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Origin and relationships of the Ictidosauria to non-mammalian cynodonts and mammals

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ABSTRACT

Ictidosaurian genera are allocated to two families, Tritheledontidae and Therioherpetidae. This paper provides a diagnosis for Ictidosauria. The previously named family Brasilodontidae is shown to be a junior synonym of a family, Therioherpetidae. It is concluded that Ictidosauria originated from Late Permian procynosuchid non-mammalian cynodonts rather than from Middle Triassic probainognathid non-mammalian cynodonts. The structure of the skull and jaws of a derived traversodontid *Ischignathus sudamericanus* from the early Late Triassic of Argentina supports an earlier view that tritylodontids are more closely related to traversodontid than probainognathid non-mammalian cynodonts. Tritylodontids should not be included in Ictidosauria, nor should they be considered to be a sister group to mammaliaforms.

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Introduction

The aim of this paper is to discuss the origin and relationships of Ictidosauria (Broom 1912b). In 1929, Broom included the southern African genera *Pachygenelus*, *Karoomys* and *Tritheledon* in this clade. One other genus he originally included, *Lychorhinus*, later proved to be an ornithischian dinosaur (Charig & Crompton 1974). Broom (1932) included two additional specimens in Ictidosauria which he referred to as ‘ictidosaurian A and B’. Since then, several authors have suggested additional genera to be included in or omitted from this clade, and have discussed the origin of Ictidosauria and its relationship to non-mammalian cynodonts, tritylodontids and mammals. A brief review is given below.

Crompton (Crompton 1958) assigned to ‘ictidosaurian B’ *Diarthrognathus broomi* and later (Crompton 1963) identified ‘ictidosaurian A’ as the same species. He proposed that *Diarthrognathus* could be ‘ancestral to some of the mammals’ (p. 214) because of the presence of a squamosal/dentary articulation, yet concluded that it could not have derived from ‘cynodonts’ but rather from an unidentified scalposaurian therocephalian. This is based partially on the shared characteristics of both a slender zygomatic arch and interpterygoid vacuity. Hopson and Barghusen (Hopson & Barghusen 1986) suggested that these features were simply juvenile features and disputed the presence of a squamosal/dentary articulation (see also Gow 1980) in *Diarthrognathus*. This genus lacks a squamosal glenoid, but it does possess a small condyle on the posterolateral edge of the articular process of the dentary that contacts the inner surface of the squamosal (Crompton 1963). Hopson and Kitching (1972) suggested that *Diarthrognathus*

was synonymous with *Pachygenelus* and included this genus in the family, Tritheledontidae (Broom 1912a). Bonaparte and Barbarena (1975) pointed out that a new specimen, which they named *Therioherpeton cargnini*, from the Santa Maria Formation in Brazil, shares many features with *Diarthrognathus* and *Pachygenelus* such as a squamosal/dentary contact. Initially they ruled out a ‘close affinity between *Therioherpeton* and ictidosaurians,’ (Bonaparte & Barbarena 1975, p. 935). Gow (1980) described in detail the dentitions of *Diarthrognathus*, *Pachygenelus* and *Tritheledon* and pointed out the close similarity between the dentition of *Pachygenelus* and *Therioherpeton cargnini*. He concluded that the dentition of tritheledontids could have been derived from those of primitive ‘cynodonts’ such as *Thrinaxodon* or *Probainognathus*. The most complete published reconstructions of *Pachygenelus*, based mainly on uncatalogued specimens in the South African Museum, are those of Allin and Hopson (1992). Hopson and Kitching (2001), in their review of the phylogeny of non-mammalian cynodonts, favored a view that tritheledontids were a sister group to morganucodontids and were derived from probainognathid rather than traversodontid non-mammalian cynodonts. They supported the view (Crompton & Ellenberger 1957) that tritylodontids were derived from the herbivorous non-mammalian cynodonts (Gomphodontidae) rather than carnivorous probainognathid non-mammalian cynodonts (Kemp 1983).

Recently several additional genera have been discovered and included in Tritheledontidae: *Chalimimia musteloides* (Bonaparte 1980), *Irajatherium hernandezii* (Martinelli et al. 2005), *Riograndia guaibensis* (Bonaparte & Barbarena 2001), *Elliotherium kersten* (Sidor & Hancox 2006). Martinelli and Rougier (2007) divided

the genera assigned to Tritheledontidae into two subfamilies: Chalimininae for *Riograndia*, *Chaliminia*, *Elliotherium*, and Pachygenelidae for *Pachygenelus*, *Diarthrognathus* and *Tritheledon*. Chalimininae genera are characterized by a large number (12–13) of simple postcanines lacking buccal and lingual cingula, whereas Pachygenelidae are characterized by transversely wide upper postcanines with the major axes of the postcanines mesio-disto-labially oriented (Gow 1980). *Riograndia* should perhaps be placed in a separate subfamily, as proposed by Bonaparte et al. (2010), because it lacks a edentulous tip of the premaxilla, its jaw articulation occurred only between a large articular and quadrate/quadratojugal complex, and the dentary lacks a lateral ridge that comes close to the squamosal jaw articulation.

Bonaparte et al. (2003) described two small insectivorous probainognathian non-mammalian cynodonts, *Brasilodon quadrangularis* and *Brasilitherium riograndensis*, from the late Triassic of Brazil. Initially these were not assigned to a specific family but were shown to be closely related to mammaliaforms on the one hand and tritheledontids on the other. Bonaparte et al. (2010) placed them in Ictidosauria, which they divided into three families: Riograndidae (for the genus *Riograndia*), Tritheledontidae (for *Chaliminia*, *Irajatherium*, *Elliotherium*, *Tritheledon*, *Diarthrognathus*, and *Pachygenelus*), and Brasilodontidae (for *Therioherpeton*, *Brasilodon*, *Brasilitherium*, and *Minicynodon* from the Late Triassic and *Protheriodon* from the Middle Triassic). Bonaparte (2013) added the Early Triassic *Panchetocynodon damodariensis* (Das & Gupta 2012) to Brasilodontidae. Brasilodontidae taxa comprise the longest known biochron of derived non-mammalian cynodonts. Of all the Ictidosauria genera the most complete and best known are *Brasilitherium riograndensis* (Bonaparte et al. 2003, 2005, 2010, 2012; Bonaparte 2012, 2013; Rodrigues et al. 2013; Ruf et al. 2014) and *Riograndia guaibensis* (Soares et al. 2011).

The relationships of tritylodonts to ictidosaurs (=tritheledontids) remains controversial. Early studies by Kemp (1983) dismissed the Hopson and Kitching (2001) view of a close relationship between tritylodontids and traversodontid non-mammalian cynodonts, and concluded that traversodontids and tritylodontids had independently evolved specialized dentitions for an herbivorous diet. Based upon a series of cranial and postcranial characteristics, Kemp also concluded that ‘...tritylodontids are the cynodont group most closely related to morganucodontids.’ (1983, pp 370). Mammals and tritylodontids, he suggested, shared a common ancestor that lacked tritylodontid specializations, such as a herbivorous dentition (somewhat convergent on that of traversodontids), and had lost the secondary jaw articulation between the lower jaw and the squamosal. This common ancestor nevertheless possessed uniquely mammalian features present in tritylodontids such as an advanced periotic, loss of prefrontal and postorbital bones, and several features of the mammalian postcranial skeleton. Kemp (2005) recognized the possibility that tritheledontids may have a closer relationship to mammals than tritylodontids. Luo and Crompton (1994) favored tritheledontids as the sister group of mammals, but only by a narrow margin over tritylodontids.

With the exception of Hopson and Kitching (2001), there is universal agreement that Ictidosauria, Tritylodontia, and Mammalia all arose from probainognathid non-mammalian cynodonts.

Several proposals on the possible relationships of ictidosaurian genera, to one another, tritylodontids, and mammaliaforms are published. Luo and Crompton (1994), Sidor and Hancox (2006), Martinelli et al. (2005), Martinelli and Rougier (2007), Shubin et al. (1991), Liu and Olsen (2010) and Luo et al. (2002, 2015) all agree that the tritheledontids were closer to mammaliaforms and mammals than tritylodontids. Bonaparte et al. (2003, 2012) and Bonaparte (2013) refined this relationship by suggesting that, out of all the ictidosaurian genera, only one, namely *Brasilitherium*, is a sister group to mammaliaforms and mammals. Abdala (2007) and Martinelli et al. (2016) agree with the *Brasilitherium*/mammaliaform relationship (Figure 1), but also agree with Kemp (1983) in considering Tritylodontidae more closely related to *Brasilitherium* and mammaliaforms than Tritheledontidae and *Riograndia*.

In this paper we introduce and discuss the evidence provided by the absence of postorbital and prefrontal bones in ictidosaurs from the Middle Triassic (Dinodontosaurus Assemblage Zone of southern Brazil), as well as a sequence of therioherpetid species that range from the late Carnian to the early Norian of the Triassic. These taxa comprise the longest known biochron of derived non-mammalian cynodonts (Table 1). We suggest a revision to the overwhelmingly accepted view that morganucodontids arose from probainognathid non-mammalian cynodonts (sensu Hopson & Kitching 2001). Probainognathids possess more derived characters than the earliest mammals (Bonaparte and Migale 2015) including the presence of a pterygo-parasphenoid crest providing a strong connection between the neurocranium and the masticatory region.

Institutional Abbreviations

MCN-PV, Vertebrate Paleontology, Natural Science Museum, Porto Alegre, Brazil.

PVL, Vertebrate Paleontology, Instituto-Fundación Lillo, National University of Tucumán, Tucumán, Argentina.

P.A.R., Patronato Alves Ramos, Santa Maria City, Santa Maria, Rio Grande do Sul, Brazil.

SAM- South African Museum.

UFRGS. PV- Universidad Federal de Rio Grande do Sul- Dept. of Geology, Brazil.

Materials and methods

The followings specimens were studied: the type specimen of *Riograndia guailbaensis*, MCN-PV 2265; UFRGS-PV 0596, and additional specimens not catalogued at UFRGS; the type

Table 1. Faunal assemblage zones of the middle and late Triassic from Southern Brazil indicating the presence of Therioherpetidae. The older species show the more plesiomorphic characters. Modified from Horn et al. (2014).

EARLY NORIAN 215 m. y.	<i>Riograndia</i> Assemblage Zone <i>Brasilodon</i> <i>Brasilitherium</i> <i>Minicynodon</i>
LATE CARNIAN 225 m. y.	<i>Hyperodapedon</i> Assemblage Zone <i>Therioherpeton</i> .
LADINIAN 238 m. y.	<i>Dinodontosaurus</i> Assemblage Zone: <i>Protheriodon</i>

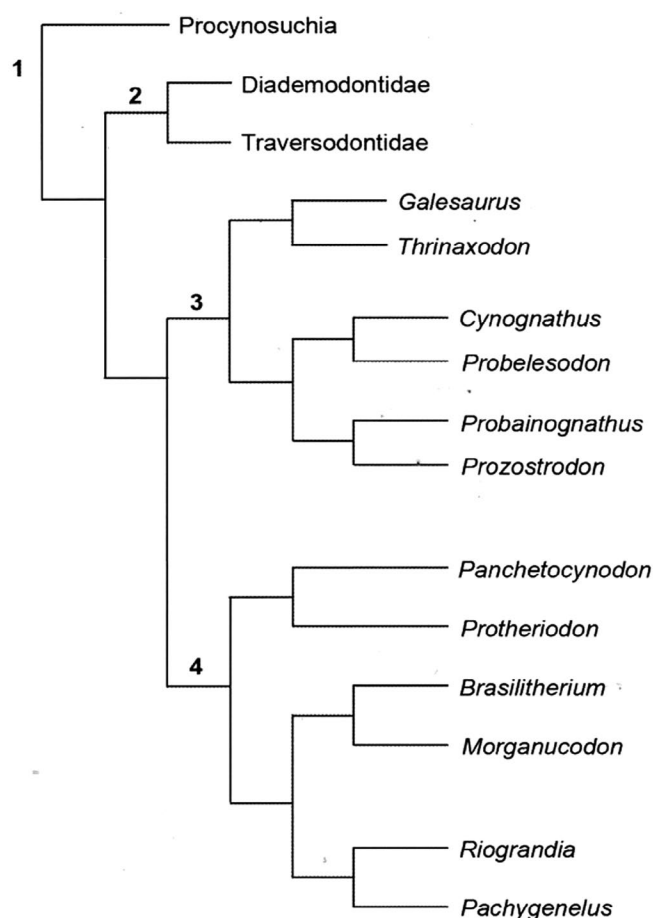


Figure 1. Tentative cladogram by Bonaparte, Soares and Martinelli (2012); to show the phylogenetic difference between gomphodontia [2] + galesauria [3] from the Ictidosauria + Morganucodontidae [4]; while Tritylodontidae was considered part of gomphodontia.

specimen of *Chalimnia musteloides*, PVL 3857; the type specimen of *Therioherpeton cargini*, an uncatalogued specimen in the collection of P.A.R.; the type specimen of *Brasilodon quadrangularis*, UFRGS.PV 0611T; UFRGS.PV 0716T; UFRGS.PV 0628T; the type specimen of *Brasilitherium riograndensis*, UFRGS.PV 0594T; UFRGS.PV 0759T; UFRGS.PV 0760T; UFRGS.PV 0603T; UFRGS.PV 0595T; UFRGS.PV 0598T; UFRS.PV 1043; the type specimen of *Protheriodon estudianti*, UFRGS.PV 0962T; the type specimen of *Minicynodon maieri*, UFRGS.PV 1030T; the type specimen of *Irajatherium hernandezi*, UFRGS.PV 0599T, and the type specimen of *Prozostrodon brasiliensis*, UFRGS.PV 0248T.

Unpublished figures of *Pachygenelus* and *Morganucodon*, supplied by J. Hopson and Zhe-Xi Luo, respectively, were also used in this research, as well a comprehensive review of relevant literature, dating from the work of Broom (1912b).

Special attention was given to the recognition of character states as the fundamental source for understanding the evolution of morphology. Cladistic procedures were used to augment observations and comparisons, but were limited by the amount of homoplasy present in some Triassic and Jurassic cynodonts.

Results

Systematics: therioherpetidae and tritheledontidae

Therioherpetidae (Bonaparte & Barberena 1975)

Based on the type specimen of *Therioherpeton* (Bonaparte & Barberena 1975, 2001), consisting of an incomplete skull, fragments of lower jaw, and some isolated postcanine teeth (Figure 2), *Therioherpeton* was placed in the new family, Therioherpetidae. The characters of this family included: absence of a postorbital arch, slender zygomatic arch, frontals wedged between parietals, postcanines with three or four cusps in a line, lack of a lingual expansion, and incipient bifurcation of the postcanine roots.

Bonaparte et al. (2003) described *Brasilodon* and *Brasilitherium* as small probainognathids closely related to *Morganucodon*, without assigning them to a known family. Later, Bonaparte et al. (2005) argued that the genera *Brasilodon* and *Brasilitherium* should in fact be placed in a new family, the Brasilodontidae. The diagnostic features of this family include: lack of a postorbital arch, frontal bordering the orbital, long frontal-parietal contact, slender zygomatic arch, postcanines with three or four cusps inline, incipient bifurcation of the postcanine roots, and slender, long lower jaws with an unfused mandibular symphysis. These characteristics indicate that Therioherpetidae (Bonaparte & Barberena 1975, 2001) and Brasilodontidae (Bonaparte et al. 2005, 2010; Bonaparte 2012) are synonymous families, and Brasilodontidae must be considered a junior synonym of Therioherpetidae.

We consider the taxonomic unit ‘family’ to include genera with a set of distinguishing characteristics not present in other families (Simpson 1971; Mckenna & Bell 1997). Based on this definition the following genera recorded only from the Middle to Late Triassic of southern Brazil are now assigned to Therioherpetidae:

Protheriodon estudianti (Bonaparte et al. 2006), lower Santa Maria Formation, *Dinodontosaurus* Assemblage Zone (Horn et al. 2014), late Ladinian to early Carnian;

Therioherpeton cargini (Bonaparte & Barberena 1975, 2001), upper Santa Maria Formation, *Hyperodapedon* Assemblage Zone (Horn et al. 2014), approximately late Carnian.

Brasilodon quadrangularis (Bonaparte et al. 2003), lower section of the Caturrita Formation, *Riograndia* Assemblage Zone (Horn et al. 2014), Early Norian.

Brasilitherium riograndensis (Bonaparte et al. 2003). Same providence and age as the latter. Liu and Olsen (2010) proposed synonymy of this genus with *Brasilodon* but this is rejected because of dental differences (Bonaparte 2012).

Minicynodon maieri (Bonaparte et al. 2010). Same providence and age as the latter.

Panchetocynodon damodarensis (Das & Gupta 2012), Lower Triassic Panchet Formation, Damodar Valley. This taxon is represented by a fragmentary lower jaw with postcanines features similar to those of Therioherpetidae genera. We prefer to assign this taxon only tentatively to Therioherpetidae because of its fragmentary condition.

On the basis of characteristics common to the specimens discussed above, a diagnosis for Therioherpetidae is as follows: these small Triassic insectivorous non-mammalian cynodonts had

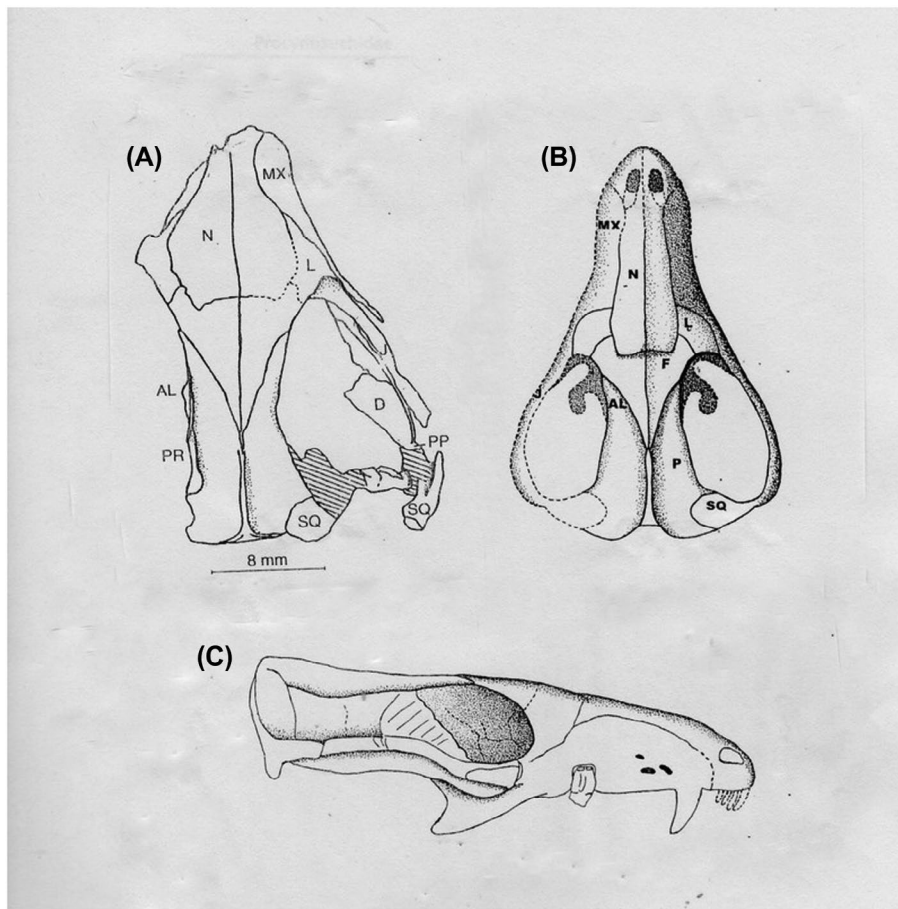


Figure 2. *Therioherpeton cargini*. A, dorsal view of the skull of the type specimen as preserved; B, reconstruction of the skull in dorsal view; and C, reconstruction of the skull in lateral view.

generalized triconodont dentitions, including three or four cusps axially aligned, with cusps A and 'a' larger than B, C, D, and 'b', 'c', 'd'; upper buccal cusps and lower lingual cingular cusps were present in derived forms, including modest lingual expansions; postcanines with incipient bifurcation at the roots; maxilla with three incisiforms and premaxilla with four; upper incisors projected ventrally; three lower incisors (procumbent in derived species) present; postorbital bar, postorbital, and prefrontal absent; wide frontal bordering the orbit; a slender zygomatic arch; axially short squamosal; dorso-ventrally reduced parietal crest; petrosal promontorium (documented only in *Brasilitherium*); braincase laterally expanded; slender cultiform process of the parasphenoid dividing the interpterygoid vacuity; articular process of the dentary close to the squamosal in plesiomorphic species; small dentary condyle and squamosal glenoid in derived species; large postdentary bones in plesiomorphic species, reduced in derived ones; slender elongated dentary; and unfused symphysis.

If we are correct in assigning the poorly known *Panchetocynodon damodarensis* to Therioherpetidae it indicates that this family had a long biochron, extending from the Anisian to the early Norian, about 25 million years (Table 1).

***Tritheledontidae* (Hopson & Barghusen 1986)**

Tritheledontidae are known from the Late Triassic to the Early Jurassic. Martinelli and Rougier (2007) include the following

genera: *Tritheledon* (Broom 1912a, Lower Jurassic, South Africa), *Pachygenelus* (Watson 1913, Lower Jurassic, South Africa), *Diarthrognathus* (Crompton 1958, Lower Jurassic, South Africa), *Chalimiania* (Bonaparte 1980, Upper Los Colorados Formation, Late Norian of Argentina), *Riograndia* (Bonaparte & Barbarena 2001, Lower Caturrita Formation, Early Norian, Southern Brazil), *Irajatherium* (Martinelli et al. 2005, Caturrita Formation, early Norian, Southern Brazil), *Elliotherium* (Sidor & Hancox 2006, Late Triassic [Rhaetic], Southern Africa).

The genera placed in the Tritheledontidae share several characteristics with the Therioherpetidae: lack of prefrontal and postorbital; interpterygoid vacuity; slender zygomatic arch; unfused mandibular symphysis; secondary palate extending as far posteriorly as the postcanine teeth; lateral ridge on the articular process of the dentary approaching the squamosal. Luo et al. (1995) state that one tritheledontid, *Pachygenelus*, lacks a promontorium on the petrosal bone (fusion of the opisthotic and prootic). However, a small promontorium appears to be present in a juvenile *Pachygenelus monus* (SAM Ki350) (AWC personal observation).

Tritheledontidae possess several diagnostic features that distinguish them from Therioherpetidae: more derived upper and lower postcanines; a relatively deep dentary; edentulous tip of the premaxilla; procumbent lower incisors; ventral border of the posterior region of the secondary palate extending ventrally as far as the tips of the postcanines; a deep groove separating the

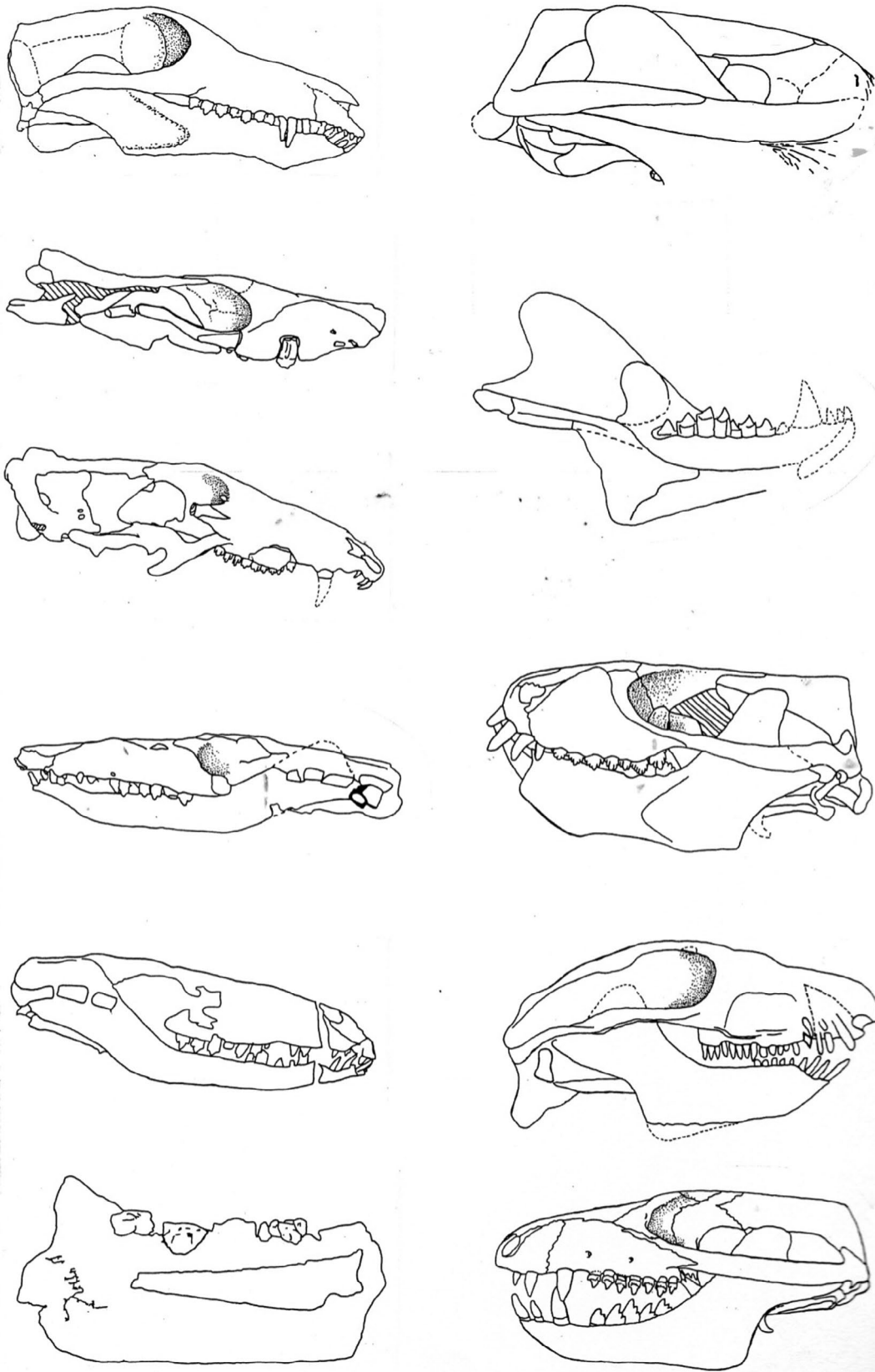


Figure 3. Genera of ictidosaur. Left, from top to bottom: *Protheriodon*, *Therioherpeton*, *Brasilodon*, *Brasilitherium*, *Minicynodon*, and tentatively *Panchetocynodon*'s the fragmentary lower jaw. Right: *Diarthrognathus*, *Diarthrognathus*' lower jaw, *Riograndia*, *Chalimimia*, *Pachygenelus*. Not to scale.

postcanine row from the secondary palate; and a bulbous central cusp dominating the crown of slightly transverse postcanines.

Ictidosauria (Figure 3)

Martinelli and Rougier (2007) included Tritheledontidae within Ictidosauria. We conclude that Therioherpetidae should also be included in Ictidosauria. The diagnostic features of Ictidosauria are as follows: absent postorbital arch, postorbital, and prefrontal; a slender zygomatic arch with a long jugal and short squamosal; a dorsoventrally short parietal crest and transversally wide braincase; interpterygoid vacuity; ventral contact of the frontal with the orbital process of the palatine; an unfused lower jaw symphysis; a well-developed articular process of the dentary contacting the squamosal; and a petrosal promontorium.

Therioherpetidae share several features with mammaliaforms: a slender zygomatic arch, squamosal dentary contact, unfused dental symphysis, petrosal promontorium, transversely narrow postcanines with axially aligned cusps and an incipient cingulum, and a transversely expanded brain case. In Therioherpetidae and *Morganucodon* the medial edges of the pterygoids lack the powerful ventral crest formed by the parasphenoid and pterygoids in probainognathids. There appears to be a closer relationship between Therioherpetidae and mammaliaforms than between Tritheledontidae and mammaliaforms. Therioherpetidae lack the features present in derived Tritheledontidae such as *Pachygenelus*: procumbent first lower incisors occluding between the first upper incisors, an edentulous tip of the premaxilla, and transversely widened postcanines.

We conclude that Therioherpetidae is the sister group to Mammaliaformes. As *Brasilitherium* is the best known genus within Therioherpetidae, this view is basically in agreement with the view of Martinelli and Soares (Martinelli et al. 2016), Bonaparte and Martinelli (Bonaparte et al. 2005), and Abdala et al. (Abdala et al. 2005), who consider *Brasilitherium* to be the sister group to Mammaliaformes. Three distinct groups have been included in Mammaliaformes. One includes forms such as *Morganucodon*, *Megazostrodon* and *Sinoconodon*; a second group consists of genera included in Docodonta that diversified in the Middle Jurassic (Luo 2007; Luo et al. 2015); and a third group includes early haramiyids such as *Haramiyavia* (Luo et al. 2015). *Brasilitherium* is closer to the first group than the more derived second and third groups. *Brasilitherium* is almost identical to *Morganucodon*, except that the latter has a mammalian tooth replacement pattern (single replacement of the incisors, canines, and premolars, and no replacement of the molars), double rooted molars, and the orbital flange of the palatine forms a medial wall to the orbit (Crompton et al. 2017).

Interpterygoid vacuity

We consider an interpterygoid vacuity in procynosuchids, non-mammalian cynodonts, and ictosaurs to be an important diagnostic feature despite the fact that it also appears in juvenile Triassic non-mammalian cynodonts (*Thrinaxodon* and *Lumkuia*). In adult Triassic non-mammalian cynodonts the medial edges of the pterygoids seem to grow towards the midline to meet the parasphenoid and form a strong ventral crest. The interpterygoid vacuity arises in Therioherpetidae,

Tritheledontidae, procynosuchids and typical reptiles such as *Sphenodon* (Moore 1981) because the medial edges of the pterygoids do not approach the midline. The parasphenoid either wholly or partially divides the interpterygoid vacuity down the middle. It is seldom pointed out that in all non-mammalian cynodonts, ictosaurs and mammaliaforms the basicranial axis of the chondrocranium does not ossify anterior to the basisphenoid in the adult skull. In these groups, as in reptiles, a cartilaginous basicranial axis (interorbital septum or trabeculae) contacted the grooved dorsal surface of the parasphenoid. A characteristic feature of mammals is the increased ossification of the chondrocranium anterior to the basisphenoid to form a presphenoid and ossified nasal capsule. Even in extant mammals the pterygoids and palatines do not meet in the midline and the space between them, a remnant of the interpterygoid vacuity, is filled by a presphenoid.

Ictidosaur origins

Hopson and Kitching (2001), Kielan-Jaworowska et al. (2004); Kemp (2005) Martinelli and Rougier (2007), and Martinelli et al. (2016) all agree that Ictidosauria (=Tritheledontidae) are related to probainognathids. We wish to suggest the possibility of a closer relationship to procynosuchids than to probainognathids.

The late Permian genus *Procynosuchus* (Broom 1937) has been described in detail by Kemp (1979, 1980, 1982, 2005). Broom (1948) included *Procynosuchus* in the family Procynosuchidae. Hopson and Kitching (1972) considered several genera to be synonyms of *Procynosuchus* and assigned additional genera to Procynosuchidae. Kemp (1979) claimed that *Procynosuchus* was the sister group of later cynodonts, and wrote, ‘...the skeleton of *Procynosuchus* is close to the expected structure of the common ancestral form of all cynodonts that followed it,’ (Kemp 1979, p. 118)

In the features used to characterize Cynodontia, Hopson and Kitching (2001) include several characters common to Triassic cynodonts and the Late Permian *Procynosuchus*. However, several features present in *Procynosuchus* are absent in probainognathids (sensu Hopson & Kitching 2001), but present in Ictidosauria. These include: interpterygoid vacuities (present only in juvenile probainognathids); a slender zygomatic arch; incisiforms present at the junction of premaxilla and maxilla; a low and elongated dentary; and an unfused lower jaw symphysis.

These five characters suggest a closer relationship between procynosuchids and Ictidosauria than between probainognathids and Ictidosauria. Several features of probainognathids that are absent in Ictidosauria include: a strong ventral crest joining the basisphenoid to the palate that is formed by the pterygoids and parasphenoid; absence of an interpterygoid vacuity in adults; a deep zygomatic arch; surangular/squamosal contact lateral to the articular/quadrangle jaw articulation; fusion of the lower jaw symphysis; absence of incisiforms at the union of the maxilla and premaxilla; canines in an anterior position; a short and wide snout; and a generally larger body. Probainognathids and tritheledontids do share some synapomorphies (Hopson and Kitching 2001—postcanine lingual cingula and medial shift of maxillary tooth rows—but if tritheledontids were derived from probainognathids, it would imply a loss of the pterygoparasphenoid ventral ridge and reacquisition of an interpterygoid vacuity,

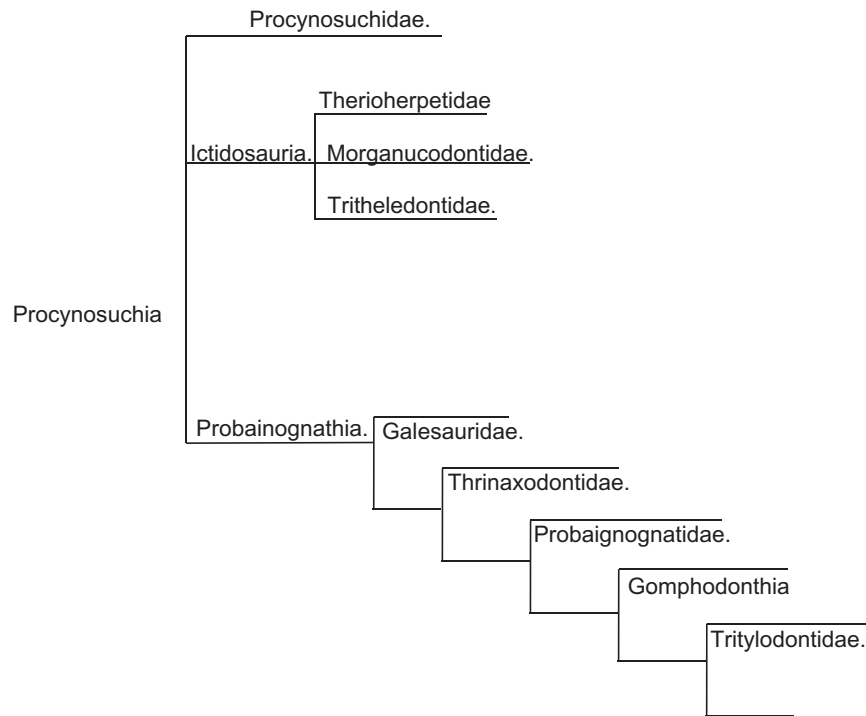


Figure 4. Cladogram showing the possible relationships of Ictidosauria and Tritylodontia.

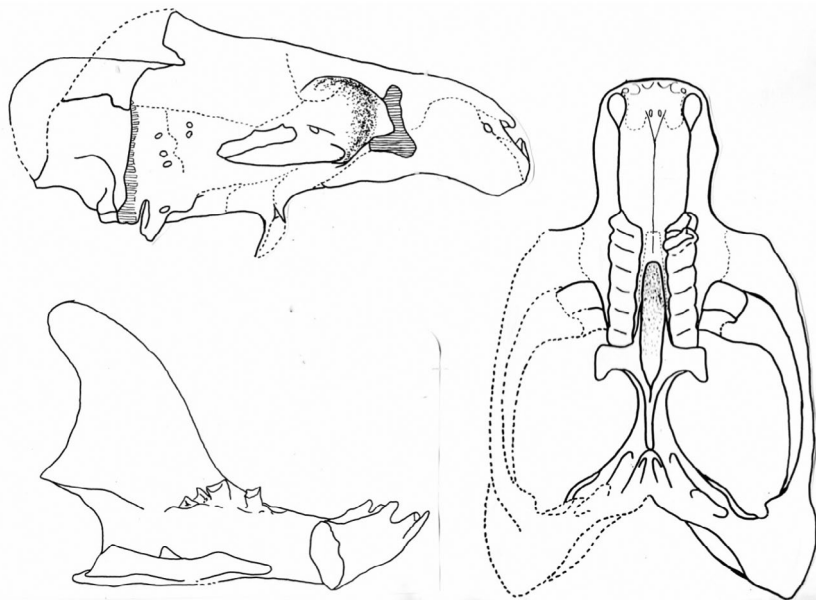


Figure 5. Specimen PVL2564 in right lateral and palatine skull views, and a medial view of the left lower jaw. This type specimen of the traversodontid *Ischignathus sudamericanus* illustrates morphological affinities with Tritylodontidae (from Bonaparte 1963). Length of skull: 60 cm. The significant features of this specimen include parallel upper postcanine rows, a large diastoma between postcanines and the anterior dentition located in the more distal portion of the maxilla and premaxilla, and the internal nares in an anterior position relative to the postcanine row. Note that in lateral view the skull is posteriorly elevated.

reduction of the deep zygoma, and loss of an external auditory meatus. While this theoretically possible, we consider a procynosuchid/ictidosaur relationship a stronger possibility.

We suggest two phylogenetic lines, one leading from procynosuchids to ictidosaurians and the other from procynosuchids to epicynodonts and eucynodonts. One line evolves towards the mammalian condition, with a loss of circumorbital bones

(prefrontal, postfrontal, and postorbital), retention of an interpterygoid vacuity, a slender zygomatic arch, dentary/squamosal contact, and a long snout. The second evolves towards advanced non-mammalian cynodonts and tritylodontids with loss of the interpterygoid vacuity (present in juveniles), formation of a strong ventral crest formed by the pterygoids and parasphenoid, a very deep zygomatic arch, a tall dentary, and a short and wide snout.

The cladogram shown in Figure 4 proposes one possible origin for Ictidosauria plus Mammalia as distinct from that for Epicynodontia. On the basis of the known fossil record, we find it plausible that Ictidosauria arose from the Procynosuchidae. Still, differences in the component bones of the circumorbital area and the position and shape of the frontals require caution. Unknown intermediate species would have required considerable time to develop such modifications.

Origin of *Tritylodontidae*

The cranial structure of the Epicynodont *Ischignathus*, from the early Late Triassic of Argentina (Bonaparte 1963), possesses tritylodontid features in the skull and lower jaws, while retaining features of the postcanines present in Middle Triassic traversodontids (Figure 5). This appears to support a close relationship of Tritylodontidae to Traversodontidae (Hopson & Kitching 2001) rather than to Probainognathidae (Kemp 2005; Abdala 2007; Liu & Olsen 2010; Martinelli et al. 2016). However, support for a Probainognathidae/Tritylodontidae relationship would be greatly strengthened if fossils clearly related to probainognathids were found to possess features such as parallel rows of postcanines designed for an herbivorous diet, and the loss of a surangular squamosal contact, while simultaneously possessing mammalian features such as a closed medial wall to the orbit.

Conclusion

We consider the view that ictidosaur and mammaliaforms arose from Permian procynosuchid non-mammalian cynodonts more plausible than the claim for dual origin of ictidosaur and tritylodontids from Middle Triassic probainognathid non-mammalian cynodonts. We acknowledge the origin of similar features in both proposed phylogenetic lines. However, the origin of ictidosaur from probainognathids implies that the latter regained an interpterygoid vacuity, reduced the depth of the zygoma, and lost the surangular/dentary contact while developing a dentary condyle/squamosal contact and retaining simple single rooted postcanines. On the other hand, if tritylodontids originated from probainognathids this would require greatly increasing the depth of the zygoma and dentary, retaining a strong junction between the basisphenoid and the palate (no interpterygoid vacuity is found in adults), acquiring transversely wide multi-rooted postcanines, and retaining and strengthening the primitive articular/quadrangle jaw articulation while losing the surangular/quadrangle contact.

We find the view that mammaliaforms arose from forms similar to *Brasilitherium* more plausible than the suggestion that mammaliaforms arose from a hypothetical probainognathid that is considered to be ancestral to both tritylodontids and ictidosaur.

The conclusions of this paper represent a new interpretation of the structure and phylogeny of cynodonts, informed by recent discoveries from the Late Triassic of Southern Brazil.

New discoveries of small insectivorous cynodonts, and further anatomical comparison with specimens of *Therioherpeton* and *Brasilodon-Brasilitherium* indicate that 'Brasilodontidae' is a junior synonymy of Therioherpetidae.

Common characters recorded in Therioherpetidae and Trithledontidae, such as interpterygoid vacuities, a slender zygomatic arch, the absence of prefrontal and postorbital arches, a reduced parietal crest, and wide braincase justify the inclusion of both families within the clade Ictidosauria.

The Ictidosauria retained a set of primitive features present in Procynosuchidae, whereas Probainognathidae evolved a set of more advanced characters. We suggest a closer relationship between Procynosuchidae and Ictidosauria than between probainognathid cynodonts and ictidosaur.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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