the Liassic mammal *Sinoconodon* . *Zoological Journal of the Linnean Society* 85: 99-119. [Links]

31. Dubost, G. 1968. Les mammif ères souterrains. *Revue d'Écologie et de Biologie du Sol* 5: 99-197. [Links] Ferigolo, J. 2000. Esfenodontídeos do Neo-triássico/?Jurássico do Estado do Rio Grande do Sul, Brasil. In: M. Holz and L.F. De Ros (eds.), *Paleontologia do Rio Grande do Sul* , CIGO/UFRGS Porto Alegre, pp. 236-245. [Links]

32. Fourie, S. 1963. Tooth replacement in the gomphodont cynodont *Diademodon* . *South African Journal of Science* 59:211-213. [Links]

33. Gambaryan, P.P. and Averianov, A.O. 2001. Femur of a morganucodontid mammal from the Middle Jurassic of Central Russia. *Acta Paleontologica Polonica* 46: 99-112. [Links]

34. Gambaryan, P.P. and Kielan-Jaworowska, Z. 1997. Sprawling *versus* parasagittal stance in multituberculate mammals. *Acta Paleontologica Polonica* 42: 13-44. [Links]

35. Goloboff, P.A. 1993. "NONA", Version 2.0. Program and documentation. [Links] Goñi, R. 1986. Reemplazo de dientes postcaninos en *Andescynodon mendozensis* Bonaparte (Cynodontia, Traversodontidae). *4º Congreso Argentino de Paleontología y Bioestratigrafia* (Mendoza) , *Actas* 2: 7-14. [Links]

36. Go ñi, R. and Goin, F.J. 1987. El origen de los postcaninos gonfodontes de *Andescynodon mendozensis* Bonaparte (Cynodontia, Traversodontidae). *Ameghiniana* 24: 235-239. [Links]

37. Gow, C.E. 1980. The dentitions of the Tritheledontidae (Therapsida: Cynodontia). *Proceedings of the Royal Society of London* B 208: 461-481. [Links]

38. Gow, C.E. 1986. A new skull of *Megazostrodon* (Mammalia, Triconodonta) from the Elliot Formation (Lower Jurassic) of Southern Africa . *Palaeontologia Africana* 26: 13-23. [Links]

39. Gow, C.E. 1994. New find of *Diarthrognathus* (Therapsida: Cynodontia) after seventy years. *Palaeontologia Africana* 31: 52-54. [Links]

40. Gow, C.E. 2001. A partial skeleton of the tritheledontid *Pachygenelus* (Therapsida: Cynodontia). *Palaeontologia Africana* 37: 93-97. [Links]

41. Groenewald, G.H., Welman, J. and MacEachern, J.A. 2001. Vertebrate burrow complexes from the Early Triassic *Cynognathus* Zone (Driekoppen Formation, Beaufort Group) of the Karoo Basin, South Africa. *Palaios* 16: 148-160. [Links]

42. Hickman, G.C. 1990. The Chrysochloridae: studies toward a broader perspective of adaptation in subterranean mammals. In: E. Nevo and O.A. Reig (eds.), *Evolution of Subterranean Mammals at the Organismal and Molecular Levels* , Alan R. Liss, Inc., pp. 23-48. [Links]

43. Hopson, J.A. 1971. Postcanines replacement in the gomphodont cynodont *Diademodon* . In: Kermack, D.M. and Kermack, K.A. (eds.), Early mammals, *Zoological Journal of the Linnean Society* 50 (Suppl. 1), pp. 1-21. [Links]

44. Hopson, J.A. and Barghusen, H. 1986. An analysis of therapsid relationships. In: Hotton, N.; MacLean, P.D.; Roth, J.J.; Roth, E.C. (eds.), *The ecology and biology of mammal-like reptiles* . Smithsonian Institution Press, Washington, pp. 83-106. [Links]

45. Hopson, J.A. and Kitching, J.W. 1972. A revised classification of cynodonts (Reptilia, Therapsida). *Palaeontologia Africana* 14: 71-85. [Links]

46. Hopson, J.A. and Kitching, J.W. 2001. A probainognathian cynodont from South Africa and the phylogeny of non-mammalian cynodonts. *Bulletin of the Museum Comparative Zoology* 156: 5-35. [Links]

47. Jenkins, F.A. 1970. The Cha ñares (Argentina) Triassic reptile fauna. VII. The postcranial skeleton of the traversodontid *Massetognathus pascuali* (Therapsida, Cynodontia). *Breviora* 352: 1-16. [Links]

48. Jenkins, F.A. 1971. The postcranial skeleton of African cynodonts. *Bulletin, Peabody Museum of Natural History* , Yale University 36: 1-216. [Links]

49. Jenkins, F.A. and Parrington, F.R. 1976. The postcranial skeletons of the Triassic mammals *Eozostrodon* , *Megazostrodon* and *Erythrotherium* . *Philosophical Transactions of the Royal Society of London, Biological Sciences* 273: 387-431. [Links]

50. Jenkins, F.A. and Weijs, W.A. 1979. The functional anatomy of the shoulder in the Virginian opossum (*Didelphis virginiana*). *Journal of Zoology* 188: 379-410. [Links]

51. Kemp, T.S. 1980. Aspect of the structure and functional anatomy of the Middle Triassic cynodont *Luangwa* . *Journal of Zoology* 191: 193-239. [Links]

52. Kemp, T.S. 1982. *Mammal-like reptiles and the origin of mammals* . Academic Press, London, 363 pp. [Links] Kemp, T.S. 1983. The interrelationships of mammals. *Zoological Journal of the Linnean Society* 77: 353-384. [Links]

53. Kermack, K.A., Mussett, F. and Rigney, H. W. 1973. The lower jaw of *Morganucodon* . *Zoological Journal of the Linnean Society* 53: 87-175. [Links]

54. Kermack, K.A., Mussett, F. and Rigney, H.W. 1981. The skull of *Morganucodon* . *Zoological Journal of the Linnean Society* 71: 1-158. [Links]

55. Kielan-Jaworoska, Z. and Qi, T. 1990. Fossorial adaptations of a taeniolabidoid multituberculate mammals from the Eocene of China. *Vertebrata PalAsiatica* 28: 81-94 [Links]

56. Kischlat, E.-E. and Lucas, S.G. 2003. A phytosaur from the Upper Triassic of Brazil. *Journal of Vertebrate Paleontology* 23: 464-467. [Links]

57. K ühne, W.G. 1956. *The Liassic therapsid* Oligokyphus. London: Trustees of the British Museum (Natural History), 149 pp. [Links]

58. Luo, Z.-X. 1994. Sister-group relationships of mammals and transformations of diagnostic mammalian characters. In: N.C. Frazer and H.D. Sues (eds.), *In the Shadow of the Dinosaurs* . Early Mesozoic tetrapods, Cambridge, United Kingdom: Cambridge University Press, pp. 98-128. [Links]

59. Luo, Z.-X. 2001. The inner ear and its bony housing in tritylodontids and implications for evolution of the mammalian ear. *Bulletin of the Museum of Comparative Zoology* 156: 81-97. [Links]

60. Luo, Z.-X. and Crompton, A. W. 1994. Transformation of the quadrate (incus) through the transition from non-mammalian cynodonts to mammals. *Journal of Vertebrate Paleontology* 14: 341-374. [Links]

61. Luo, Z.-X., Crompton, A. W. and Sun, A.-L. 2001. A new mammaliaform from the Early Jurassic and evolution of the mammalian characteristics. *Science* 292: 1535-1540. [Links]

62. Luo, Z.-X., Kielan-Jaworowska, Z. and Cifelli, R.L. 2002. In quest for a phylogeny of Mesozoic mammals. *Acta Palaeontologica Polonica* 47: 1-78. [Links]

63. Martinez, R.N. and Forster, C.A. 1996. The skull of *Probelesodon sanjuanensis* , sp. nov., from the Late Triassic Ischigualasto Formation of Argentina. *Journal of Vertebrate Paleontology* 16: 285-291. [Links]

64. Martinez, R.N., May C.L. and Forster, C.A. 1996. A new carnivorous cynodonts from the Ischigualasto Formation (Late Triassic, Argentina), with comment on eucynodont phylogeny. *Journal of Vertebrate Paleontology* 16: 271-284. [Links]

65. Miall, A.D. 1996. *Geology of Fluvial Deposits. Sedimentary Facies, Basin Analysis and Petroleum Geology* . Berlin, Spriger Verlag, 582 pp. [Links]

66. Mills, J.R.R. 1971. The dentition of *Morganucodon* . In: Kermack, D.M. and Kermack, K.A. (eds.), Early Mammals, *Zoological Journal of Linnean Society* 50 (Suppl. 1): 26-63. [Links]

67. Montardo, D.K. 1982. [*Estudos geológicos dos sedimentitos do gonduana Superior no regiao de Santa Cruz e Candelária, Rio Grande do Sul, Brasil* . M.S. dissertion. Universidad Federal do Rio Grande do Sul, Brazil: Postgraduation in Geosciences, 147 pp. Unpublished] [Links].

68. Muizon, C. de. 1998. *Mayulestes ferox* , a borhyaenoid (Metatheria, Mammalia) from the early Paleocene of Bolivia. Phylogenetic and palaeobiologic implications. *Geodiversitas* 20: 19-142. [Links]

69. Murray, P.F. 1978. Late Cenozoic monotreme anteaters. In: Augee M.L. (ed.), Monotreme Biology. *The Australian Zoologist* 20: 29-55. [Links]

70. Nixon, K.C. 1999. Winclada (Beta) version 0.9.9. Published by the author. Ithaca, New York. [Links] Owen, R. 1845. *Odontography; or, a treatise on the comparative anatomy of the teeth; their morphological relations, mode of development, and microscopic structure in vertebrate animals* . Part. 3. Hippolyte Baillière, London: 296-655. [Links]

71. Parrington, F.R. 1936. On tooth replacement in the theriodont reptiles. *Philosophical Transaction of the Royal Society* 226: 121-142. [Links]

72. Parrington, F.R. 1973. The dentition of earliest mammals. *Zoological Journal of the Linnean Society* 52: 85-95. [Links]

73. Romer, A.S. 1969a. The Brazilian Triassic cynodonts reptiles *Belesodon* and *Chiniquodon* . *Breviora* 332: 1-16. [Links]

74. Romer, A.S. 1969b. The Cha ñares (Argentina) Triassic reptile fauna. V. A new chiniquodontid cynodont, *Probelesodon lewisi* - cynodont ancestry. *Breviora* 333: 1-24. [Links]

75. Romer, A.S. 1970. The Cha ñares (Argentina) Triassic reptile fauna. VI. A chiniquodontid cynodont with incipient squamosaldentary jaw articulation. *Breviora* 344: 1-18. [Links]

76. Romer, A.S. and Lewis, A.D. 1973. The Cha ñares (Argentina) Triassic reptile fauna. XIX. Postcranial materials of the cynodonts *Probelesodon* and *Probainognathus* . *Breviora* 407: 1-26. [Links]

77. Rougier, G.W. 1993. [Vincelestes neuquenianus *Bonaparte (Mammalia, Theria) un primitivo mamífero del Cretácico Inferior de la Cuenca Neuquina* . Ph. D. dissertation, University of Buenos Aires, Argentina, 720 pp. Unpublished] [Links].

78. Rougier, G.W., Novacek, M.J., McKenna, M.C. and Wible, J.R. 2001. Gobiconodonts from the Early Cretaceous of Oshih (Ashile), Mongolia. *American Museum Novitates* 3348: 1-30. [Links]

79. Rowe, T. 1988. Definition, diagnosis, and origin of Mammalia. *Journal of Vertebrate Paleontology* 8: 241-264. [Links]

80. Shapiro, M.D. and Jenkins, F.A. 2001. A new cynodont from the Upper Triassic of East Greenlandic: tooth replacement and double-rootedness. *Bulletin of the Museum Comparative Zoology* 156: 49-58. [Links]

81. Shubin, N.H., Crompton, A.W., Sues, H.-D. and Olsen, P.E., 1991. New fossil evidence on the sister-group of mammals and early Mesozoic faunal distributions. *Science* 251: 1063-1065. [Links]

82. Sidor, C.A. and Hopson, J.A. 1998. Ghost lineages and "mammalness": assessing the temporal pattern of character acquisition in the Synapsida. *Paleobiology* 24: 254-273. [Links]

83. Sues, H.-D. 1983. [*Advanced Mammal-like Reptiles from the Early Jurassic of Arizona* . Ph.D. dissertation, Harvard University, Massachusetts, 302 pp. Unpublished] [Links].

84. Sues, H.-D. 1985. The relationships of the Tritylodontidae (Synapsida). *Zoological Journal of the Linnean Society* 85: 205- 217. [Links] Sues, H.-D. 2001. On *Microconodon* , a Late Triassic cynodont from the Newark Supergroup of Eastern North America. *Bulletin of the Museum Comparative Zoology* 156: 37-48. [Links]

85. Teixeira, A.M. 1982. Um novo cinodonte carnívoro (*Probelesodon kitchingi* sp. nov.) do Triássico do Rio Grande do Sul, Brasil. *Comunicações do Museu de Ciências da PUCRGS* 24: 1-31. [Links]

86. Watson, D.M.S. 1913. On a new cynodont from the Stormberg. *Geological Magazine* 10: 145-148. [Links]

87. Wible, J. R. 1991. Origin of Mammalia: the craniodental evidence reexamined. *Journal of Vertebrate Paleontology* 11: 1-28. [Links]

88. Zerfass, H., Lavina, E.L., Schultz, C.L., Garcia, A.J.V., Faccini, U.F. and Chemale Jr. F. 2003. Sequence stratigrapy of continental Triassic strata of Southernmost Brazil: A contribution to Southwestern Gondwana palaeogeography and palaeoclimate. *Sedimentary Geology* 161: 85-105. [Links]

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