



A revision of the putative Late Cretaceous triconodonts from South America



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ABSTRACT

Austrotroconodon mckennai and *Austrotroconodon sepulvedai*, from the Campanian Los Alamos Formation, Patagonia, Argentina were originally described as triconodont mammals and the sole members of the family Austrotroconodontidae. 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 *Austrotroconodon* with other Late Cretaceous taxa and conclude that *Austrotroconodon* 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 Alamos 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 Alamos 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 (*Austrotroconodon mckennai* Bonaparte, 1986a and *Austrotroconodon sepulvedai* Bonaparte, 1992) and included them in the monotypic family Austrotroconodontidae (Bonaparte, 1992).

Although other Jurassic and Cretaceous mammaliaforms were later found in South America (see section 2), *Austrotroconodon* long remained the only Mesozoic “triconodont” known from this subcontinent. It was not until the description of *Argentoconodon fariatorum* 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 fariatorum* and *Condorodon spanios*, the identification of the “triconodonts” from the Los Alamos 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 Alamos 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*

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

Rougier et al. (2011a) questioned the “triconodont” affinities suggested for *Austroriconodon* and interpreted the specimens as meridiolestid dryolestoids. Rougier et al. based their hypothesis on the similarities between the lower teeth of *Austroriconodon* and some premolariforms assigned to *Coloniatherium cilinskii* and *Cronopio dentiactutus*. 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. Meridiolestids 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 meridiolestids. Hence, we will simply refer to meridiolestids 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 *Austroriconodon* 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 meridiolestids (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

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