A revision of the putative Late Cretaceous triconodonts from South America

L.C. Gaetano [a,*], C.A. Marsicano [a], G.W. Rougier [b]

[a] Instituto de Estudios Andinos "Don Pablo Groeber" (UBA − CONICET), Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Intendente Güiraldes 2160, Ciudad Universitaria, Pabellón II, C1428EGA Ciudad Autónoma de Buenos Aires, Argentina
[b] Department of Anatomical Sciences and Neurobiology, University of Louisville, 500 S. Preston St., Louisville, KY 40292, USA

ABSTRACT

Austrotriconodon mckennai and Austrotriconodon sepulvedai, from the Campanian Los Alamitos Formation, Patagonia, Argentina were originally described as triconodont mammals and the sole members of the family Austrotriconodontidae. These mammals were represented by isolated cheek teeth originally regarded as molariforms, but their peculiar morphology later raised doubts about their purported triconodont affinities. Nevertheless, the morphological bases supporting the alternative taxonomic views have not been fully documented. We present here detailed comparisons of Austrotriconodon with other Late Cretaceous taxa and conclude that Austrotriconodon specimens should be assigned to Meridiolestida and Mesungulatoidea. These isolated teeth are likely premolars and might represent unknown dental positions of already described species or correspond to taxa that are yet to be formally recognized. According to our interpretation, there is still no record of Cretaceous triconodonts in South America, but we support the triconodont affinities for Jurassic taxa from the Cañadón Asfalto Formation in central Patagonia.

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1. Introduction

The presence of Mesozoic mammaliaforms in South America was first documented by the description of the ichnogenus Ameghinichnus patagonicus Casamiquela, 1964 from the Middle−Late Jurassic La Matilde Formation, Santa Cruz Province, Argentina (Casamiquela, 1964). However, it was more than 20 years later that the first osteological remains of Mesozoic mammaliaforms were found; in 1985, Bonaparte and Soria described an isolated molariform from the Late Cretaceous Los Alamitos Formation, Río Negro Province, Argentina. This specimen, initially thought to represent an upper molar of a basal ungulate, served as the basis for what was later recognized as a non-tribosphenic mammal, Mesungulatum houssayi Bonaparte and Soria, 1985. After this initial publication, intensive work of Bonaparte over the following 20 years resulted in the recognition of a diverse mammaliaform fauna from Los Alamitos Formation represented by 17 genera and 19 species (Bonaparte and Soria, 1985; Bonaparte, 1986a,b,c, 1987, 1990, 1992, 1994, 2002).

Among these taxa, Bonaparte reported two "triconodont" species represented by isolated upper and lower cheek teeth (Austrotriconodon mckennai Bonaparte, 1986a and Austrotriconodon sepulvedai Bonaparte, 1992) and included them in the monotypic family Austrotriconodontidae (Bonaparte, 1992).

Although other Jurassic and Cretaceous mammaliaforms were later found in South America (see section 2), Austrotriconodon long remained the only Mesozoic "triconodont" known from this subcontinent. It was not until the description of Argentoconodon fariasorum Rougier et al., 2007a and Condorodon spanios Gaetano and Rougier, 2012 from the Jurassic (Wilf et al., 2013; Cúneo et al., 2013) Cañadón Asfalto Formation, Chubut Province, Argentina that new information on South American Mesozoic "triconodonts" became available.

Unlike the widely supported "triconodont" affinities of Argentoconodon fariasorum and Condorodon spanios, the identification of the "triconodonts" from the Los Alamitos Formation (Bonaparte, 1986a, 1992) has been disputed (Rougier et al., 2007a, 2011a). In this context, the morphology exhibited by the Jurassic triconodonts was recognized to be clearly different from those of Los Alamitos Formation, suggesting that these forms might not be closely related (Rougier et al., 2007a; Gaetano and Rougier, 2011, 2012). Additionally, the discovery of Cretaceous mammaliaforms with relatively complete or complete dentitions (Coloniatherium cilinskii

* Corresponding author. Tel.: +54 11 4576 3400x255.
E-mail addresses: lcgaetano@gl.fcen.uba.ar, leandrogaetano@gmail.com (L.C. Gaetano), claumar@gl.fcen.uba.ar (C.A. Marsicano), grougier@louisville.edu (G.W. Rougier).

Rougier et al., 2009b and *Cronopio dentiacutus* Rougier et al., 2011a) raised doubts about the triconodont affinities of *Austrotriconodon* (see Rougier et al., 2011a).

Rougier et al. (2011a) questioned the "triconodont" affinities suggested for *Austrotriconodon* and interpreted the specimens as meridiolestid dryolestoids. Rougier et al. based their hypothesis on the similarities between the lower teeth of *Austrotriconodon* and some premolariforms assigned to *Coloniatherium cilinskii* and *Cronopio dentiacutus*. However, except for the mention of a similar cusp pattern, a general resemblance of the teeth, and a comparative figure, Rougier et al. (2011a) did not make explicit the particular shared traits that supported their interpretations. Meridiolestidans have been alternatively interpreted as dryolestoids (Rougier et al., 2011a; Chimento et al., 2012), derived cladotherians (Rougier et al., 2012), and basal trechnotherians closely related to spalacotheriids (Averianov et al., 2013). It is beyond the scope of this paper to solve the phylogenetic affinities of meridiolestidans. Hence, we will simply refer to meridiolestidans without making any suggestion of their high-level relationships. Despite the disagreement regarding their relationships, it is clear that Meridiolestida are a natural group that includes several endemic Argentinean taxa with relatively mesiodistally compressed cheek teeth (i.e., *Cronopio*, *Leonardus* Bonaparte, 1990, and *Necrolestes* Ameghino, 1891) and the probably omnivorous/herbivorous mesungulatids and allies (i.e., *Coloniatherium*, *Mesungulatum*, *Peligrotherium* Bonaparte et al., 1993, and *Reigitherium* Bonaparte, 1990) (see Rougier et al., 2011a, 2012; Chimento et al., 2012; Averianov et al., 2013). The main aim of this contribution is to provide a better documentation of *Austrotriconodon* and a detailed morphological analysis of the specimens assigned to this genus by Bonaparte (1986a, 1992) to clarify their taxonomic affinities.

The term "triconodont" is used informally here to refer to specimens with three major cusps in line, the members of the traditional, and non-monophyletic, Order Triconodonta Osborn, 1888 and forms similar to them (see for example Kielan-Jaworowska et al., 2004; Gaetano and Rougier, 2011, 2012; Gaetano, 2013); for the sake of simplicity the quotation marks will be omitted on the remainder of this paper.

Cusp nomenclature follows the usual convention by employing letter designations for triconodont teeth and tribosphenic nomenclature for meridiolestidans (e.g., Kielan-Jaworowska et al., 2004; Rougier et al., 2009a,b, 2011a, 2012; Chimento et al., 2012; Averianov et al., 2013). Cusp homology between forms with triangulated and non-triangulated cusps is beyond the scope of this contribution.

1.1. Institutional abbreviations

MACNRN-PV, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", colección Río Negro.

2. South American Mesozoic mammaliaform discoveries through time

Almost 30 years have passed since the first discoveries of Mesozoic mammaliaforms in South America. A number of paleontological expeditions have been devoted to search these elusive forms. However, findings are restricted to a single Jurassic and a handful of Cretaceous localities.

The Jurassic Queso Rallado locality, Cañadón Asfalto Formation, Chubut Province, Argentina has yielded five mammaliaforms. Two of them, *Asfaltomylos patagonicus* Rauhut et al., 2002 and *Henosferus molus* Rougier et al., 2007c, have been recognized as basal members of Australosphenida (see Rougier et al., 2007c), whereas two other taxa are triconodonts, a derived triconodontid

Fig. 1. Location map of South America with a detail of Patagonia, Argentina showing the localities where Mesozoic mammaliaforms have been found. **References**: **1**. Laguna Manantiales, La Matilde Fm., Santa Cruz Province, Argentina; **2**. Queso Rallado, Cañadón Asfalto Fm.; Chubut Province, Argentina; **3**. La Amarga, La Amarga Fm., Neuquén Province, Argentina; **4**. La Buitrera, Candeleros Fm., Río Negro Province, Argentina; **5**. Cerro Cuadrado, Los Alamitos Fm., Río Negro Province, Argentina; **6**. Cerro Tortuga, Allen Fm., Río Negro Province, Argentina; **7**. La Colonia, La Colonia Fm., Chubut Province, Argentina; **8**. Paso Córdoba, Río Colorado Fm., Río Negro Province, Argentina; **9**. Lago Los Barreales, Los Bastos Fm., Neuquén Province, Argentina; **10**. Adamantina Fm., Sao Paulo, Brazil; **11**. Pajcha Pata, El Molino Fm., Bolivia; **12**. Laguna Umayo, Muñani Fm., Perú; **13**. Fundo el Triunfo, Fundo el Triunfo Fm., Perú. Modified from Rougier et al. (2011b).

(*Argentoconodon fariasorum*) and an "amphilestid" amphilestherian (*Condorodon spanios*). The last taxon from Queso Rallado, a purported allotherian (Gaetano and Rougier, 2010), has not been yet published.

Vincelestes neuquenianus Bonaparte, 1986a is the only Early Cretaceous South American mammaliaform known. *Vincelestes* was found in the lower member of La Amarga Formation, Neuquén Province, Argentina (Bonaparte, 1986a; Bonaparte and Rougier, 1987; Rougier, 1993) and is probably of Barremian age (Leanza and Hugo, 1995, 1997; Salgado et al., 2006). *Vincelestes* is represented by several relatively complete specimens including cranial and postcranial material from a single locality (Rougier, 1993).

The Late Cretaceous taxa represent several time intervals, are more abundant, and in some instances are better preserved than the Jurassic ones. Late Cretaceous mammaliaforms have been discovered in Argentina, Bolivia, Brazil, and Perú (see Kielan-Jaworowska et al., 2004 and Rougier et al., 2011b for a review; Forasiepi et al., 2012; Fig. 1). The Argentinean localities from which Late Cretaceous mammaliaforms have been reported are: La Buitrera, Cerro Cuadrado, Paso Córdoba, and Cerro Tortuga in Río Negro Province; La Colonia in Chubut Province; and Lago Los Barreales in Neuquén Province.

The fossiliferous outcrops of La Buitrera locality have been assigned to the Candeleros Formation (Leanza et al., 2004) and are regarded as early Cenomanian age (Garrido, 2010). Early Late

Cretaceous mammaliaforms from South America have been found only in this locality. Rougier et al. (2011a) reported *Cronopio dentiacutus* and an as yet undescribed taxon.

The Lago Los Barreales locality has yielded only an edentulous lower jaw found in a level probably belonging to the Los Bastos Formation of early to middle Coniacian age (Garrido, 2010, 2011; Forasiepi et al., 2012). The genus and species of this specimen were left in open nomenclature but the authors suggested affinities with mesungulatid meridiolestidans (Forasiepi et al., 2012). If so, this finding represents the geologically oldest mesungulatid known to date.

The most diverse South American mammaliaform Cretaceous assemblage comes from Cerro Cuadrado locality, Los Alamitos Formation (Bonaparte and Soria, 1985; Bonaparte, 1986a,b,c, 1990, 1992, 1994, 2002; Bonaparte and Kielan-Jaworowska, 1987). The Los Alamitos Formation is regarded to be of Campanian age (Bonaparte, 1986a, 1987; Rougier et al., 2009a,b). Bonaparte collected a large number of specimens which he regarded as dryolestoids, gondwanatheriids, multituberculates, symmetrodonts, and triconodonts (see Pascual et al., 1999; Kielan-Jaworowska et al., 2004; Rougier et al., 2007a, 2011a,b; and Averianov et al., 2013 for an alternative view). The mammaliaforms from the Cerro Cuadrado locality are part of a fauna of Gondwanan nature that includes several endemic South American forms (Bonaparte, 1986a,b,c, 1990, 1992, 1994, 2002).

The Campanian–Maastrichtian Anacleto Formation outcrops at the Paso Córdoba locality yielded only an edentulous, incomplete lower jaw which has been identified as a marsupial by Goin et al. (1986); however, this specimen was later re-interpreted as a dryolestoid (Martinelli and Forasiepi, 2004), an identification followed by other authors (Rougier et al., 2011b) and here.

In outcrops of the Maastrichtian Allen Formation at the Cerro Tortuga locality, seven isolated mammaliaform teeth have been found (Rougier et al., 2009a). The Cerro Tortuga mammaliaform fauna is comparable to that of Cerro Cuadrado in that both faunas include ferugliotheriids and dryolestoids (Rougier et al., 2009a). Several of the supraspecific taxa found at Cerro Tortuga are co-generic with those reported from the Los Alamitos Formation (i.e., *Barberenia* Bonaparte, 1990 and *Mesungulatum*) but represent different species (i.e., *B. allenensis* Rougier et al., 2009a and *M. lamarquensis* Rougier et al., 2009a). Additionally, there are shared taxa between the faunas of Cerro Tortuga and Cerro Cuadrado (i.e., *Groebertherium stipanicici* Bonaparte, 1986a and cf. *Brandonia* Bonaparte, 1990). Other forms, that up to now have only been reported from Cerro Tortuga locality (i.e., *Trapalcotherium matuastensis* Rougier et al., 2009a), are closely related to mammals from Los Alamitos Formation.

At the La Colonia locality, outcrops of the homonymous formation have provided mammaliaform remains of Maastrichtian age (Rougier et al., 2009b). Some of these taxa (i.e., ferugliotheriids, mesungulatids, and reigitheriids) are also known from the Cerro Cuadrado locality (see Rougier et al., 2011b for a review). The most common form at La Colonia has been identified as *Coloniatherium cilinskii*, a mesungulatid only reported from this site and represented by teeth, jaws, and petrosals (Rougier et al., 2009b).

Mammals of the Tiupampa locality, Bolivia, were originally thought to be of Cretaceous age (Marshall and Muizon, 1988; Muizon, 1994; Muizon et al., 1997; Marshall and Sigogneau-Russell, 1995). However, these outcrops were later recognized to be from the early Paleogene and assigned to the Santa Lucía Formation (Van Valen, 1988; Gayet et al., 1991; Muizon, 1998). Presently, the only Bolivian site where Mesozoic mammaliaforms have been found is Pajcha Pata (Kielan-Jaworowska et al., 2004; Rougier et al., 2011b). Two complete teeth and a fragmentary one have been

reported from this locality; they have been interpreted as representing a dryolestoid and a therian (Gayet et al., 2001) but some of them could represent meridiolestidans (Rougier et al., 2011b).

Bertini et al. (1993) published a fragmentary lower jaw from the Adamantina Formation (Cenomanian–Campanian?), Sao Paulo, Brazil and attributed the specimen to Eutheria. However, there is insufficient evidence to exclude other mammaliaform affinities (Rougier et al., 2011b).

Mesozoic mammaliaforms from Perú are restricted to the findings at two Cretaceous localities: Laguna Umayo (Muñani Formation, Maastrichtian) and Fundo el Triunfo (Fundo el Triunfo Formation, Campanian–Maastrichtian) (Kielan-Jaworowska et al., 2004; Rougier et al., 2011b). Five therian taxa represented by isolated and fragmentary teeth have been found at Laguna Umayo (Grambast et al., 1967; Sigé, 1971, 1972; Van Valen, 1978; Crochet, 1980; Marshall et al., 1983). On the other hand, only a single therian tooth of uncertain affinities has been reported from Fundo el Triunfo (Sigé, 1971).

The poor record and debatable affinities of Mesozoic mammaliaforms from Bolivia, Brazil, and Perú make it difficult to characterize the taxonomic composition of the mammaliaform assemblages. Argentinean Cretaceous mammaliaform faunas seem to have been dominated by relatively basal forms; the presence of therian remains is still to be convincingly demonstrated.

3. Triconodont hypothesis: a comparative analysis

The tooth morphology of *Austrotriconodon* is peculiar and very different from that of other triconodonts. Following the interpretations of Bonaparte (1986a, 1990, 1992, 1994), the purported lower molariforms of *Austrotriconodon* are characterized by the mesiodistal alignment of three main cusps. The crown is dominated by a main cusp (**a**) and two very reduced minor ones (**b** and **c**). Cusp **b** is approximately 1/3 of the height of cusp **a**. Cusp **c** is substantially smaller than **b** and, depending on the specimen, can be as tall as cusp **d** or slightly taller. The cusp proportions result in molariforms that are markedly asymmetrical in lateral view. Additionally, there are well-developed cingula and wear facets. A similar morphology is recognized in the only lower premolariform (MACNPV-RN240) described by Bonaparte (1992). However, in this lower premolariform, the anterior root is more robust than the posterior one, the main cusp (**a**) is more centrally placed on the crown, cusp **b** is minute, and there is a relatively large distal cusp (identified as **cd** by Bonaparte, 1992) and a very small accessory cusp at the distal end of the crown.

There is a single upper tooth referred to *Austrotriconodon* and identified as a molariform (Bonaparte, 1992). Its morphology is unique among mammaliaforms (Bonaparte, 1992). According to Bonaparte, this tooth has four poorly separated main cusps (**A**–**D**) forming a continuous lamina ("en empalizada" disposition *sensu* Bonaparte, 1992) that decrease in height distally (**B** > **A** > **C** > **D**). There is a concavity on the mesial face of cusp **B** that is not limited by well-defined crests or cusps and was interpreted by Bonaparte (1992) as part of an interlocking mechanism between adjacent molariforms. A lingual cingulum extending along most of the length of the crown is present. Bonaparte (1992) hypothesized that the lower molariform might have occluded in the shelf defined by the cingulum.

Basal triconodonts, which are some of the most basal mammaliaforms (e.g., Huene, 1933; Parrington, 1941; Kühne, 1949; Patterson and Olson, 1961; Rigney, 1963; Crompton, 1964; Crompton and Jenkins, 1968; Freeman, 1979; Clemens, 1980, 2011; Jenkins et al., 1983; Sigogneau-Russell, 1983; Yadagiri, 1984; Lucas and Hunt, 1990; Hahn, 1993; Datta and Das, 1996, 2001; Butler et al., 2012), have molariforms that are not as compressed

labiolingually as those of more derived triconodonts. The crown of the molariforms is dominated by cusp **A**/**a** followed in height by cusp **C**/**c**. Cusp **B**/**b** is relatively small and can be part of a mesial cingulum in some forms. The cingula are well-developed and usually bear numerous relatively large cingular cuspules.

Triconodontids and closely related taxa (e.g., Simpson, 1925a,b, 1928; Patterson, 1951; Fox, 1969; Sigogneau-Russell, 1995; Cifelli and Madsen, 1998; Cifelli et al., 1998, 1999; Meng et al., 2006, 2011; Rougier et al., 2007a; Montellano et al., 2008; Kusuhashi et al., 2009) are a group of derived triconodonts consistently regarded as monophyletic (Ji et al., 1999; Rougier et al., 2001, 2007b; Luo et al., 2002, 2007; Kielan-Jaworowska et al., 2004; Hu et al., 2005; Montellano et al., 2008; Kusuhashi et al., 2009; Gao et al., 2010; Meng et al., 2011; Gaetano and Rougier, 2011, 2012). These forms have molariforms with three main mesiodistally aligned cusps (**A**/**a**, **B**/**b**, and **C**/**c**) that are generally similar in height. Cingula and cingular cusps might be present but they are not as well-developed as in basal triconodonts or austrotriconodontids. A relatively small distal accessory cusp (**D**/**d**) is present in basal triconodontids but it is tall in more derived forms (i.e., alticonodontines).

In volaticotherine triconodonts, which Gaetano and Rougier (2011) place within Alticonodontinae, the main cusps are recumbent, there is no mesial accessory cusp **e** in lower molariforms (present in some non-volaticotherine alticonodontines), and there are no cingula (Sigogneau-Russell, 1995; Meng et al., 2006; Gaetano and Rougier, 2011). Unlike other triconodontids, the upper molariforms of volaticotherines have relatively more labiolingually compressed crowns, a well-developed mesial accessory cusp (**E**), no cingula, and a distally overhanging cusp **D**.

"Amphilestids" (e.g., Owen, 1838, 1859; Simpson, 1925b; Prasad and Manhas, 1997; Heinrich, 1998; Kretzoi and Kretzoi, 2000; Sigogneau-Russell, 2003; Averianov et al., 2005; Rougier et al., 2007b; Gao et al., 2010; Lopatin et al., 2010; Gaetano and Rougier, 2012), a paraphyletic assemblage of derived triconodonts more closely related to cladotherians than to triconodontids (Rougier et al., 2007b; Montellano et al., 2008; Kusuhashi et al., 2009; Gao et al., 2010; Gaetano and Rougier, 2011, 2012; see Luo et al., 2002, 2007; Kielan-Jaworowska et al., 2004; Hu et al., 2005 for an alternative view), have molariforms with five bulbous cusps (**A**/**a**–**E**/**e**). The cusps are mesiodistally aligned or might show a slight triangulation. Cusp **A**/**a** is the largest and tallest of the cusps; it is centered on the crown and flanked by two smaller cusps (**B**/**b** and **C**/**c**) that are subequal in height. Mesially and distally, two small accessory cusps of similar size are present (**D**/**d** and **E**/**e**). Additionally, a small mesial accessory cusp **F**/**f** may be present. Cusp **A**/**a** is erect. Cusp **B**/**b** and **C**/**c** are divergent from cusp **A**/**a**, pointing mesially and distally, respectively. The valleys between the main cusps are not very deep so the cusps are not completely separated.

Dental interlocking mechanisms in triconodonts are mainly known from lower dentitions (see references above). Typically, the distal accessory cusp contacts a concave surface on the mesial face of the adjacent posterior molariform. In most basal triconodonts and "amphilestids", the mesial concavity is limited by two relatively small mesial cusps. These cusps have been identified as **b** and **e** in the lower molariforms of basal triconodonts and as **e** and **f** in the lower molariforms of "amphilestids". On the other hand, non-volaticotherine triconodontids lack a mesial accessory cusp (**e**) on the lower molariforms; thus, the mesial concave surface contacted by cusp **d** of the anterior molariform is limited by well-developed ridges on the sides of the relatively large cusp **b**. In non-volaticotherine alticonodontines, this triconodontid condition is much further developed as the mesial concavity continues on to a groove extending along the mesial face of the anterior root. In volaticotherines, as in some basal triconodonts and "amphilestids", the molariforms lack any special interlocking structure and, in
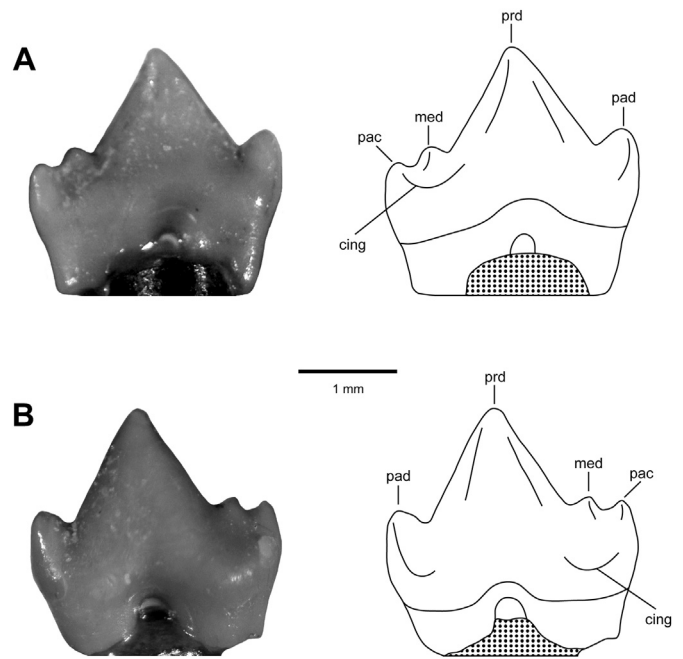
Fig. 2. Photo and line drawing of *Austrotriconodon mckennai* lower right premolariform (MACNPV-RN21) in labial (**A**) and lingual (**B**) views. **Abbreviations**: **cing**, cingulum; **med**, metaconid; **pac**, posterior accessory cusp; **pad**, paraconid; **prd**, protoconid. Dotted areas represent covered surfaces.

some forms, the posterior cheek teeth are imbricated (a derived character; see Gaetano and Rougier, 2011, 2012).

Austrotriconodon differs strikingly from the other known triconodonts reviewed above in dental features such as the relative size and proportion of the cusps, the development of cingula and cingular cuspules, and the structure of the mesial concavity associated with an interlocking mechanism. On the other hand, close similarity can be recognized between *Austrotriconodon* specimens and some Argentinean meridiolestidans (see Section 4).

4. Systematic paleontology

Unnamed rank MAMMALIAFORMES Rowe, 1988
Class Mammalia Linnaeus, 1758
Unnamed rank Trechnotheria McKenna, 1975
Unnamed rank Meridiolestida Rougier, Apesteguía and Gaetano, 2011a
Genus *AUSTROTRICONODON* Bonaparte, 1986a
Type species. Austrotriconodon mckennai Bonaparte, 1986a
Emended diagnosis. The same as for the type species.
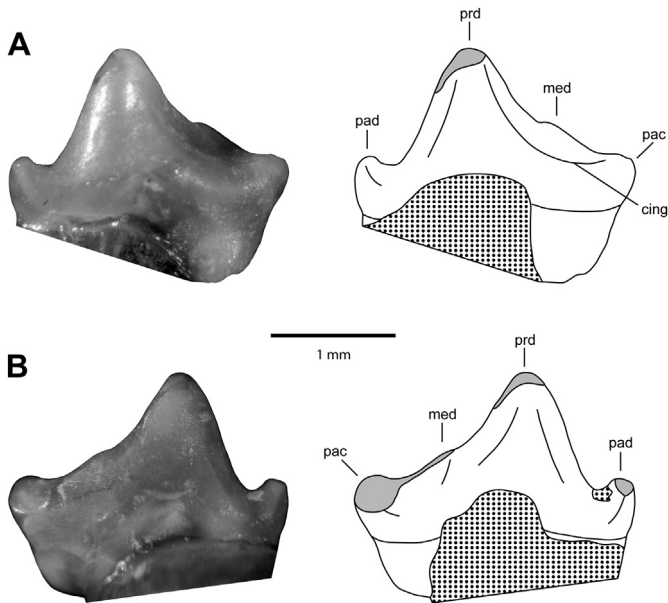*Austrotriconodon mckennai* Bonaparte, 1986a
Figs. 2 and 3

Holotype. MACNPV-RN21, complete lower right premolariform (Fig. 2).
Hypodigm. MACNPV-RN234, complete lower left premolariform (Fig. 3).
Synonym. *Austrotriconodon ferox* Bonaparte, 1986c.
Geographic and stratigraphic provenance. Middle section of the Los Alamitos Formation, Cerro Cuadrado locality, southwest slope of the Cerro Cuadrado, Estancia Los Alamitos, Arroyo Verde area, southeast Río Negro province, Argentina; probably of Campanian age (Bonaparte, 1986a, 1987).
Emended diagnosis. Meridiolestidan with labiolingually compressed premolariforms, asymmetric in lateral aspect. Lingual face more concave than the labial one in occlusal view. With four crown

Fig. 3. Photo and line drawing of *Austrotriconodon mckennai* lower left premolariform (MACNPV-RN234) in labial (**A**) and lingual (**B**) views. **Abbreviations**: **cing**, cingulum; **med**, metaconid; **pac**, posterior accessory cusp; **pad**, paraconid; **prd**, protoconid. Dotted areas represent covered surfaces; shaded areas represent worn surfaces.

cusps: protoconid, paraconid, metaconid, and a distal accessory cusp. Protoconid larger than the other cusps and mesially placed. Distinct paraconid, emerging at the same level than the metaconid and the distal accessory cusp. Well-developed labial cingulid between the protoconid and the distal accessory cusp. Two roots present, the posterior root larger than the anterior one. It can be distinguished from *Cronopio dentiacutus*, the most similar taxon, by the presence of a relatively large paraconid, a larger posterior than anterior root, and the bases of the paraconid, metaconid, and distal accessory cusp at the same level.

Discussion. Bonaparte (1986a: 53) designed MACNPV-RN21 and MACNPV-RN234 the holotype and paratype of *Austrotriconodon mckennai*, respectively. Nevertheless, Bonaparte (1986c: 86) illustrated and labeled MACNPV-RN21 specimen as *Austrotriconodon ferox*, indicating that it was the holotype of a new taxon published by himself in the same volume (i.e., Bonaparte, 1986a: 53). According to the International Code of Zoological Nomenclature (ICZN), 1999, the name *Austrotriconodon ferox* Bonaparte, 1986c is available (Art. 13). Hence, it is an objective synonym of *Austrotriconodon mckennai* Bonaparte, 1986a. Nevertheless, the name employed by Bonaparte (1986c) in reference to MACNPV-RN21 is probably a mistake as Bonaparte did not make explicit his intention of performing a nomenclatorial action nor did he present a proper description accompanying the illustration in Bonaparte, 1986c (page 86). Moreover, no other researcher has made reference to MACNPV-RN21 as *Austrotriconodon ferox.* Thus, we acknowledge *Austrotriconodon mckennai* to be the valid name for the taxon represented by MACNPV-RN21 (holotype) and MACNPV-RN234 (paratype) (see Art. 24 of the ICZN).

The known lower premolariforms of *A. mckennai* (MACNPV-RN21 and 234) are similar to the p2 of *Cronopio dentiacutus*. On the basis of these comparisons, MACNPV-RN21 and MACNPV-RN234 are re-interpreted here as right and left lower premolariforms, respectively (see below); not as left lower molariforms (Bonaparte, 1986a). MACNPV-RN21, MACNPV-RN234, and the p2 of *Cronopio* share the labiolingual compression and the asymmetry of the crown in lateral view. The lingual face of the crown is more concave

than the labial one in occlusal view. In these teeth, the slightly mesial protoconid dominates the crown. The mesial margin of the protoconid is convex whereas the distal one is concave. These teeth bear an erect metaconid and a labial cingulid between the protoconid and the distal accessory cusp.

In MACNPV-RN234 and the p2 of *Cronopio* the distal half of the tooth is higher relative to the base of the crown and the distal margin of the protoconid is relatively shorter than the mesial one when compared to MACNPV-RN21. MACNPV-RN234 differs from the second lower premolariform of *Cronopio* and MACNPV-RN21 in the presence of a procumbent paraconid well separated from the protoconid by a comparatively wide valley and a distal accessory cusp that is aligned with the rest of the cusps (not labially displaced). Unlike the p2 of *Cronopio*, MACNPV-RN21 and MACNPV-RN234 present a relatively large paraconid whose base is at the same level as the metaconid and the distal accessory cusp (not basal to them as in *Cronopio*). Additionally, the posterior root is larger than the anterior one in MACNPV-RN21 and MACNPV-RN234, whereas the opposite is observed in the p2 of *Cronopio*.

Based on the similarities recognized, we conclude that *Austrotriconodon mckennai* is more closely related to meridiolestidans than to triconodonts, a hypothesis also suggested by previous authors (Rougier et al., 2011a). However, as expressed in the diagnosis, *Austrotriconodon mckennai* and *Cronopio* differ in details and were found in rocks that differ in age by approximately 30 Ma apart; co-generic affinities between these taxa seem unlikely.

Several meridiolestidan taxa have been reported from the Allen, La Colonia, and Los Alamitos formations (Bonaparte and Soria, 1985; Bonaparte, 1986a, 1990, 1992, 1994, 2002; Rougier et al., 2009a,b). These forms are known from isolated teeth or incomplete dentitions, mostly molariform loci, and could even represent different tooth positions of the same taxon (e.g., Rougier et al., 2011a). Although of similar age, MACNPV-RN21 and MACNPV-RN234 cannot be unambiguously assigned to any of these taxa on the basis of the available evidence.

Relatively complete dentitions of meridiolestidans are only known for *Cronopio*, *Necrolestes*, and *Peligrotherium* (Rougier et al., 2011a, 2012; Páez Arango, 2008). In *Cronopio* and *Necrolestes*, the premolariforms are longer mesiodistally than the molariforms. This is also true for the lower teeth of *Peligrotherium*, whereas the upper premolariforms are shorter mesiodistally than the molariforms. If our interpretation is correct that MACNPV-RN21 and MACNPV-RN234 are lower premolariforms, then it is likely that the length ratio of the lower molariforms *vs* molariforms of *A. mckennai* would be comparable to that of *Cronopio*, *Necrolestes*, and *Peligrotherium*.

Late Cretaceous mammaliaforms that could have similar proportions are: *Trapalcotherium* from the Allen Formation; *Alamitherium* Bonaparte, 2002, *Bondesius* Bonaparte, 1990, *Casamiquelia* Bonaparte, 1990, *Ferugliotherium* Bonaparte, 1986a, *Leonardus* Bonaparte, 1990, *Reigitherium* Bonaparte, 1990, *Rougietherium* Bonaparte, 2002, and *Vucetichia* Bonaparte, 1990 from the Los Alamitos Formation; and *Barberenia* Bonaparte, 1990, *Brandonia*, and *Groebertherium* from both the Allen and Los Alamitos formations. These taxa do not compare closely to MACNPV-RN21 (or MACNPV-RN234). However, if co-generic or co-specific affinities of these forms are demonstrated, the cases of synonymy should be addressed. In this latter scenario, the names *Alamitherium*, *Barberenia*, *Bondesius*, *Brandonia*, *Casamiquelia*, *Leonardus*, *Reigitherium*, *Rougietherium*, *Trapalcotherium*, and *Vucetichia* would be junior synonyms of *Austrotriconodon*. On the other hand, as *Austrotriconodon*, *Ferugliotherium*, and *Groebertherium* were all published in the same paper (Bonaparte, 1986a) and the ICZN does not establish that publication page is a criterion to establish name priority (Art. 23), a decision would need to be made on the name priority (Art. 24).
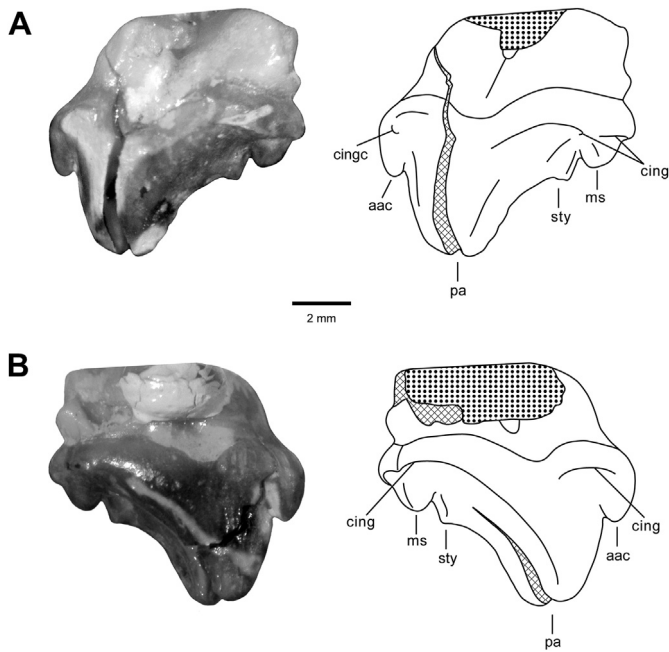
Fig. 4. Photo and line drawing of a left P1 of a mesungulatid indet. (MACNPV-RN239) in labial (**A**) and lingual (**B**) views. **Abbreviations**: **aac**, anterior accessory cusp; **cing**, cingulum; **cingc**, cingular cusp; **ms**, metastyle; **pa**, paracone; **sty**, stylocone. Dotted areas represent covered surfaces; striped areas represent broken surfaces.

Fig. 5. Photo and line drawing of a left p1 of a mesungulatid indet. (MACNPV-RN240) in labial (**A**) and lingual (**B**) views. **Abbreviations**: **cing**, cingulum; **med**, metaconid; **pac**, posterior accessory cusp; **pad**, paraconid; **prd**, protoconid. Dotted areas represent covered surfaces; striped areas represent broken surfaces.

Considering the uncertain taxonomic affinities of MACNPV-RN21 and MACNPV-RN234, we prefer to provisionally follow Bonaparte (1986a, 1992) in recognizing *Austrotriconodon mckennai* as a valid taxon but including this species in the clade Meridiolestida.

Unnamed rank MAMMALIAFORMES Rowe, 1988
Class Mammalia Linnaeus, 1758
Unnamed rank Trechnotheria McKenna, 1975
Unnamed rank Meridiolestida Rougier, Apesteguía and Gaetano, 2011a
Family Mesungulatidae Bonaparte, 1986a
Genus and species indet.

Referred material. MACNPV-RN239, complete left P1 (Fig. 4); MACNPV-RN240, complete left p1 (Fig. 5).
Synonym. Austrotriconodon sepulvedai Bonaparte, 1992
Geographic and stratigraphic provenance. Middle section of the Los Alamitos Formation, Cerro Cuadrado locality, southwest slope of the Cerro Cuadrado, Estancia Los Alamitos, Arroyo Verde area, southeast Río Negro province, Argentina; probably of Campanian age (Bonaparte, 1986a, 1987).
Description. These specimens were originally interpreted by Bonaparte (1992) as triconodont teeth. Herein we consider MACNPV-RN239 and MACNPV-RN240 to be upper and lower premolariforms, respectively (see below), of a slender mesungulatid and describe them as such.
MACNPV-RN239 and MACNPV-RN240 are labiolingually compressed teeth with four mesiodistally aligned cusps centered on the crown. They are very similar to the P/p1 of *Coloniatherium cilinskii* but significantly smaller and without well-developed cingula. MACNPV-RN239 has a dominant paracone, a metastyle subequal to the mesial accessory cusp, a stylocone reduced and developed on the distal margin of the paracone, labial and lingual cingula continuous distally, a distinct mesial lingual cingulum, and the posterior root is longer mesiodistally than the anterior one.
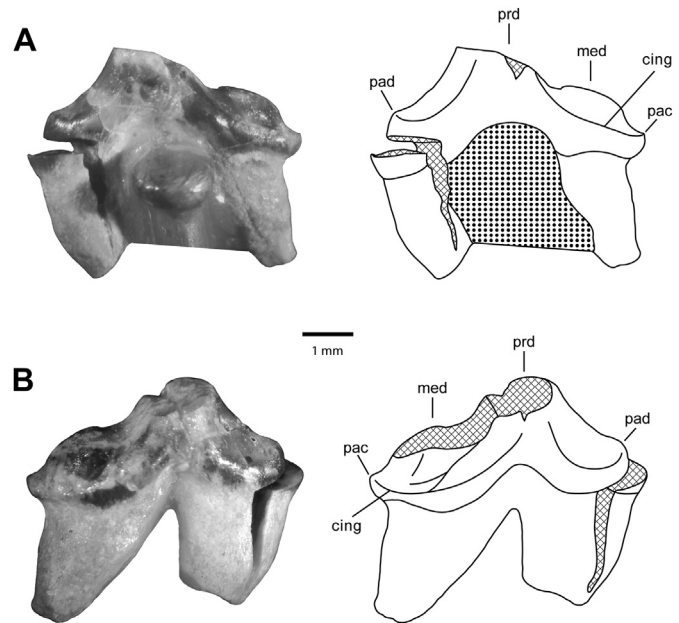
MACNPV-RN240 has a dominant protoconid centered on the crown, a well-developed metaconid, a small paraconid similar in size to the distal accessory cusp, a very conspicuous distal cingulum, a vertically oriented anterior root, and a posteriorly oriented posterior root.
Discussion. MACNPV-RN239 was identified by Bonaparte (1992) as a triconodont lower left molariform and designated it as the holotype of *A. sepulvedai*. Nevertheless, comparison with *C. cilinskii* shows that MACNPV-RN239 is remarkably similar to the P1 of this taxon (see Rougier et al., 2011a: Fig. S4B). Thus, MACNPV-RN239 is re-interpreted here as a P1. MACNPV-RN239 and the P1 of *C. cilinskii* are labiolingually compressed teeth with a mesially placed paracone, a small metastyle similar in size to the mesial accessory cusp, a tiny stylocone developed on the crest that connects the paracone and the metastyle, cingula labial and lingual to the metastyle, and a small anterior root when compared to the posterior one.
MACNPV-RN240, initially interpreted as a last lower right premolariform of *A. sepulvedai* (Bonaparte, 1992), is understood here as a p1 based on comparisons with the p1 of *C. cilinskii* (Fig. 6). MACNPV-RN240 and the p1 of *C. cilinskii* share the labiolingual compression of the crown and the presence of four mesiodistally aligned cusps. In both teeth the metaconid (cusp **cd** in MACNPV-RN240 *sensu* Bonaparte, 1992) is relatively large and is developed on the distal margin of the protoconid. Distally, there is a small accessory cusp, similar in size to the paraconid, and overhanging the posterior root. The two roots are labiolingually compressed. The anterior root is nearly vertical whereas the posterior one is posteriorly oriented. On the other hand, unlike the p1 of *C. cilinskii*, MACNPV-RN240 has well-developed cingula. This trait has also been recognized in more distal postcanines of *C. cilinskii* and is common among other mesungulatids (see Rougier et al., 2009b).
Although, there is not enough evidence to unambiguously consider MACNPV-RN239 and MACNPV-RN240 as co-specific, in our view, these specimens should remain provisionally as the sole representatives of their respective species, following the original
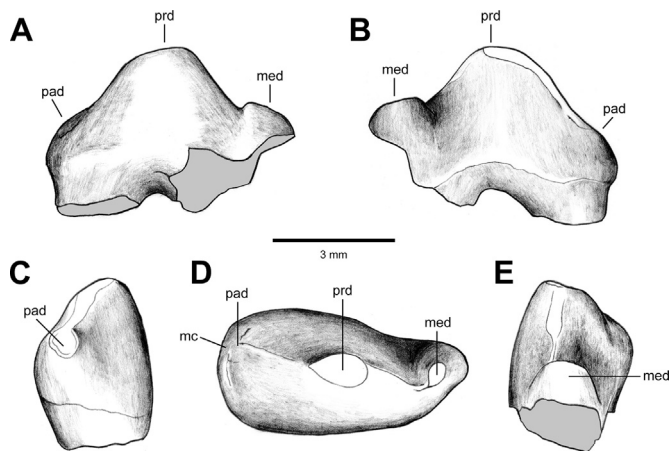
Fig. 6. Drawing of *Coloniatherium cilinskii* left p1 in labial (**A**), lingual (**B**), mesial (**C**), occlusal (**D**), and distal (**E**) views. **Abbreviations**: **mc**, mesial cingulum; **med**, meta-conid; **pad**, paraconid; **prd**, protoconid. Courtesy of A. Martinelli; used with permission of the author.

intention of Bonaparte (1992). However, the type species of the genus *Austrotriconodon* (i.e., *A. mckennai* Bonaparte, 1986a) is thought to belong to a different family than *A. sepulvedai* Bonaparte, 1992 (see above). Thus, the combination *Austrotriconodon sepulvedai* Bonaparte, 1992 is not valid and must be changed. Nevertheless, to avoid the proliferation of new names of poorly known taxa, we prefer to leave MACNPV-RN239 and MACNPV-RN240 in open nomenclature.

The close comparison between MACNPV-RN239 and MACNPV-RN240 to *C. cilinskii* suggests that the former triconodont specimens should be re-interpreted as mesungulatids. However, despite the morphological resemblance of these specimens, *C. cilinskii* is substantially larger than MACNPV-RN239 and MACNPV-RN240. Hence, we believe that MACNPV-RN239 and MACNPV-RN240 cannot be assigned to *C. cilinskii*. Considering the taxa present at the Cerro Cuadrado locality and based on their relative sizes, *Mesungulatum houssayi* is the most likely candidate to be co-specific with MACNPV-RN239 and MACNPV-RN240. If that were the case *Austrotriconodon sepulvedai* Bonaparte, 1992 would be a junior synonym of *Mesungulatum houssayi* Bonaparte and Soria, 1985.

Unnamed rank MAMMALIAFORMES Rowe, 1988
Class Mammalia Linnaeus, 1758
Unnamed rank Trechnotheria McKenna, 1975
Unnamed rank Meridiolestida Rougier, Apesteguía and Gaetano, 2011a
Genus and species indet.

Referred material. MACNPV-RN241, complete right upper pre-molariform (Fig. 7).
Geographic and stratigraphic provenance. Middle section of the Los Alamitos Formation, Cerro Cuadrado locality, southwest slope of the Cerro Cuadrado, Estancia Los Alamitos, Arroyo Verde area, southeast Río Negro province, Argentina; probably of Campanian age (Bonaparte, 1986a, 1987).
Description. This specimen was originally interpreted by Bonaparte (1992) as a triconodont upper molariform. Herein we consider, MACNPV-RN241 to be a meridiolestidan upper premolariform (see below) and describe it as such.
The labiolingually compressed crown is triangular in occlusal aspect, tapering mesially and with a constricted central part defining a mesial and a distal lobe. There are three compressed main cusps (paracone, stylocone, and metastyle) that decrease in
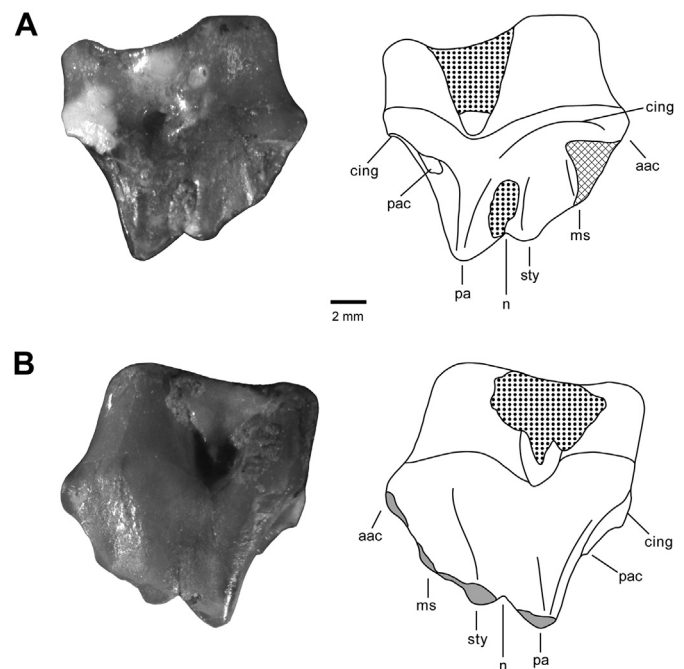
Fig. 7. Photo and line drawing of a meridiolestidan incertae sedis upper right pre-molariform (MACNPV-RN241) in labial (**A**) and lingual (**B**) views. **Abbreviations**: **aac**, anterior accessory cusp; **cing**, cingulum; **ms**, metastyle; **n**, notch; **pa**, paracone; **pac**, posterior accessory cusp; **sty**, stylocone. Dotted areas represent covered surfaces; shaded areas represent worn surfaces; striped areas represent broken surfaces.

height mesially. These cusps are mesiodistally aligned and connected by crests, forming a continuous lamina ("en empalizada" disposition *sensu* Bonaparte, 1992). Bonaparte (1992) identified four main cusps (**A**–**D**) but we were not able to recognize the cusp **C** of Bonaparte (1992).
The paracone is recumbent and occupies almost completely the distal half of the tooth, excluding the stylocone from the distal lobe of the crown. The paracone is set apart from the other main cusps by a valley that is more deeply incised than the one between the stylocone and the metastyle. The distal face of the paracone is a concave surface limited laterally by crests, probably the pre- and post-paracrista, and basally by a cingulum. The distal cingulum bears a labially placed accessory cusp. The stylocone and the metastyle are distally oriented and occupy the mesial lobe of the tooth. There is no valley between these cusps. Poorly defined grooves separate the stylocone and the metastyle labially and lingually; the labial grove is better defined. Mesial to the meta-style (cusp **D** *sensu* Bonaparte, 1992), there is a small accessory cusp that is not supported by the anterior root. The area between the metastyle and the accessory cusp is damaged; thus, their degree of separation cannot be evaluated. Labially, between the paracone and the mesial accessory cusp, there is a well-developed cingulum. Wear is present only on the lingual face of the crown, on the apical region of the main cusps and on the mesial accessory cusp.
The tooth has two roots. The anterior one is larger and supports the mesial lobe of the crown (but not the mesial accessory cusp). It is compressed labiolingually and long mesiodistally. On the other hand, the posterior root is smaller and subcircular in cross-section. It is restricted to the distal lobe of the crown.
Discussion. MACNPV-RN241 is a complete tooth except for the tips of the roots. Although there is some damage on the crown, it does not prevent the recognition of the main features of the tooth. MACNPV-RN241 was interpreted as an upper right molariform and

assigned to the derived triconodont *Austrotriconodon mckennai* by Bonaparte (1992). The co-specific affinities of MACNPV-RN241 with MACNPV-RN21 and MACNPV-RN234 proposed by Bonaparte (1992), are not supported by detailed comparisons of the specimens (see the corresponding descriptions above). Moreover, MACNPV-RN241 is noticeably larger than MACNPV-RN21 and MACNPV-RN234. Hence, we propose that MACNPV-RN241 should be excluded from the hypodigm of *A. mckennai* as this specimen probably represents a different taxon. Nevertheless, to avoid the proliferation of taxa defined on the basis of unique and isolated teeth, and due to the uncertainties regarding the specific affinities of MACNPV-RN241 (see below), we consider the genus and species of this specimen as indeterminate.

MACNPV-RN241 has a peculiar morphology that makes this tooth unique among known Mesozoic mammaliaforms. Kielan-Jaworowska et al. (2004) stated that MACNPV-RN241 has an advanced "triconodont" aspect and could represent the last upper molariform; thus, its morphology and, especially, the cusp proportions would not be representative of the tooth series. Moreover, in agreement with Bonaparte (1992), Kielan-Jaworowska et al. (2004) interpreted the concavity in the purported mesial face of the main cusp as indicative of the presence of an interlocking mechanism, similar to what is observed in some triconodonts. Nevertheless, if MACNPV-RN241 is oriented in life position (i.e., with the gum line horizontal), the mentioned concavity is far away from the mesial margin, unlike what is observed in triconodontids (e.g., Simpson, 1925a,b, 1928; Patterson, 1951; Fox, 1969; Cifelli and Madsen, 1998; Cifelli et al., 1998, 1999; Kusuhashi et al., 2009). Hence, it is questionable if this concavity is part of a dental interlocking mechanism.

Our analysis shows that the arguments employed by previous authors (Bonaparte, 1992; Kielan-Jaworowska et al., 2004) to support the derived triconodont affinities of MACNPV-RN241 (i.e., morphological crown traits and an interlocking mechanism) are not valid. On the other hand, the morphology of MACNPV-RN241 suggests possible affinities with meridiolestidans.

Comparing the isolated teeth from Los Alamitos (Bonaparte and Soria, 1985; Bonaparte, 1986a, 1990, 1994, 2002) with more complete specimens (Páez Arango, 2008; Rougier et al., 2011a), Rougier et al., 2011a considered that the holotype specimens of two of these taxa, *Barberenia araujoae* Bonaparte, 1990 and *Quirogatherium major* Bonaparte, 1990, represented upper premolariforms. Rougier et al. (2011a) and Averianov et al. (2013) stated that the holotypes of *Barberenia* and *Quirogatherium* are similar to the deciduous premolariforms of dryolestoids from the Late Jurassic of Europe and North America (Martin, 1997, 1999, 2002; Kielan-Jaworowska et al., 2004; Bonaparte and Migale, 2010; Rougier et al., 2011a) and to some of the upper premolariforms of Argentinean meridiolestidans (i.e., the P2 of *Peligrotherium tropicalis* Bonaparte et al., 1993 and *Coloniatherium cilinskii* Rougier et al., 2009b and the P3 of *Cronopio dentiacutus*). Like MACNPV-RN241, these teeth have one or more relatively low (mesial) cusps followed by a larger cusp (distally). Additionally, as in MACNPV-RN241, there is a distal cingulum with at least an accessory cusp in *Barberenia araujoae*, *Coloniatherium*, *Peligrotherium*, and *Quirogatherium*. MACNPV-RN241 shares with *Barberenia araujoae*, *Coloniatherium*, *Cronopio*, and *Quirogatherium* the presence of a mesiodistally long root and a smaller subcircular root. As seen in MACNPV-RN241, *Barberenia araujoae*, *Coloniatherium*, and *Quirogatherium* have triangular crowns in occlusal view. In MACNPV-RN241 and *Cronopio* the labiolingual compression of the crowns is more accentuated than in *Barberenia araujoae*, *Coloniatherium*, and *Quirogatherium*, differing greatly from the noncompressed P2 of *Peligrotherium*.

Additionally, Bonaparte described isolated purported upper molariforms as *Alamitherium bishopi* Bonaparte, 2002 and
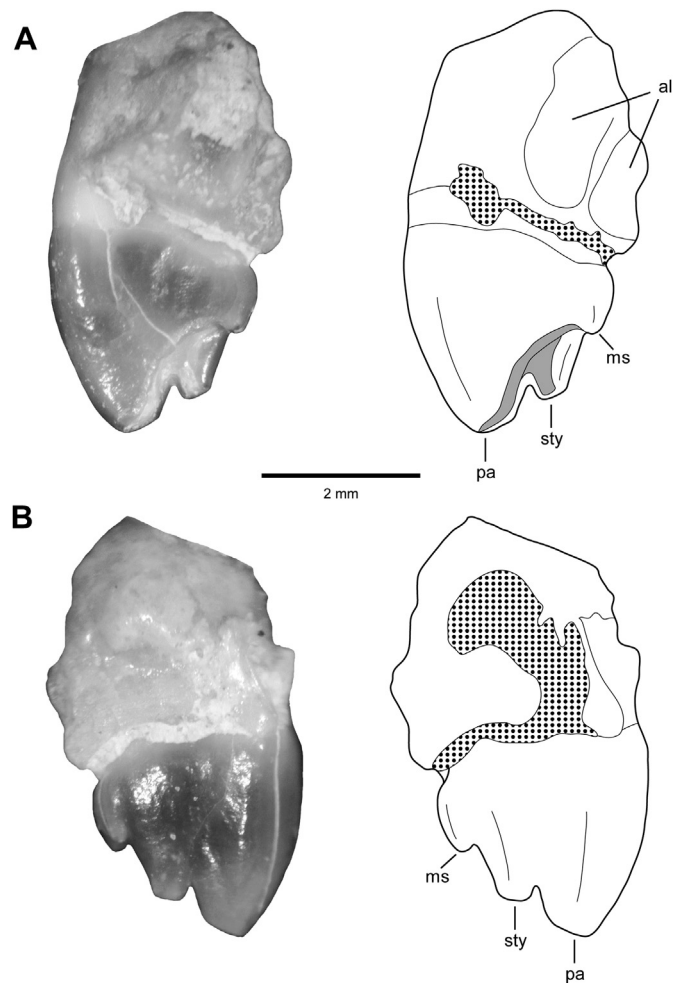
Fig. 8. Photo and line drawing of *Alamitherium bishopi* upper right molariform (MACNPV-RN1035) in distal (**A**) and mesial (**B**) views. **Abbreviations**: **al**, alveolus; **ms**, metastyle; **pa**, paracone; **sty**, stylocone. Dotted areas represent covered surfaces; shaded areas represent worn surfaces.

Rougietherium tricuspes Bonaparte, 2002, also from the Los Alamitos Formation. These teeth are very similar to each other, suggesting that the differences between them might respond to different *loci* of the same taxon; however, following the interpretation of Bonaparte (2002), we prefer to consider them different taxa until unambiguous evidence to decide on this matter is available. *Alamitherium* was identified as a dryolestoid by Bonaparte (2002). The holotype of this taxon (MACNPV-RN1034) was described with the long axis of the tooth oriented labiolingually, although Bonaparte (2002) did not state the basis for this interpretation. An unpublished specimen (MACNPV-RN1035; Fig. 8), identified by Bonaparte as belonging to *Alamitherium*, is a small right maxillary fragment with two empty alveoli and a molariform very similar to MACNPV-RN1034. Thus, the analysis of MACNPV-RN1035 suggests that the orientation for the holotype of *Alamitherium* proposed by Bonaparte (2002) is correct.

Rougietherium is only known by an isolated tooth (MACNPV-RN162). Originally, Bonaparte (1990) described this specimen as an upper molariform of the purported symmetrodont *Bondesius ferox* Bonaparte, 1990. Bonaparte (1990) described MACNPV-RN162 as a labiolingually compressed tooth with four mesiodistally aligned cusps, a well-developed lingual cingulum, and a small labial basin. Later, Bonaparte (2002) re-interpreted MACNPV-RN162 as a mesiodistally compressed upper molariform with labiolingually

aligned cusps that represented a new dryolestoid taxon, *Rougietherium tricuspes*. This last proposal is in accordance with the orientation of the teeth assigned to *Alamitherium* and is consistent with the wear facets recognized in MACNPV-RN162; thus, it is the interpretation followed here.

MACNPV-RN241 is especially similar to MACNPV-RN162. Both teeth have compressed crowns with aligned cusps, a well-developed mesial cingulum parallel to the cusp row, the main cusp set apart from the lower cusps by a more deeply incised valley than the one between the two lower cusps, a small subcircular root under the larger cusp, and a larger longitudinally elongated root under the smaller cusps. Additionally, the concave surface and the small basal cingulum in the mesiolingual face of the largest cusp of *Rougietherium* can also be identified in MACNPV-RN241, although better developed in the latter.

On the other hand, some of the structures recognized by Bonaparte (2002) in *Rougietherium* (i.e., an anterior basin, a metacrista limiting the trigon basin, and a paracrista) are not identified in MACNPV-RN241. Moreover, the main cusp is recurved in opposite directions in *Rougietherium* and MACNPV-RN241. Unlike *Rougietherium*, in MACNPV-RN241 there is no wear on the external region of the longitudinal cingulum (trigon basin *sensu* Bonaparte, 2002) and there is a small cusp in the short cingulum associated with the main cusp (mesial cingulum *sensu* Bonaparte, 2002).

These comparisons hint that MACNPV-RN241 is an upper tooth. Furthermore, despite the similarity with the upper molariforms of *Rougietherium*, the relatively simple crown, the fact that wear is restricted to one side of the tooth, and the presence of a cusp comparable to the distal cusp in *Barberenia araujoae*, *Quirogatherium*, the P2 of *Coloniatherium* and *Peligrotherium*, and the P3 of *Cronopio*, point to a mesiodistal orientation of the long axis of the tooth and suggest that MACNPV-RN241 is a premolariform.

MACNPV-RN241 might be a previously unrecognized taxon closely related to some Argentinean Late Cretaceous mammaliaforms such as *Alamitherium*, *Barberenia araujoae*, *Cronopio*, *Quirogatherium*, *Peligrotherium*, and *Rougietherium*. On the other hand, it cannot be ruled out that MACNPV-RN241 represents an as yet unknown dental position of one of these forms. Hence, we prefer to consider the genus and species of MACNPV-RN241 as an indeterminate meridiolestidan.

5. Concluding remarks

Our analysis leads to the conclusion that the only South American Mesozoic triconodonts (i.e., triconodontids and "amphilestids") are the Early–Middle Jurassic forms from Queso Rallado locality, Cañadon Asfalto Formation: *Argentoconodon fariasorum* and *Condorodon spanios*.

The Late Cretaceous specimens assigned to the purported triconodont genus *Austrotriconodon* are re-interpreted as meridiolestidans, in agreement with some previous hypotheses (Rougier et al., 2007a, 2011a). MACNPV-RN239 and MACNPV-RN240, identified as *Austrotriconodon mckennai* molariforms, are thought to be lower molariforms of a small meridiolestidan similar to *Cronopio dentiacutus*.

MACNPV-RN241, originally the only upper molariform of *Austrotriconodon mckennai*, is here understood as an upper premolariform and might represent a still unnamed meridiolestidan phylogenetically close to *Alamitherium*, *Barberenia araujoae*, *Cronopio*, *Quirogatherium*, *Peligrotherium* and *Rougietherium* or a tooth of an indeterminate tooth locus of any of these taxa.

In our view, *Austrotriconodon sepulvedai* is not a valid binomen and if retained as a valid taxon, the generic name should be replaced. A new combination is not proposed here in order to avoid the proliferation of names referring to poorly known taxa which ultimately may be a junior synonym of other taxa from the same locality. This species is thought to be represented by a P1 and a p1 very similar to the P/p1 of *Coloniatherium cilinskii*. We propose that this former triconodont may be understood as a relatively gracile mesungulatid meridiolestidan.

References

Ameghino, F., 1891. Nuevos restos de mamíferos fósiles descubiertos por Carlos Ameghino en el Eoceno inferior de la Patagonia austral. Especies nuevas adiciones y correcciones. Revista Argentina de Historia Natural 1, 289–328.

Averianov, A.O., Martin, T., Lopatin, A.V., 2013. A new phylogeny for basal Trechnotheria and Cladotheria and affinities of South American endemic Late Cretaceous mammals. Naturwissenschaften 100, 311–326.

Averianov, A.O., Skutschas, P.P., Lopatin, A.V., Leshchinskiy, S.V., Rezvyi, A.S., Fayngerts, A.V., 2005. Early Cretaceous mammals from Bol'shoi Kemchug 3 locality in West Siberia, Russia. Russian Journal of Theriology 4, 1–12.

Bertini, R.J., Marshall, L.G., Gayet, M., Brito, P., 1993. Vertebrate faunas from the Adamantina and Marilia formations (upper Bauru Group, Late Cretaceous, Brazil) in their stratigraphic and paleobiogeographic context. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 188, 71–101.

Bonaparte, J.F., 1986a. Sobre *Mesungulatum houssayi* y nuevos mamíferos cretácicos de Patagonia. Actas IV Congreso Argentino de Paleontología y Bioestratigrafía, Argentina, pp. 48–61.

Bonaparte, J.F., 1986b. A new and unusual Late Cretaceous mammal from Patagonia. Journal of Vertebrate Paleontology 6, 264–270.

Bonaparte, J.F., 1986c. History of the terrestrial Cretaceous vertebrates of Gondwana. Actas IV Congreso Argentino de Paleontología y Bioestratigrafía 2, 63–95.

Bonaparte, J.F., 1987. The Late Cretaceous fauna of Los Alamitos, Patagonia, Argentina. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" 3, 103–178.

Bonaparte, J.F., 1990. New Late Cretaceous mammals from the Los Alamitos Formation, northern Patagonia. National Geographic Research 6, 63–93.

Bonaparte, J.F., 1992. Una nueva especie de Triconodonta (Mammalia), de la Formación Los Alamitos, Provincia de Río Negro y comentarios sobre su fauna de mamíferos. Ameghiniana 29, 99–110.

Bonaparte, J.F., 1994. Approach to the significance of the Late Cretaceous mammals of South America. Berliner geowissenschafliche Abhandlungen E 13, 31–44.

Bonaparte, J.F., 2002. New Dryolestida (Theria) from the Late Cretaceous of Los Alamitos, Argentina, and paleogeographical comments. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 224, 339–371.

Bonaparte, J.F., Kielan-Jaworowska, Z., 1987. Late cretaceous dinosaur and mammal faunas of Laurasia and Gondwana. In: Currie, P.M., Koster, E.H. (Eds.), Fourth Symposium on Mesozoic Terrestrial Ecosystems short papers, pp. 24–29.

Bonaparte, J.F., Migale, L.A., 2010. Protomamíferos y mamíferos Mesozoicos de América del Sur. Museo de Ciencias Naturales Carlos Ameghino, Mercedes, Buenos Aires.

Bonaparte, J.F., Rougier, G.W., 1987. Mamíferos del Cretácico Inferior de Patagonia. IV Congreso Latinoamericano de Paleontología 1, 343–359.

Bonaparte, J.F., Soria, M.F., 1985. Nota sobre el primer mamífero del Cretácico argentino, Campaniano–Maastrichtiano (Condylarthra). Ameghiniana 21, 177–183.

Bonaparte, J.F., Van Valen, L.M., Kramarz, A., 1993. La fauna local de Punta Peligro, Paleoceno Inferior, de la Provincia del Chubut, Patagonia, Argentina. Evolutionary Monographs 14, 1–61.

Butler, P.M., Sigogneau-Russell, D., Ensom, P.C., 2012. Possible persistence of the morganucodontans in the Lower Cretaceous of Purbeck Limestone Group (Dorset, England). Cretaceous Research 33, 135–145.

Casamiquela, R.M., 1964. Sobre la presencia de un mamífero en el primer elenco (icnológico) de vertebrados del Jurásico de la Patagonia. Physis 22, 225–233.

Chimento, N.R., Agnolin, F.L., Novas, F.E., 2012. The Patagonian fossil mammal *Necrolestes*: a Neogene survivor of Dryolestoidea. Revista del Museo Argentino de Ciencias Naturales 14, 261–306.

Cifelli, R.L., Lipka, T.R., Schaff, C.R., Rowe, T.B., 1999. First Early Cretaceous mammal from the eastern seaboard of the United States. Journal of Vertebrate Paleontology 19, 199–203.

Cifelli, R.L., Madsen, S.K., 1998. Triconodont mammals from the medial Cretaceous of Utah. Journal of Vertebrate Paleontology 18, 403–411.

Cifelli, R.L., Wible, J.R., Jenkins Jr., F.A., 1998. Triconodont mammals from the Cloverly Formation (Lower Cretaceous), Montana and Wyoming. Journal of Vertebrate Paleontology 18, 237–241.

Clemens, W.A., 1980. Rhaeto–Liassic mammals from Switzerland and West Germany. Zitteliana, Abhandlungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie 5, 51–92.

Clemens, W.A., 2011. New morganucodontans from an Early Jurassic fissure filling in Wales (United Kingdom). Palaeontology 54, 1139–1156.

Crochet, J.-Y., 1980. Les Marsupiaux du Tertiaire d'Europe. Editions de la Fondation Singer-Polignac, Paris.

Crompton, A.W., 1964. A preliminary description of a new mammal from the Upper Triassic of South Africa. Proceedings of the Zoological Society of London 142, 441–452.

Crompton, A.W., Jenkins Jr., F.A., 1968. Molar occlusion in Late Triassic mammals. Biological Reviews 43, 427–458.

Cúneo, R., Ramezani, J., Scasso, R., Pol, D., Escapa, I., Zavattieri, A., Bowring, S.A., 2013. High-precision U-Pb geochronology and a new chronostratigraphy for the Cañadón Asfalto Basin, Chubut, central Patagonia: implications for terrestrial faunal and floral evolution in Jurassic. Gondwana Research 24, 1267–1275.

Datta, P.M., Das, D.P., 1996. Discovery of the oldest fossil mammal from India. India Minerals 50, 217–222.

Datta, P.M., Das, D.P., 2001. *Indozostrodon simpsoni*, gen. et sp. nov., an Early Jurassic megazostrodontid mammal from India. Journal of Vertebrate Paleontology 21, 528–534.

Forasiepi, A.M., Coria, R.A., Hurum, J., Currie, P.J., 2012. First dryolestoid (Mammalia, Dryolestoidea, Meridiolestida) from the Coniacian of Patagonia and new evidence on their early radiation in South America. Ameghiniana 49, 497–504.

Fox, R.C., 1969. Studies of Late Cretaceous vertebrates. III. A triconodont mammal from Alberta. Canadian Journal of Zoology 47, 1253–1256.

Freeman, E.F., 1979. A Middle Jurassic mammal bed from Oxfordshire. Palaeontology 22, 135–166.

Gaetano, L.C., 2013. *Argentoconodon fariasorum*, un mamaliaforme del Jurásico de Patagonia, Argentina: descripción, relaciones filogenéticas e implicancias evolutivas y paleobiogeográficas. Doctoral Tesis. Universidad de Buenos Aires, Buenos Aires.

Gaetano, L.C., Rougier, G.W., 2010. New specimens and phylogenetic relationships of the South American Jurassic triconodont *Argentoconodon fariasorum*. Journal of Vertebrate Paleontology 28, 93A.

Gaetano, L.C., Rougier, G.W., 2011. New materials of *Argentoconodon fariasorum* (Mammaliaformes, Triconodontidae) from the Jurassic of Argentina and its bearing on triconodont phylogeny. Journal of Vertebrate Paleontology 31, 829–843.

Gaetano, L.C., Rougier, G.W., 2012. First amphilestid from South America: A molariform from the Jurassic Cañadón Asfalto Formation, Patagonia, Argentina. Journal of Mammalian Evolution 19, 235–248.

Gao, C.-L., Wilson, G.P., Luo, Z.-X., Murat Maga, A., Meng, Q., Wang, X., 2010. A new mammal skull from the Lower Cretaceous of China with implications for the evolution of obtuse–angled molars and 'amphilestid' eutriconodonts. Proceedings of the Royal Society of London B 276, 237–246.

Garrido, A.C., 2010. Estratigrafía del Grupo Neuquén, Cretácico Superior de la Cuenca Neuquina (República Argentina): Nueva propuesta de ordenamiento litoestratigráfico. Revista del Museo Argentino de Ciencias Naturales, nueva serie 12, 121–177.

Garrido, A.C., 2011. Grupo Neuquén (Cenomaniano–Campaniano). 18° Congreso Geológico Argentino (Neuquén), Relatorio, p. 231–244.

Gayet, M., Marshall, L.G., Sempere, T., 1991. The Mesozoic and Paleocene vertebrates of Bolivia and their stratigraphic context: a review. In: Suárez Soruco, R. (Ed.), Fósiles y Facies de Bolivia, Vertebrados, Volumen I. Revista Técnica de Yacimientos Petrolíferos Fiscales Bolivianos, Santa Cruz, pp. 393–434.

Gayet, M., Marshall, L.G., Sempere, T., Meunier, J., Cappetta, H., Rage, J.-C., 2001. Middle Maastrichtian vertebrates (fishes, amphibians, dinosaurs and other reptiles, mammals) from Pajcha Pata (Bolivia). Biostratigraphic, palaeoecologic and palaeobiogeographic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 169, 39–68.

Goin, F.J., Carlini, A.A., Pascual, R., 1986. Un probable marsupial del Cretácico tardío del norte de Patagonia, Argentina. IV Congreso de Paleontología y Bioestratigrafía 2, 43–47.

Grambast, L., Martinez, M., Mattauer, M., Thaler, L., 1967. *Peratherium altiplanense*, nov. gen., nov. sp., premier Mammifère mésozoïque d'Amérique du Sud. Comptes Rendus del'Académie des Sciences, Paris, sér. D 264, 707–710.

Hahn, G., 1993. The systematic arrangement of the Paulchoffatiidae (Multituberculata) revisited. Geologica et Paleontologica 27, 201–214.

Heinrich, W.-D., 1998. Late Jurassic Mammals from Tendaguru, Tanzania, East Africa. Journal of Mammalian Evolution 5, 269–290.

Hu, Y., Meng, J., Wang, Y.-Q., Li, C., 2005. Large Mesozoic mammals fed on young dinosaurs. Nature 433, 149–152.

Huene, F. von, 1933. Zur Kenntnis des württembergischen Rhätbonebeds mit Zahnfunden neuer Säuger und Säugerähnlicher Reptilien. Jahreshefte der Vereins Vaterländische Naturkunde Württemburg 89, 65–128.

International Commission on Zoological Nomenclature, 1999. International Code of Zoological Nomenclature. International Trust for Zoological Nomenclature, ISBN 0-85301-006-4.

Jenkins Jr., F.A., Crompton, A.W., Downs, W.R., 1983. Mesozoic mammals from Arizona: new evidence on mammalian evolution. Science 222, 1233–1235.

Ji, Q., Luo, Z.-X., Ji, S.-A., 1999. A Chinese triconodont mammal and mosaic evolution of mammalian skeleton. Nature 398, 326–330.

Kielan-Jaworowska, Z., Cifelli, R.L., Luo, Z.-X., 2004. Mammals from the Age of Dinosaurs. Origins, Evolution, and Structure. Columbia University Press, New York.

Kretzoi, M., Kretzoi, M., 2000. Fossilium Catalogus 1: Animalia. Pars 137—Index Generum et Subgenerum Mammalium. Backhuys Publishers, Leiden.

Kühne, W.G., 1949. On a triconodont tooth of a new pattern from a fissure–filling in South Glamorgan. Proceedings of the Zoological Society of London 119, 345–350.

Kusuhashi, N., Hu, Y., Wang, Y., Hirasawa, S., Matsuoka, H., 2009. New triconodontids (Mammalia) from the Lower Cretaceous Shahai and Fuxin formations, northeastern China. Geobios 42, 765–781.

Leanza, H.A., Apesteguía, S., Novas, F.E., Fuente de la, M.S., 2004. Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. Cretaceous Research 25, 61–87.

Leanza, H.A., Hugo, C.A., 1995. Revisión estratigráfica del Cretácico inferior continental en el ámbito sudoriental de la Cuenca Neuquina. Revista de la Asociación Geológica Argentina 50, 30–32.

Leanza, H.A., Hugo, C.A., 1997. Hoja Geológica 3969-IIIe Picún Leufú, provincias del Neuquén y Río Negro. Instituto de Geología y Recursos Naturales, SEGEMAR, Boletín 218, 1–135.

Linnaeus, C., 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. In: Regnum animale. Editio decima, reformata, vol. 1. Laurentii Salvii, Stockholm.

Lopatin, A.V., Maschenko, E.N., Averianov, A.O., 2010. A new genus of triconodont mammals from the Early Cretaceous of Western Siberia. Doklady Biological Sciences 433, 282–285.

Lucas, S.G., Hunt, A.P., 1990. The oldest mammal. New Mexico Journal of Science 30, 41–49.

Luo, Z.-X., Chen, P., Li, G., Chen, M., 2007. A new eutriconodont mammal and evolutionary development in early mammals. Nature 446, 288–293.

Luo, Z.-X., Kielan-Jaworowska, Z., Cifelli, R.L., 2002. In quest for a phylogeny of Mesozoic mammals. Acta Palaeontologica Polonica 47, 1–78.

Marshall, L.G., Muizon, C. de, 1988. The dawn of the age of mammals in South America. National Geographic Research 4, 23–55.

Marshall, L.G., Muizon, C, de, Sigé, B., 1983. *Peratherium altiplanense*, un notoungulé du Crétacé supérieur du Pérou. Palaeovertebrata, Montpellier 13, 145–155.

Marshall, L.G., Sigogneau-Russell, D., 1995. Part III: Postcranial skeleton. In: Muizon, C. de (Ed.), *Pucadelphys andinus* (Marsupialia, Mammalia) from the Early Paleocene of Bolivia. Mémoires du Muséum national d'Histoire naturelle 165, Paris, pp. 91–164.

Martin, T., 1997. Tooth replacement in Late Jurassic Dryolestidae (Eupantotheria, Mammalia). Journal of Mammalian Evolution 4, 1–18.

Martin, T., 1999. Dryolestidae (Dryolestoidea, Mammalia) aus dem Oberen Jura von Portugal. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 550, 1–119.

Martin, T., 2002. New stem-line representatives of Zatheria (Mammalia) from the Late Jurassic of Portugal. Journal of Vertebrate Paleontology 22, 332–348.

Martinelli, A.G., Forasiepi, A., 2004. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Río Negro Province, Argentina, with a description of a new sauropod dinosaur (Titanosauridae). Revista del Museo Argentino de Ciencias Naturales, Nueva serie 6, 257–305.

McKenna, M.C., 1975. Toward a phylogenetic classification of the Mammalia. In: Luckett, W.P., Szalay, F.S. (Eds.), Phylogeny of the Primates. Plenum Press, New York, pp. 21–46.

Meng, J., Hu, Y.-M., Wang, Y., Wang, X., Li, C., 2006. A Mesozoic gliding mammal from northeastern China. Nature 444, 889–893.

Meng, J., Wang, Y., Li, C., 2011. Transitional mammalian middle ear from a new Cretaceous Jehol eutriconodont. Nature 472, 181–185.

Montellano, M., Hopson, J.A., Clark, J.M., 2008. Late Early Jurassic mammaliaforms from Huizachal Canyon, Tamaulipas, Mexico. Journal of Vertebrate Paleontology 28, 1130–1143.

Muizon, de, C., 1994. A new carnivorous marsupial from the Palaeocene of Bolivia and the problem of marsupial monophyly. Nature 370, 208–211.

Muizon, de, C., 1998. *Mayulestes ferox*, a borhyaenoid (Metatheria, Mammalia) from the early Palaeocene of Bolivia. Phylogenetic and palaeobiologic implications. Geodiversitas 20, 19–142.

Muizon, de, C., Cifelli, R.L., Céspedes, R., 1997. The origin of dog-like marsupials and the early evolution of Gondwanian marsupials. Nature 389, 486–489.

Osborn, H.F., 1888. On the structure and classification of the Mesozoic Mammalia. Journal of the Academy of Natural Sciences, Philadelphia 9, 186–265.

Owen, R., 1838. On the jaws of the *Thylacotherium prevostii* (Valenciennes) from Stonesfield. Proceedings of the Geological Society of London 3, 5–9.

Owen, R., 1859. Palaeontology. In: Encyclopaedia Britannica, eighth edition, Volume 17. Adam and Black, Edinburgh, pp. 91–176.

Páez Arango, N., 2008. Dental and craniomandibular anatomy of *Peligrotherium tropicalis*: the evolutionary radiation of South American dryolestoid mammals. Master Thesis. University of Louisville.

Parrington, F.R., 1941. On two mammalian teeth from the lower Rhaetic of Somerset. Annals and Magazine of Natural History, Series 11 8, 140–144.

Pascual, R., Goin, F.J., Krause, D.W., Ortiz-Jaureguizar, E., Carlini, A.A., 1999. The first gnathic remains of *Sudamerica*: implications for gondwanathere relationships. Journal of Vertebrate Paleontology 19, 373–382.

Patterson, B., 1951. Early Cretaceous mammals from northern Texas. American Journal of Science 249, 31–46.

Patterson, B., Olson, E.C., 1961. A triconodontid mammal from the Triassic of Yunan. In: Vandebroek, G. (Ed.), International Colloquium on the Evolution of Lower and Non-Specialized Mammals. Koninklijke Vlaamse Academie voor Wetenschappen, Litteren en Schone Kunsten van Belgie, Brussels, pp. 129–191.

Prasad, G.V.R., Manhas, B.K., 1997. A new symmetrodont mammal from the Lower Jurassic Kota Formation, Pranhita–Godavari Valley, India. Géobios 30, 563–572.

Rauhut, O.W.M., Martin, T., Ortiz-Jaureguizar, E., Puerta, P., 2002. A Jurassic mammal from South America. Nature 416, 165–168.

Rigney, H.W., 1963. A specimen of *Morganucodon* from Yunnan. Nature 197, 1122–1123.

Rougier, G.W., 1993. *Vincelestes neuquenianus* Bonaparte (Mammalia, Theria) un primitivo mamífero del Cretácico Inferior de la Cuenca Neuquina. Doctoral Tesis. Universidad de Buenos Aires, Buenos Aires.

Rougier, G.W., Apesteguía, S., Gaetano, L.C., 2011a. Highly specialized mammalian skulls from the Late Cretaceous of South America. Nature 479, 98–102.

Rougier, G.W., Chornogubsky, L., Casadio, S., Páez Arango, N., Giallombardo, A., 2009a. Mammals from the Allen Formation, Late Cretaceous, Argentina. Cretaceous Research 30, 223–238.

Rougier, G.W., Forasiepi, A.M., Hill, R.V., Novacek, M., 2009b. New mammalian remains from the Late Cretaceous La Colonia Formation, Patagonia, Argentina. Acta Paleontologica Polonica 54, 195–212.

Rougier, G.W., Gaetano, L.C., Drury, B., Páez Arango, N., Colella, R., 2011b. A review of the Mesozoic mammalian record of South America. In: Calvo, J., Porfiri, J., Gonzales Riga, B., Dos Santos, D. (Eds.), Paleontología y dinosaurios desde América Latina, 1° edición. Editorial de la Universidad Nacional de Cuyo – EDIUNC, Mendoza, Argentina, pp. 195–214.

Rougier, G.W., Garrido, A., Gaetano, L.C., Puerta, P., Corbitt, C., Novacek, M.J., 2007a. First Jurassic triconodont from South America. American Museum Novitates 3580, 1–17.

Rougier, G.W., Isaji, S., Manabe, M., 2007b. An Early Cretaceous mammal from the Kuwajima Formation (Tetori Group), Japan, and a reassessment of triconodont phylogeny. Annals of the Carnegie Museum 70, 73–115.

Rougier, G.W., Martinelli, A.G., Forasiepi, A.M., Novacek, M.J., 2007c. New Jurassic mammals from Patagonia, Argentina: a reappraisal of australosphenidan morphology and interrelationships. American Museum Novitates 3566, 1–54.

Rougier, G.W., Novacek, M.J., McKenna, M.C., Wible, J.R., 2001. Gobiconodonts from the Early Cretaceous of Oshih (Ashile), Mongolia. American Museum Novitates 3348, 1–30.

Rougier, G.W., Wible, J.R., Beck, R.M.D., Apesteguía, S., 2012. The Miocene mammal *Necrolestes* demonstrates the survival of a Mesozoic nontherian lineage into the late Cenozoic of South America. Proceedings of the National Academy of Sciences 109, 20053–20058.

Rowe, T.B., 1988. Definition, diagnosis, and origin of Mammalia. Journal of Vertebrate Paleontology 8, 241–264.

Salgado, L., Souza Carvalho, de, I., Garrido, A.C., 2006. *Zapalasaurus bonapartei*, un nuevo dinosaurio saurópodo de la Formación La Amarga (Cretácico inferior), noroeste de Patagonia, Provincia de Neuquén, Argentina. Géobios 39, 695–707.

Sigé, B., 1971. Les Didelphoidea de Laguna Umayo (Formation Vilquechico, Crétacé Supérieur, Pérou), et le peuplement marsupial d'Amérique du Sud. Comptes Rendus de l'Académie des Sciences, Paris 273, 2479–2481.

Sigé, B., 1972. La faunule des mammifères du Crétacé supérieur de Laguna Umayo (Andes péruviennes). Bulletin du Muséum national d'Histoire naturelle, sér. 3, Sciences de la Terre 99, 375–405.

Sigogneau-Russell, D., 1983. A new therian mammal from the Rhaetic locality of Saint–Nicolas–de–Port (France). Zoological Journal of the Linnean Society 78, 175–186.

Sigogneau-Russell, D., 1995. Two possibly aquatic triconodont mammals from the Early Cretaceous of Morocco. Acta Palaeontologica Polonica 40, 149–162.

Sigogneau-Russell, D., 2003. Diversity of triconodont mammals from the Early Cretaceous of North Africa – Affinities of the amphilestids. Palaeovertebrata 32, 27–55.

Simpson, G.G., 1925a. Mesozoic Mammalia. I. American triconodonts, part 1. American Journal of Science 10, 145–165.

Simpson, G.G., 1925b. Mesozoic Mammalia. I. American triconodonts: part 2. American Journal of Science 10, 334–358.

Simpson, G.G., 1928. A Catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum. Trustees of the British Museum, London.

Van Valen, L., 1978. The beginning of the age of mammals. Evolutionary Theory 4, 45–80.

Van Valen, L., 1988. Paleocene dinosaurs or Cretaceous ungulates in South America? Evolutionary Monographs 10, 1–79.

Wilf, P., Cúneo, N.R., Escapa, I.H., Pol, D., Woodburne, M.O., 2013. Splendid and Seldom Isolated: The Paleobiogeography of Patagonia. Annual Review of Earth and Planetary Sciences 41, 561–603.

Yadagiri, P., 1984. New symmetrodonts from the Kota Formation. Journal of the Geological Society of India 25, 512–521.