

## Mammals from the Allen Formation, Late Cretaceous, Argentina

Guillermo W. Rougier<sup>a,\*</sup>, Laura Chornogubsky<sup>b</sup>, Silvio Casadio<sup>c</sup>, Natalia Paéz Arango<sup>a</sup>,  
Andres Giallombardo<sup>d,e</sup>

<sup>a</sup> Department of Anatomical Sciences and Neurobiology, University of Louisville, Louisville, KY 40292, USA

<sup>b</sup> CONICET, Department of Vertebrate Paleontology, Museo Argentino de Ciencias Naturales "B. Rivadavia", Av. Ángel Gallardo 470, C1405DRJ Buenos Aires, Argentina

<sup>c</sup> CONICET, Universidad Nacional de La Pampa, Uruguay 151, 6300 Santa Rosa, La Pampa, Argentina

<sup>d</sup> Division of Paleontology, American Museum of Natural History, New York, NY 10024, USA

<sup>e</sup> Department of Earth and Environmental Sciences, Columbia University, Lamont-Doherty Earth Observatory, LDEO, P.O. Box 1000, 61 Route 9W, Palisades, New York, NY 10964-1000, USA

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### ABSTRACT

A mammalian fauna from the Late Cretaceous locality of "Cerro Tortuga," Allen Formation, Río Negro Province, Argentina, is described here based on a sample, represented by 7 isolated teeth which shows similarities with those reported from the Late Cretaceous Los Alamitos Formation. These two mammalian faunas largely agree on their overall composition at the supraspecific level but new species are recognized for some of the specimens described. Small-sized dryolestoids, mesungulatids and ferugliotheriids are present in Cerro Tortuga. A new species of *Mesungulatum*, [Bonaparte, J.F., Soria, M.F., 1985. Nota sobre el primer mamífero del Cretácico Argentino, Campaniano-Maastrichtiano, (Condylarthra). *Ameghiniana* 21, 177–183] leads to a reassessment of mesungulid diversity in the Late Cretaceous South American mammalian faunas and some provisional considerations on the relative age of the mammal-bearing units. The South American Late Cretaceous radiation of dryolestoids has its origins in the early Late Cretaceous, at the latest, and extends into the Paleocene when their last remnants are obliterated possibly in relation to the incoming Laurasian tribosphenic mammals. The Late Cretaceous non-tribosphenic mammals have no clear link with the Jurassic and Early Cretaceous South American mammals, emphasizing the distinctiveness and episodic nature of the Mesozoic South American mammalian assemblages. The scant number of fossils and geochronologically discontinuous record may artificially accentuate the distinctiveness of the as yet poorly known pre-Late Cretaceous South American mammals, in particular if an epic sea separated South America into northern and southern realms.

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### 1. Introduction

Because of geological, historical, and social factors, not all areas of the globe are equally represented in the fossil record. Northern continents, with a long tradition of fossil research, account for 68% of the total number of terrestrial fossil genera (computed from McKenna and Bell, 1997), while in the present fauna they represent only 41% (Nowak, 1991). The case is even more dramatic when the Mesozoic record is examined; 84% of the Mesozoic fossil genera have been collected from the northern continents (from Kielan-Jaworowska et al., 2004 and further additions). Mesozoic Mammals have been known in the Northern Hemisphere since the 1800s (Owen, 1871; Marsh, 1879, 1889a, b,

1892; Osborn, 1887, 1888, 1893 1907; Goodrich, 1894), while our knowledge of them in the Southern Hemisphere is still in its infancy. In South America, the first skeletal record of a Mesozoic mammal is slightly over twenty years old (Bonaparte and Soria, 1985). Our understanding of early mammalian faunas in Gondwana in general, and of South America in particular, has been dramatically improved by a flurry of activity in the mid 1980s and 90s (Bonaparte, 1986a,b,c, 1990, 1992, 1994; Bonaparte and Rougier, 1987; Bonaparte and Pascual, 1987; Bonaparte, 1987; Krause and Bonaparte, 1990; Krause et al., 1992). The pioneering work of Dr. José Bonaparte opened new avenues to colleagues and students who, at least partially based on the information Bonaparte produced from the late Cretaceous locality of Los Alamitos in central Río Negro Province (Patagonia, Argentina), expanded the search to other Mesozoic and Paleocene rocks in Patagonia (Pascual et al., 1992, 1993, 2000a,b, 2002; Pascual and Goin, 2001; Gelfo and Pascual, 2001; Rougier et al., 2000, 2001, 2007a,b; Rauhut et al., 2002; Martin and Rauhut, 2005; Gurovich, 2006; Pascual and Ortíz-Jaureguizar, 2007).

\* Corresponding author.

E-mail addresses: [grougier@louisville.edu](mailto:grougier@louisville.edu) (G.W. Rougier), [lchorno@macn.gov.ar](mailto:lchorno@macn.gov.ar) (L. Chornogubsky), [scasadio@cpenet.com.ar](mailto:scasadio@cpenet.com.ar) (S. Casadio), [giallomb@amnh.org](mailto:giallomb@amnh.org) (A. Giallombardo).

Los Alamos has had an unparalleled impact on our appreciation of Cretaceous South American faunas. It was not until Pascual and collaborators explored la Colonia Formation in Chubut Province (Pascual et al., 2000b) that a second Late Cretaceous locality with mammalian dental remains was reported. In here we describe a few mammalian teeth from a third Late Cretaceous Patagonian locality. The new locality, Cerro Tortuga (Allen Formation), is roughly contemporaneous with Los Alamos and La Colonia. However tantalizing it would be to have a wider temporal representation of South American Mammals, we are fortunate to have three roughly penecontemporaneous localities allowing us to start evaluating mammalian diversity and distribution during the latest Cretaceous.

All three Late Cretaceous localities mentioned above have to be considered within a wider paleogeographic framework, in which the dominant paleobiogeographic element was the Late Cretaceous-early Paleocene Atlantic transgression that reduced Patagonia to an archipelago (Casadío, 1998; Wilson and Arens, 2001; Griffin et al., 2005; Keller et al., 2007). Malumián and Caramés (1995) estimated that a minimum area of 507,000 km<sup>2</sup> of present day Patagonia was at the time covered by the Atlantic Sea; this large flooded surface is known as Rocanense Sea. Differences in faunal composition among these mammalian localities might be due to “small” temporal discrepancies, geographic distribution and incipient insular events on this archipelago-like geography. The extra-Patagonian record of Mesozoic mammals in Brazil (Bertini et al., 1993) and Bolivia (Gayet et al., 2001) is, so far, very fragmentary and comparisons with the Patagonian forms are therefore limited.

The composition of the Cretaceous faunas from South America seems to be characterized by a dominant presence of dryolestoid lineages, which diversify remarkably in South America (Bonaparte, 1986a,c, 1994, 2002), and the bizarre ferugliotherids and sudamericids (Bonaparte, 1986a,b, 1990; Bonaparte et al., 1989; Sigogneau-Russell, et al., 1991; Krause et al., 1992; Kielan-Jaworowska and Bonaparte, 1996; Kielan-Jaworowska et al., 2007). The conspicuous absence of therian mammals (phylogenetically defined as the common ancestor of marsupials and placentals plus all their descendants [Rougier et al., 1998]) in Southern South America seems to be one of the most striking differences with the fauna from the Northern Hemisphere (Bonaparte, 1986a,b,c; Bonaparte and Kielan-Jaworowska, 1987; Pascual and Ortíz-Jaureguizar, 1990, 2007) although in the Late Cretaceous of Peru both, tribosphenic and non-tribosphenic forms are probably present (Gayet et al., 2001). Dryolestoids are well known and relatively abundant in the Jurassic of Laurasia (Prothero, 1981; Martin, 1999; Kielan-Jaworowska et al., 2004), but their Cretaceous record is more limited and possibly restricted to the Early Cretaceous (Owen, 1871; Henkel and Krebs, 1969; Canudo and Cuenca-Bescós, 1996).

The pre-Late Cretaceous mammalian record in South America is still very poor, restricted to only two localities: the Middle Jurassic Queso Rallado (Cañadón Asfalto) (Rauhut et al., 2002; Martin and Rauhut, 2005; Forasiepi et al., 2004a,b; Rougier et al., 2007a,b), and the Lower Cretaceous La Amarga (Bonaparte, 1986a; Bonaparte and Rougier, 1987; Rougier et al., 1992; Rougier 1993). The known South American Jurassic mammals represent so far either australosphenidan taxa (Rauhut et al., 2002; Martin and Rauhut, 2005; Rougier et al., 2007a) or a peculiar lineage of triconodonts (Rougier et al., 2007b) with similarities to the recently described *Volatcotherium* (Meng et al., 2007a,b). The australosphenidans have only distant affinities with regard to any of the mammals that are dominant in the Late Cretaceous, and the triconodonts are utterly unrelated to all of them (Rougier et al., 2001; Luo et al., 2002; Meng et al., 2003; Kielan-Jaworowska et al., 2004; Rougier et al., 2007c). *Vincelestes*, from the Hauterivian-Barremian La Amarga Formation, seems to be closely allied to Theria and therefore only distantly related to any of the Late Cretaceous mammals. Therefore, it is clear that some kind of faunistic discontinuity exists between the Early

Cretaceous and the Late Cretaceous (see also Pascual and Ortíz-Jaureguizar, 2007). Recently, mammalian remains have been found in the early Late Cretaceous La Buitrera locality, which are mostly undescribed as of yet (Rougier and Apesteguía, 2004). Enough is known from these taxa to show that they are highly derived dryolestoids that belong to the dryolestoid radiation recognized from the finds in Los Alamos (Bonaparte, 1986a, 1990, 1994, 2002) and La Colonia (Rougier et al., 2003b,c; 2007, in press) and therefore, dating the origin of the dryolestoid dominated faunas to at least the Early Late Cretaceous.

The Late Cretaceous Patagonian faunas typified by dryolestoids and accompanying taxa, like sudamericids, ferugliotheriids, and multituberculates, are not restricted to Patagonia, but possibly extended beyond the confines of the Rocanense Sea. Recent finds in the Late Cretaceous of Bolivia (Gayet et al., 2001) show the presence of dryolestoid-like forms and other non-tribosphenic mammals, bringing a measure of support to the idea that the mammalian fauna of Los Alamos is somewhat representative of the South American (or even Gondwanan) mammalian assemblages (Bonaparte, 1986a,c, 1990; Pascual et al., 2000a,b; Pascual and Ortíz-Jaureguizar, 2007).

Therians are dominant in the South American Early Paleogene record. However, survival of lineages with an old Mesozoic pretherian ancestry occur in the Paleocene of Salamanca Formation, where dryolestoids and the enigmatic gondwanatherians are still important components, coexisting side by side with monotremes, didelphoid metatherians, various condylarths and archaic South American ungulates (Scillato-Yane and Pascual, 1985; Bonaparte et al., 1993; Bonaparte and Morales, 1997; Pascual et al., 1992; Gelfo and Pascual, 2001; Gelfo, 2004, 2007; Gelfo et al., 2008; Rougier and Páez Arango, 2007). Our report here focuses on the description of a series of specimens that can be easily placed within some of the high level groups recognized early on by (Bonaparte 1986a) from Los Alamos. We note however what we believe are specific differences in many taxa from those present in Los Alamos. Despite the small number of specimens, we wish to report these finds as a way to stimulate prospecting and research of the promising outcrops of the Allen Formation in Río Negro Province and to take the opportunity to critically review some aspects pertaining to the Late Cretaceous South American mammals.

### 1.1. Locality and stratigraphy

A thick sedimentary section, including marine and non-marine facies, was deposited in the Neuquén Basin during the Late Cretaceous: extending over northern Patagonia and including part of the provinces of Río Negro, La Pampa, and Mendoza (Legarreta and Gulisano, 1990). During the Late Campanian and Early Maastrichtian, the Neuquén Basin underwent important compressional events related to subduction processes along the western margin of South America, which changed from back-arc to foreland basin (Legarreta et al., 1989). This new paleogeographic context saw the onset of non-marine sedimentation that originated the Albian-Campanian Neuquén Group (Dingus et al., 2000). During the Late Campanian?-Early Maastrichtian – and with a different paleogeographic distribution – began the deposition of the Malargüe Group, comprising the Allen, Jagüel, Roca and Carrizo formations. This group unconformably overlies the uppermost beds of the Neuquén Group (i.e., the Anacleto Member of the Río Colorado Formation).

The Cretaceous/Paleogene boundary in Patagonia was characterized by important climatic and paleoenvironmental changes evidenced in the rocks and faunas contained in the Malargüe Group (Casadío et al., 2005). This unit, widely distributed in northern Patagonia, is exposed at numerous localities in the province of Mendoza, along the foothills of the Andes, and north of the Somuncurá Massif in the provinces of Río Negro, Neuquén and La Pampa.

The Malargüe Group is comparable in many aspects with the Neuquén Group; however, a clear change can be recognized in the source of the two depositional systems (Legarreta et al., 1989). While the main sediment source during the Cenomanian–Albian (Neuquén Group) was towards the East, during the Maastrichtian (Malargüe Group) it shifted mainly towards the West.

The first Atlantic marine event in the Neuquén Basin occurs in the lower section of the Late Campanian?–Early Maastrichtian Allen Formation (Wichmann, 1927; Casamiquela, 1980; Parras et al., 1998). This event is represented at a few localities south of latitude 37°S by marginal marine facies. Legarreta et al. (1989) suggested that this event reached northwards into the Malargüe area about 36°S.

In the middle and upper sections of the Allen Formation, facies changed towards a more clearly marine character, denoting a rise in relative sea level. During this time, more than 40 m of siltstone were deposited under sub-tidal conditions in the Auca Mahuida area (Casadío, 1994). At the same time, in the Huantraico area to the West, the sedimentary record suggests more restricted marine conditions. Likewise, towards the eastern margin of the basin these beds are represented by intertidal facies (Casadío, 1994). This relative sea level increase was followed by an important drop that greatly reduced the flooded area, which was thus restricted to south of latitude 37°S. This can be inferred from the thickness of the evaporites recorded in the Auca Mahuida, Lago Pellegrini and Aguará areas. The upper beds of the Allen Formation exposed at Barda Baya show evidence of an important sub-aerial exposure event (Casadío, 1994).

The fossils studied here come from the bottom layers of the Allen Formation exposed at Cerro Tortuga (El Matuasto), within the Trapalcó and Santa Rosa depressions, Río Negro Province (Fig. 1). The fossiliferous layer yielded a rich collection of isolated vertebrate remains that are approximately 38 m below the top of the Allen Formation. The base of the Allen Formation is not exposed and at the top it transitionally gives way to the mainly pelitic rocks of the Jagüel Formation. The limestones of the Roca Formation overlie the latter.

The Allen Formation consists mainly of tabular and finely stratified siltstone and fine sandstone beds. Non-marine vertebrate and freshwater mollusk remains are frequent. These vertebrates, in addition to sedimentological characteristics, suggest a mainly lacustrine origin for these sediments with fluvial influence at their base. This is supported by the presence of channeled sandy bodies excavated into pelitic beds, containing abundant fossil remains such as freshwater mollusks (*Diplodon* sp., *Biomphalaria* sp. and *Paleoanculosa* sp.), dinosaur eggshells, coprolites (Parras et al., 2004), and the mammal remains studied herein, as well as fish, snake vertebrae (Apesteguía and Rougier, 2007; Gómez et al., 2008), and chelid turtles. The turtles are similar to those described from the Los Alamos Formation (Broin, 1987; Broin and de la Fuente, 1993), La Colonia Formation (Gasparini and de la Fuente, 2000), and other Late Campanian?–Early Maastrichtian lithostratigraphic units from Patagonia (Lapparent de Broin and de la Fuente, 2001; Martinelli and Forasiepi, 2004a, b).

The Jagüel Formation – at the studied localities – comprises siltstones with a few laminated beds bearing very scarce Late Maastrichtian marine bivalves, identified as *Ambigostrea clarae* (Ihering, 1907) and “*Pecten*” *mahuidaensis* Weaver, 1931. This unit carries a very abundant assemblage of calcareous nannofossils (Concheyro et al., 2002), the most relevant of which are *Cribrosphaerella daniae*, *Nephrolithus frequens*, *Prediscosphaera stoveri*, *Biscutum melaniae*, *Lithraphidites quadratus* and *Arkhangelskiella cymbiformis*. These indicate a late Maastrichtian age, CC26 Biozone (Perch-Nielsen, 1985). Overlying this nannoflora, and also within the Jagüel Formation, Concheyro et al. (2002) confirmed the occurrence of *Biantholithus sparsus*, a guide fossil for the early Danian, NP1 Zone (Martini, 1971; Perch-Nielsen, 1985; Concheyro, 1995).

The top of the Jagüel Formation is given by the base of the first shell bed with *Pycnodonte* (*Phygraea*) *burckhardtii* (Böhm, 1903) and

*Gryphaeostrea callophyla* (Ihering, 1903). In the studied area, the Jagüel Formation contains the Cretaceous/Paleogene boundary.

The age of the sediments providing the specimens described here is difficult to establish beyond general terms. It is obviously Late Cretaceous, because of the position of the Cretaceous–Paleogene boundary inside the overlying Jagüel Formation. Beyond this age, the estimate has to be based on faunistic similarities with the likely contemporaneous or penescontemporaneous Formations Los Alamos and La Colonia. The mammals from these three units are similar at the higher taxonomic level but differ in specific composition. Not all groups recorded in Los Alamos are present in either the Allen Formation or La Colonia Formation. The notable absence of conspicuous gondwanatherians in both La Colonia and Allen formations and of non-mesungulid dryolestoids in La Colonia may reflect either time or environmental/preservational bias. The Non-mammalian vertebrates overlap substantially among these three units (Martinelli and Forasiepi, 2004a, b; Gómez et al., 2008) and we believe they are all close in age. La Colonia Formation has large size mesungulids (Rougier et al., 2001a,b, 2002; 2) that seem to correspond with later large sized dryolestoids from the Paleocene Salamanca Formation (i.e. *Peligrotherium*). We believe that it is possible to argue for a slightly younger age for La Colonia Formation with respect to either Allen or Los Alamos formations, with the latter two closer to each other in age. The Los Alamos Formation has been attributed to Campanian –Maastrichtian based on palynological evidence (Papu and Sepúlveda, 1995). The age of the remains studied here is likely to be Maastrichtian, but not the latest Maastrichtian.

## 2. Materials and methods

The specimens were all collected by screen washing and further picking of the resulting concentrate, over the years 2002 and 2003. Several tons of sediment were taken from the Cerro Tortuga locality (GPS) (39° 47' 02.1 S; 66° 42' 17.9 W) soaked in water, and then screen washed either at the local museum in Lamarque or at “El Matuasto” ranch (GPS) (39° 46' 53.65 S; 66° 33' 44.5 W) using running water provided by a pump from a cattle pond. Members of the expedition and trained personnel at the Lamarque Museum performed the picking.

The anatomical nomenclature follows Prothero (1981) with further modifications by Rougier et al. (2003a).

Lm = maximum length

Wm = maximum width

### 2.1. Institutional abbreviations

MML-Pv; Museo Municipal de Lamarque, Paleontología de Vertebrados.

MACN-RN; Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Colección Río Negro.

## 3. Systematic Paleontology

Class: Mammalia Linnaeus, 1758

Legion: Cladotheria Mckenna, 1975

Sublegion: Dryolestoida Butler, 1939

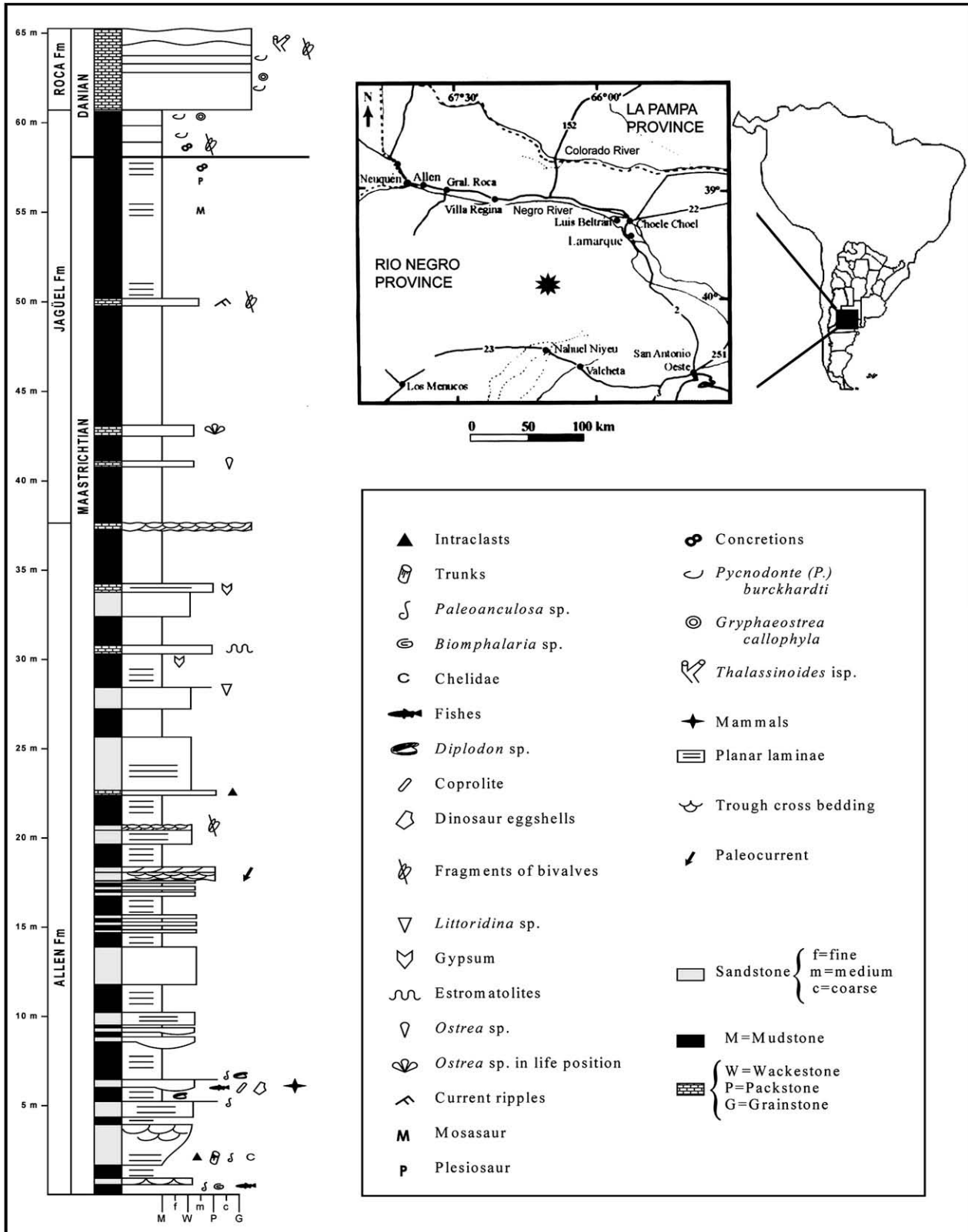


Fig. 1. Map of South America indicating the location of Cerro Tortuga (asterisk), and stratigraphic column. See text for coordinates of the locality.

Family: Mesungulatidae Bonaparte, 1986a

Mesungulatum lamarquensis sp. nov.

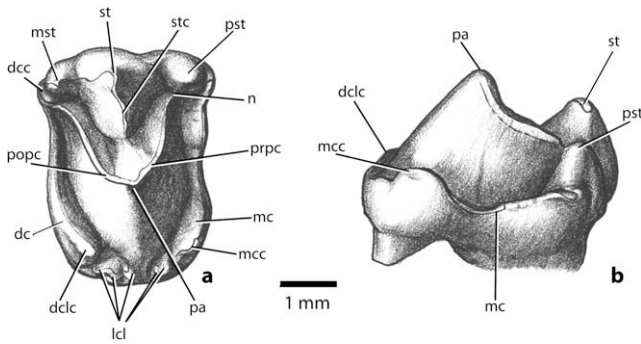
Figs. 2–4f

Genus *Mesungulatum* Bonaparte and Soria, 1985

Type-species. *Mesungulatum houssayi* Bonaparte and Soria, 1985

Derivation of the specific name. *lamarquensis*, a latinized version of Lamarque, the largest city in the area, and home of the Museo





**Fig. 2.** Drawing of the type of *Mesungulatum lamarquensis* MML-Pv 10, right upper molar. Abbreviations: **dc**: distal cingulum; **dcc**: distal cingular cusp; **dclc**: distal cingulum lingual cusp; **lcl**: lingual cusps; **mc**: mesial cingulum; **mcc**: mesial cingulum lingual cusp; **mst**: metastyle; **n**: notch; **st**: stylocone; **stc**: styloconar crest; **pa**: paracone; **prpc**: preparacrista; **pst**: parastyle; **popc**: postparacrista.

Municipal de Lamarque, which serves as repository of the specimens. The species name also recognizes the pioneering work being carried out by the personnel of this institution and their invaluable help in making collecting of these specimens possible.

**Holotype.** MML-Pv 10, a right upper molar.

**Hypodigm.** The type, MML-Pv 11, a left upper molar (fig. 2, 3); and MML-Pv 12, a lower molar fragment (fig. 4).

**Horizon and locality.** Microvertebrate layer, Cerro Tortuga, Allen Formation, 38 m below the top of the Allen Formation.

**Diagnosis.** Mesungulid of similar size to *M. houssayi*, but without lingual shifting of the stylocone, so that when the molars are oriented with the crown-root boundary horizontal, the buccal wall of the stylocone is more vertical and the apex of the stylocone is almost on the buccal margin of the tooth in *M. lamarquensis*, rather than more lingual as in *M. houssayi*. The cingula are broader in *M. lamarquensis* than in *M. houssayi*, determining a rectangular outline of the crown (also evident in MML-Pv 11, in spite of having part of the cingulum missing), while in *M. houssayi* the outline tapers lingually, having a more distinct triangular outline. The mesial and distal cingula culminate lingually in robust and distinct cusps in *M. lamarquensis*, but they are not as developed in *M. houssayi* (this feature is partially responsible for the more rectangular outline of *M. lamarquensis*). The parastyle is fully independent with a separate base and a labial surface distinct from the stylocone in relatively unworn specimens of *M. houssayi* (MACN-RN 03); on the contrary, in *M. lamarquensis* the parastyle is lower, more rounded, and not so sharply separated from the stylocone by a broad groove. There are two cusps in the metastylar area of *M. lamarquensis*, a metastyle and a distal cingular cusp; the metastyle is prominent (remnants of which can still be seen in the very much worn MML-Pv 11) and the distal cingular cusp is well differentiated. In contrast, both cusps are poorly developed in *M. houssayi* and the metastyle is missing in most specimens (although a distinct metastyle is present in MACN-RN 182). The metastyle is more labial and closely appressed in *M. houssayi* than in *M. lamarquensis*, where they are almost in line. The mesocrista (*sensu* Bonaparte, 1990; medianer Grat *sensu* Martin, 1999; median ridge *sensu* Kielan-Jaworowska et al., 2004) on the buccal slope of the paracone is poorly developed in *M. lamarquensis* but is sharp and distinct in unworn specimens of *M. houssayi*. These differences between *M. houssayi* and *M. lamarquensis* are established based on specimens likely to be neither the first nor the last molar, probably M2 (see below).

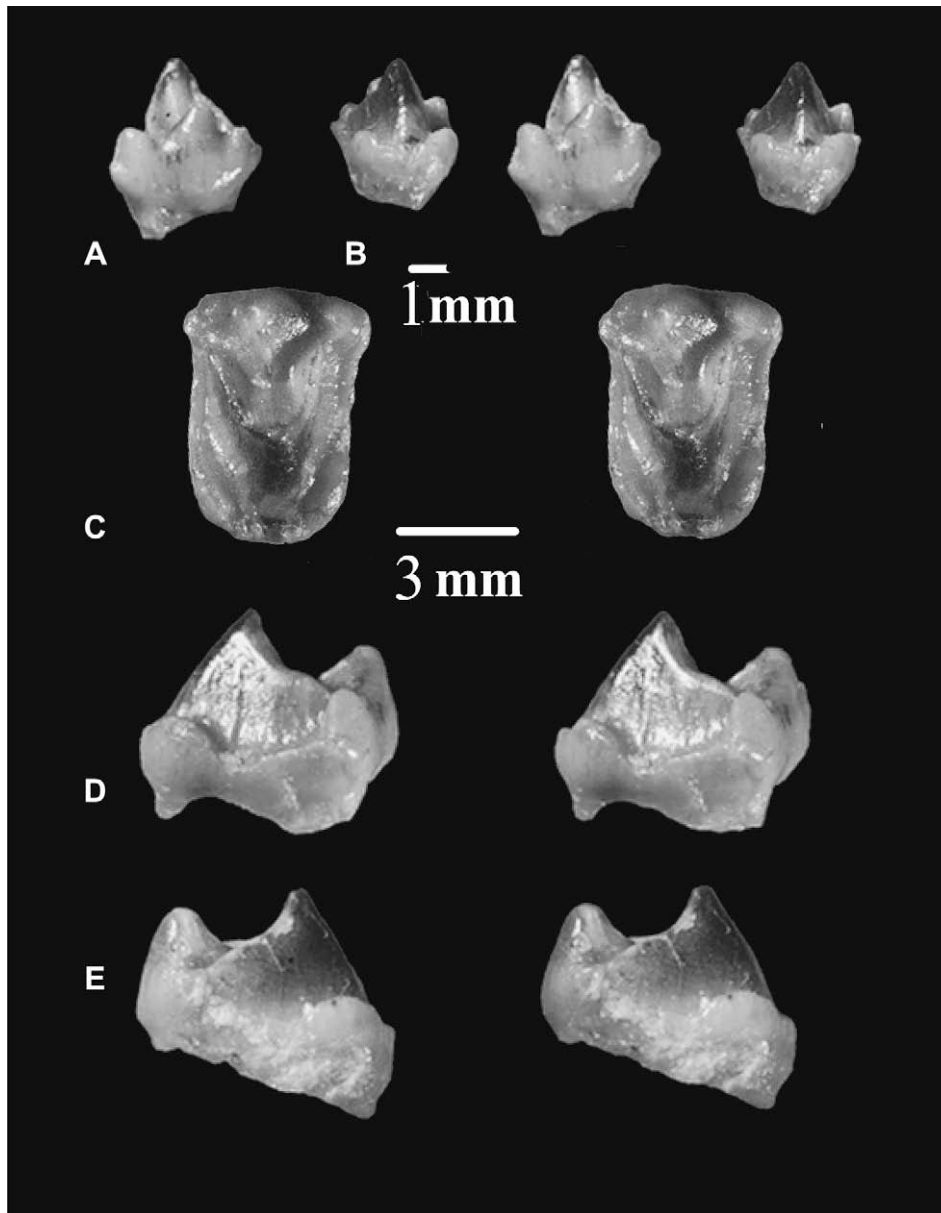
**Description.** There are two specimens, possibly three, that can be attributed to mesungulids (MML-Pv 10–12).

MML-Pv 10 is a crown of a right molar missing both roots and minor chips of the enamel along the main crests. The crown is

preserved as an empty shell of enamel with an enormous pulp chamber, without much dentine or cementum; these features strongly suggest that this molar was incompletely mineralized and probably only partially erupted. MML-Pv 10 lacks any evidence of wear except for the tip of the paracone. The broken stubs of three roots are present and suggest roots not fully formed. A single subcylindrical root was located under the paracone, while two mesiodistally compressed roots of similar size supported the labial aspect of the tooth. The molar follows closely the typical pattern of mesungulids. A dominant lingual paracone is the main cusp of the crown united to the distal cingular cusp and parastyle by two sharp crests that outline a rather symmetrical triangle. Slightly distal from the position of the paracone and along the labial margin of the crown is the second larger cusp, the stylocone. As in all mesungulids, the stylocone occupies a mid-way position between the mesial and distal styler cusps and is completely divorced from the preparacrista. The stylocone is only slightly shorter than the paracone and is not fully connected to the paracone by a crest. The sharp and distinct lingual styloconal crest stops at the embrasure at the base of the paracone/stylocone, and only a blunt raised surface continues to the lingual aspect of the paracanal apex. The paracrista (preparacrista) extends labially in the direction of the parastyle, but stops distal and slightly short of it. A small notch separates the engrossed buccal end of the preparacrista and the distal surface of the parastyle. The parastyle is conical and moderately procumbent, somewhat buccolingually compressed, and forming a rudimentary parastylar hook that projects mesially from the line determined by the preparacrista. There is no distinct metacone in mesungulids and therefore the posterior crest should be considered as the postparacrista; this crest is almost a mirror image of the preparacrista. The postparacrista ends buccally in a thickened eminence that is separated by a shallow notch from the distal cingular cusp. The metastyle is fully separated from the postparacrista, and closely abuts the stylocone. The buccal aspects of all the styler cusps are rather vertical and do not bulge much buccally; an ectoflexus is lacking. Large cingula are present mesially and distally immediately above (occlusal of Butler, 1956) the crown line. These cingula extend along the whole buccolingual extension of the tooth. The mesial cingulum is more extensive and is continued past the mesial base of the parastyle, whereas the distal one does not extend past the distal cingular cusp. The cingula reach their maximum development on the lingual surface where they show distinct robust and elongated cusps. Both cingula encroach upon the base of the paracone through a lower crest ornated by numerous cusps. Only a minute space is left lingual to the paracone base between the approaching mesial and distal cingula.

There is a second rather complete molar (MML-Pv 11) that can be attributed to a mesungulid; this molar is of similar size to the type (MML-Pv 10) and despite some uncertainty it is interpreted here as a left upper molar. The tooth is very heavily worn and is missing the metastylar area and most of the distal cingulum. The specimen conforms well to the details seen in MML-Pv 10, but probably represents a different position. Despite the wear there is evidence of a broad cingulum that forms a platform along the base of the crown (seen only in the preserved mesial cingulum). Wear has obliterated all details in the trigon including most of the stylocone, mesocrista and labial surface of the paracone. Despite overall similarities there is one clear difference between this specimen and MML-Pv 10: the close lingual continuation of the cingula seen in MML-Pv 10 is missing in MML-Pv 11, and its absence does not seem to be explained by wear.

A fragmentary mammalian tooth, MML-Pv 12, consists of half of a large cusp, a crest leading from it to a small cusp, and a cingulum at the base of the crown extending the whole buccolingual length. The enamel is rugose and the fragment is similar in size to the



**Fig. 3.** Stereophotographs of the type of *Mesungulatum lamarquensis* MML-Pv 10, right upper molar. **A:** labial, **B:** lingual, **C:** occlusal, **D:** mesial, **E:** distal views

specimens we referred to mesungulatids, but somewhat larger and robust. It is likely that this fragment also represents a lower tooth of a mesungulatid, an attribution supported by the extensive cingulum, but no further data can be gleaned from it and we are uncertain if it belongs to *M. lamarquensis*.

**Measurements.** MML- Pv 10 (Lm = 4.05 mm; Wm = 5.29 mm); MML-Pv 11 (Lm = 4.05 mm; Wm = 5.62 mm); MML-Pv 12 too fragmentary for meaningful measurements.

Class: Mammalia Linnaeus, 1758

Legion: Cladotheria Mckenna, 1975

Sublegion: Dryolestoidea Butler, 1939

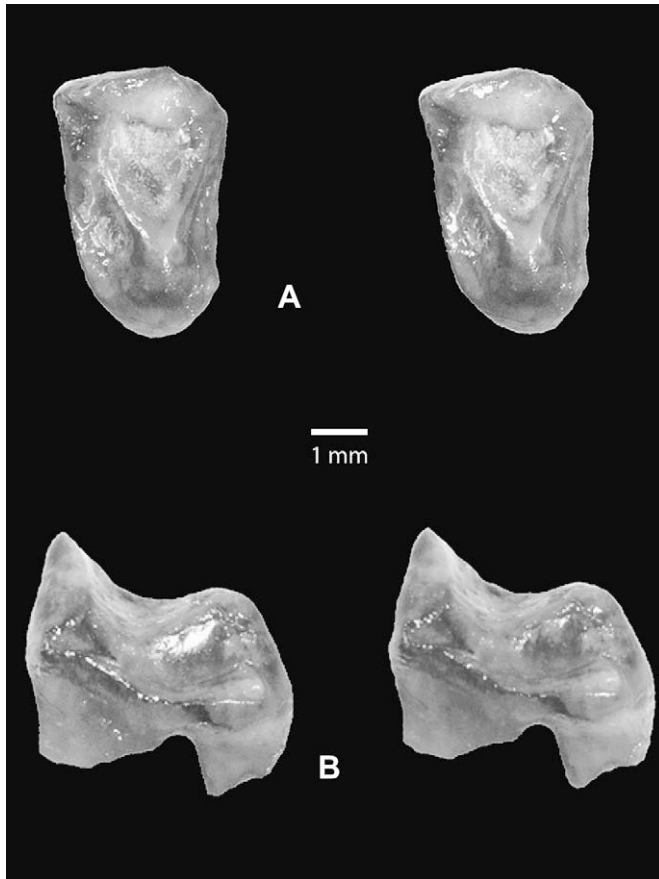
Genus: *Groebertherium* Bonaparte, 1986

*Type species.* *Groebertherium stipanicici* Bonaparte, 1986

**Referred specimen:** MML-Pv 14, a right upper molar. **Fig. 51**  
**Horizon and locality.** Microvertebrate layer, Cerro Tortuga, Allen Formation, 38 m below the top of the Allen Formation.

**Revised diagnosis.** *Groebertherium stipanicici* is a small-sized dryolestoid, with a stylocone divorced from the paracrista and a long, narrow trigon. The molars have a tall crown, they are approximately symmetrical and devoid of cingula. The parastyle forms a small hook. A centrocrista is poorly defined and, if at present, represented by the thick lingual extension of the lingual slope of the stylocone.

**Description.** There is one tooth that represents a small-sized dryolestoids in the size range of *Groebertherium* and of very similar morphology. The specimen MML-Pv 14 is a right upper molar missing the parastyle, but otherwise well preserved and unworn. The paracone is large, sharp and found at the confluence of two sharp crests, the preparacrista and the postparacrista. A low mesocrista climbs the buccal surface of the paracone, but it is barely distinguishable. No metacone is present as individual cusp, and



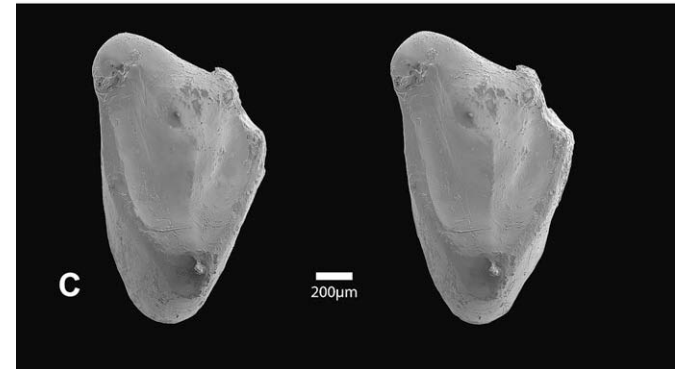
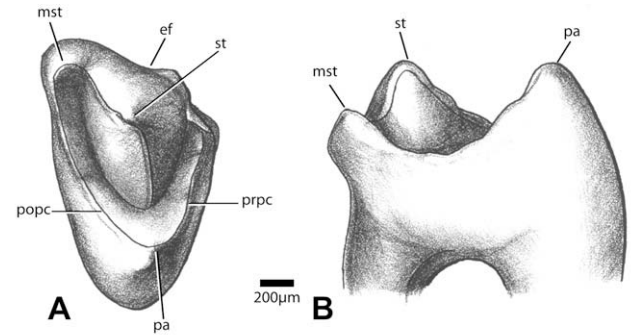
**Fig. 4.** Stereophotographs of *Mesungulatum lamarquensis* MML-Pv 11, left upper in **A**: occlusal and **B**: mesial views.

because of the little wear of the molar it is likely this cusp was absent altogether. The faint paraconal contribution to the mesocrista contacts a sharp, well defined ridge that descends from the lingual aspect of the stylocone. The mesocrista divides the crown in two halves, almost symmetrically. The stylocone is lower than the paracone and markedly triangular in plant. The posterior basin is delimited between the postparacrista, the mesocrista, the distal aspect of the stylocone, and the metastyle that marks the buccal end of the postparacrista.

The basin mesial to the mesocrista is incomplete because of the missing parastyle, and its confluence into a presumably present parastylar hook cannot be fully ascertained. It is clear, however, that a moderate ectoflexus was present, with the stylocone almost completely enclosed in the posterior lobe. The preparacrista is fully separated from the stylocone. The bases of the stylocone and the metastyle are very close together, forming a continuous surface in buccal view. No cingula are present in this specimen. Remnants of three roots are present, with a small posterior one supporting the metastyle part of the stylocone, and a complex, large mesial one. The mesial root is compressed and subdivided in two bucco-lingual lobes supporting the paracone and the parastylar area, respectively.

**Measurements.** MML-PV 14 (Lm = 1.16 mm; Wm = 1.73 mm).

**Remarks.** We accept here *Groebertherium stipanicici* and *Groebertherium novasi* as co-specific (Chornogubsky, unpub. data). *G. stipanicici* and *G. novasi* were published in the same paper (Bonaparte, 1986a). The type of *G. stipanicici* (MACN-RN 13) has been subsequently damaged to the point of being useless for systematic purposes (LC, pers. obs.); we choose therefore the type of *G. novasi* (MACN-RN 19) as the neotype of *Groebertherium stipanicici*. The



**Fig. 5.** *Groebertherium stipanicici*. MML-Pv 14, right upper molar. Drawing in occlusal (**A**) and distal (**B**) views. Stereo SEM photographs in occlusal view of the same specimen (**C**). Abbreviations: **ef**: ectoflexus; **mst**: metastyle; **pa**: paracone; **popc**: postparacrista; **prpc**: preparacrista; **st**: stylocone

two species become objective synonyms. The specimens found at Allen Formation share with *G. stipanicici* the presence of a high metastyle connected to the stylocone by a strong vertical wall, a feature, however, less accentuated on *G. stipanicici* from Los Alamitos. *Groebertherium* was originally referred to the Dryolestidae and not to mesungulatidae because of the absence of cingula in the upper molars, and the presence of a mesiodistally compressed trigonid with a somewhat transverse metacristid. The presence of a large stylocone on the center of the stylocone, plus its lack of connection with the paracrista, argue against a close relationship with Laurasian dryolestoids and possibly can be referred to a monophyletic group of South American Dryolestoids (Bonaparte, 1994) that in our opinion, would be basal to the highly autapomorphic mesungulatids.

*Groebertherium* from Cerro Tortuga and Los Alamitos are very close morphologically; this overall similarity suggests a small time difference, if any at all, present between the Allen Formation and Los Alamitos Formation yielding these mammals.

**Class:** Mammalia Linnaeus, 1758

**Legion:** Cladotheria Mckenna, 1975

**Sublegion:** Dryolestoidea Butler, 1939

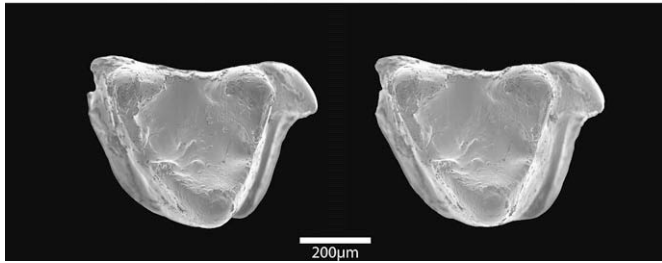
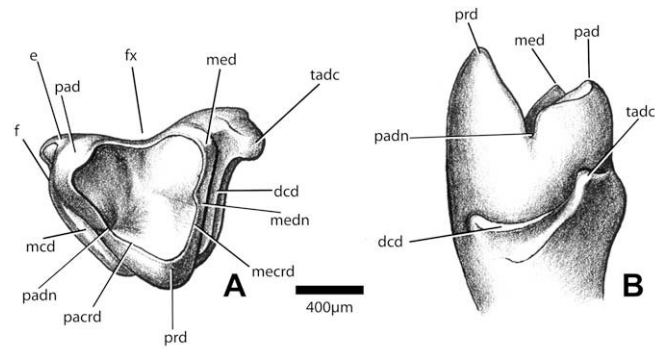
**Cf.** *Brandonia* Bonaparte, 1990

**Referred specimen.** MML-Pv 17, a left lower molar. **Fig. 6**

**Horizon and locality.** Microvertebrate layer, Cerro Tortuga, Allen Formation, 38 m below the top of the Allen Formation.

**Description.** The lower molar MML-Pv 17 is a complete left lower molar preserving most of its mesiodistally compressed roots and showing very little wear. The tooth is arranged following the





**Fig. 6.** Cf. *Brandonia* sp. MML-Pv 17, left lower molar. Drawing in occlusal (A) and distal (B) views. Stereo SEM photographs in occlusal view of the same specimen (C). Abbreviations: **dcd**: distal cingulid; **e**: cusp "e"; **f**: cusp "f"; **fx**: flexid; **mcd**: mesial cingulid; **mecrd**: metacristid; **med**: metaconid; **medn**: metacristid notch; **pad**: paraconid; **pacrd**: paracristid; **padn**: paracristid notch; **prd**: protoconid; **tadc**: talonid cusp.

general pattern of other dryolestoid lower molars, although the trigonid is proportionately broader.

The crown is dominated by a robust protoconid flanked by two sharp crests; the posterior one, the metacristid, leads to the metaconid, while the anterior one, the paracristid, leads to the paraconid. The buccal slope of the protoconid is convex, while the lingual one is flat or barely convex. The metaconid is found in the lingualmost extension of the metacristid, and is the second highest cusp in the tooth. The metacristid is interrupted half-way by a notch with angled walls similar to a carnassial notch, but without the characteristic tear-shaped bottom of the latter. The metacristid is not very transverse, forming an angle of approximately 72 degrees with the mesio-lingual axis of the tooth. The smaller paraconid is of triangular section and is at the end of a notched paracristid. Between the protoconid, paraconid and metaconid there is a shallowly basined trigonid that is fully open lingually. A moderate flexid divides the crown into two distinct lobes, a mesial one dominated by the paraconid, and a distal one dominated by the metaconid. Well developed cingula are present mesially and distally, but do not contact each other at the base of the protoconid; instead, a wide lingual gap remains between them. The mesial cingulum shows two distinct cingular cusps on its lingual margin. These cusps are similar to those found in other mammals in which the molar interlocking is achieved by cingular structures, and thus they are likely homologous of cusps **e** and **f** of other cladotherians. The distal cingulum culminates lingually in a sole cusp, the talonid cusp (perhaps homologous of the hypoconulid of later therians; Crompton, 1971; Bonaparte, 1990). This distal cingular cusp is more developed than its mesial counterparts and slightly posteriorly extended. The talonid cusp is interlocked with cusps **e** and **f** of the subsequent tooth, providing a distinct locking mechanism not commonly seen in Laurasian dryolestoids.

**Measurements.** MML-PV 17 (Lm = 1.49 mm; Wm = 1.16 mm).

**Remarks.** The lower molar assigned to this species is similar in size to *Brandonia*, and proper occlusal relationship between our specimen and the upper molar of *Brandonia intermedia* appears likely. There are, however, a few differences between the lower

molar attributed by Bonaparte (1990) to *Brandonia intermedia* (MACN-RN 170) and our specimen. The molar from Allen Formation is shorter relative to *B. intermedia* and has notches in both para- and metacristid, features barely distinguishable in the species from Los Alamitos Formation. It is possible that *Brandonia intermedia* and the species from Allen Formation are two closely related congeneric species, but given that the upper molar morphology has been emphasized in the systematic arrangement of South American dryolestoids, we choose not to erect a new taxon at this time when only lower molars are available.

**Class:** Mammalia Linnaeus, 1758

**Legion:** Cladotheria Mckenna, 1975

**Sublegion:** Dryolestoidea Butler, 1939

**Genus:** *Barberenia* Bonaparte, 1990

**Type species:** *Barberenia araujoae* Bonaparte, 1990

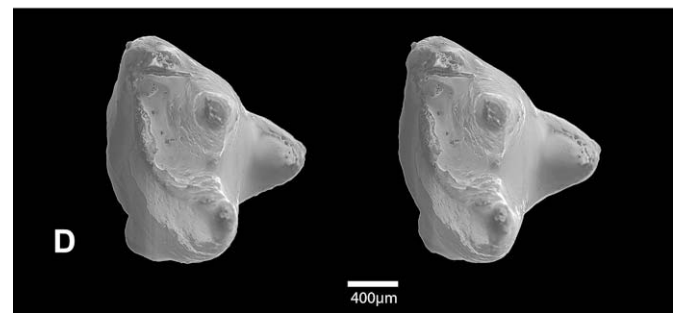
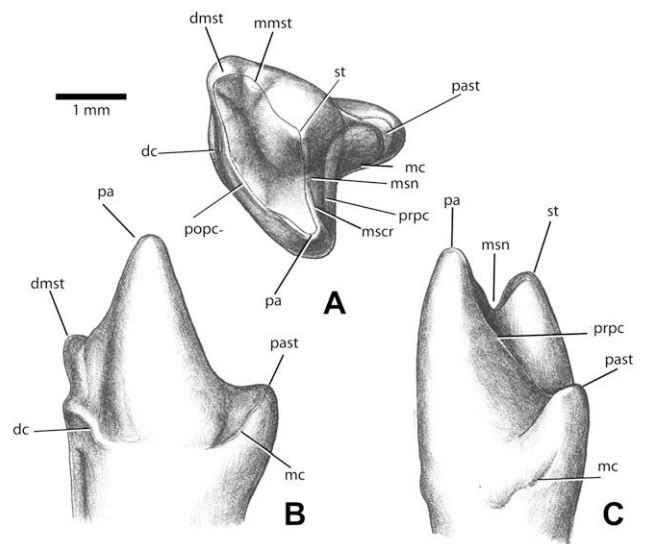
*Barberenia allenensis* sp. nov.

**Figs. 7, 8.**

**Derivation of the specific name.** A new species of the previously known genus *Barberenia*, *allenensis* after Allen Formation, the unit bearing the specimens here studied.

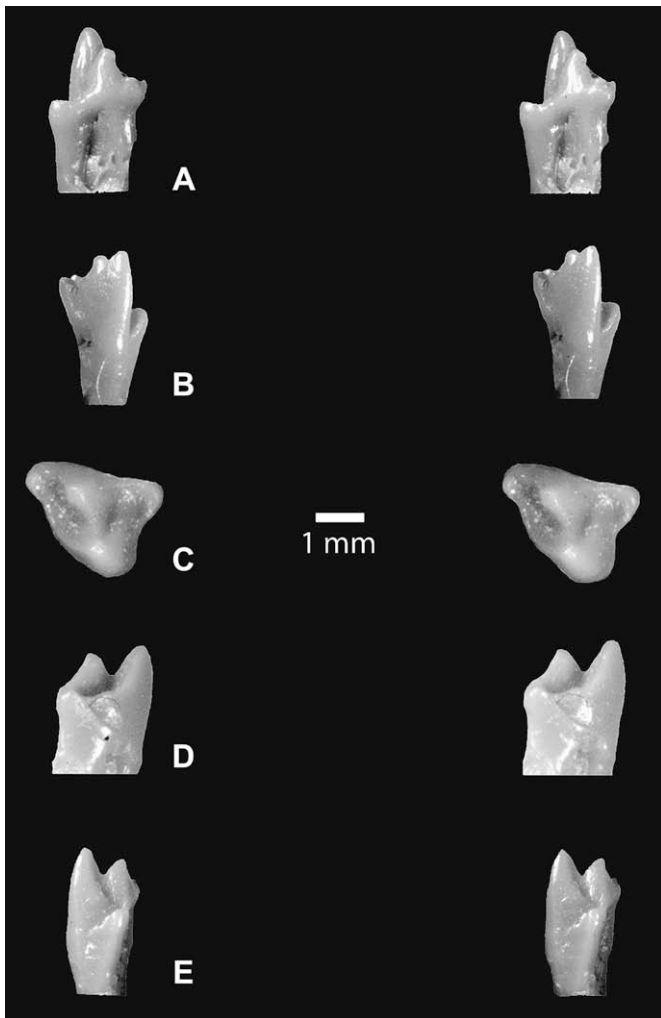
**Holotype.** MML- Pv 13, a right upper molariform (P2?)

**Horizon and locality.** Microvertebrate layer, Cerro Tortuga, Allen Formation, 38 m below the top of the Allen Formation.



**Fig. 7.** Type of *Barberenia allenensis* MML- Pv 13 right upper molariform (P2?). Drawings in occlusal (A), lingual (B), and mesial (C) views. Stereo SEM photographs in occlusal view of the same specimen (D). Abbreviations: **dc**: distal cingulum; **dmst**: distal metastyle; **mc**: mesial cingulum; **mmst**: mesial metastyle; **mscr**: mesocrista; **msn**: mesocrista notch; **pa**: paracone; **popc**: postparacrista; **prpc**: preparacrista; **past**: parastyle; **st**: stylocone.





**Fig. 8.** Type of *Barberenia allenensis* MML- Pv 13 right upper molariform (P2?). Stereophotographs in labial (A), lingual (B), occlusal (C), distal (D) and mesial (E) views.

**Diagnosis.** Medium sized dryolestoid with a skewed compressed basin similar to *Quirogatherium* and *Barberenia araujoae* (Bonaparte, 1990). Differs from *Quirogatherium* in the more gracile cusp pattern, smaller size and more skewed cusp arrangement. *Barberenia allenensis* is similar to *B. araujoae* in the sharp, tall cusps, but the Allen Formation species is distinctly larger, has a less mesio-distally elongated triangular outline with a smaller parastylar area and a less developed anterior cingulum.

The parastylar hook is relatively small, significantly smaller than the similar *Barberenia araujoae* (Bonaparte, 1990).

**Description.** The molariform MML-Pv 13 is almost complete, preserving two roots, the posterior one missing its tip. The crown is triangular in outline, with the mesial surface slightly shorter than the distal; the geometrical arrangement of the triangle is barely disturbed by the heel-like parastyle. The highest cusp is the labially positioned paracone found in the intersection of three crests variously developed. The paracone shows little wear and the lingual slope of the cusp is rather vertical, with its base only moderately more lingual than the sharp apex. The most prominent of the crests connecting with the paracone (the mesocrista *sensu* Bonaparte [1990]; medianer Grat *sensu* Martin (1997)) is labially and slightly distally directed towards the second most prominent cusp of the crown, the stylocone. The stylocone is sharp and approximately conical, with a flattened mesial slope. The axis paracone-

mesocrista-stylocone bisects the crown in a portion mesial to the mesocrista and a little larger distal portion. The mesocrista is notched halfway between the paracone and the stylocone. Stemming mesio-buccally from the paracone there is a second crest, the preparacrista. This crest is low and poorly differentiated, running in the direction of the base of the parastyle, closely abutting against the base of the mesocrista. The area directly mesial to the mesocrista resembles, thus, more a blunt ledge than a basined trigon. The preparacrista does not reach the parastyle, ending distal to it. The parastyle is far dorsal than the rest of the crown, the cusp is of triangular section and shows a wear facet mildly developed between its distolingual surface and the weak paracrista. The parastylar hook is relatively small, much smaller than in the similar *Barberenia araujoae* (Bonaparte, 1990). The cingulum extending distolingually from the parastyle towards the crown neck is very short and covers less than half the mesial view of the tooth.

The posterior half of the crown is formed by a well-delimited basin between the mesocrista and the postparacrista (see below). A trough-like basin is developed between these cusps and the labially positioned dual metastyle. A distinct metacone is absent in this tooth as it is in *B. araujoae*, however a truly minute bulge in the crest has been identified as a metacone in the type of *B. araujoae* (MACN-RN 166). A similar bulge is present in the molariforms from Allen, but we, however, refrain from calling this crest a metacrista and employ instead the term postparacrista. The postparacrista is much lower than the mesocrista and ends directly at the more distal and smaller of the two metastyles. The mesial metastyle forms a distinct buccal edge for the basin and is centrally located between the stylocone and the distal metastyle.

A small but distinct cingulum runs down from the distal metastyle to about half the length of the distal face of the tooth.

The roots are very unequal in size; the larger anterior one supports the parastyle and the paracone, while the small, round and posterior one provides support to the metastyles as well as part of the stylocone.

**Measurements.** MML-PV 13 (Lm = 2.31 mm; Am = 1.90 mm).

**Remarks.** *Barberenia allenensis* is similar to *Barberenia araujoae*; the molars of the latter have been thought to be deciduous teeth (Martin, 1999, 2002; Bonaparte, 2002; Kielan-Jaworowska et al., 2004). This supposition is mainly based on the similarity between *Barbereniás* molariforms and deciduous teeth of *Dryolestes*, from the Late Jurassic from Laurasia (Martin, 1997), and isolated elements of *Thereuodon* of Early Cretaceous age from Morocco (Sigogneau-Russell and Ensom, 1998). The family Barbereniidae was created by Bonaparte (1990) to hold the genus *Barberenia* and it was defined by the presence of a basin between the parastyle and the paracone, and another one between the paracone and metastyle, both separated by a ridge, and also by the persistence of the metacone, features not known in any other South American dryolestoid (Bonaparte, 1992). Later, several authors (e.g., Martin, 1999; Bonaparte, 2002; Kielan-Jaworowska et al., 2004) raised the possibility that the molars of *Barberenia* were molariform premolars, perhaps deciduous ones, of other Los Alamos species. Bonaparte (2002) even suggested that *Barberenia's* teeth pertained to *Groebertherium* or *Brandonia* genus. We are uncertain about the ultimate affinities of the teeth with morphologies similar to *Brandonia* and *Quirogatherium*, and we agree that they might represent deciduous teeth, or alternative molariform positions of other dryolestoids from Los Alamos, but because of the ambiguity on the attribution and the paucity of our specimens, we provisionally retain *Groebertherium*, *Barberenia* and *Brandonia* as valid genera.

Accepting *Barberenia* as a valid taxon allows the recognition of a new morph from the Allen Formation not represented by either *B. araujoae* nor *Quirogatherium*. The differences between *B. araujoae*

and *B. allenensis* are substantive: the presence of a more generalized L/W ratio (i.e., has a shorter crown) due to the significantly smaller and mesially open anterior basin in *B. allenensis*, and to a parastylar hook not so mesiodistally elongated. The parastyle is more dorsally positioned than the rest of the crown and the parastyle cingulum is smaller than that present in *B. araujoae*. Neither of these species have posterior cingulum in the upper molars. If the morphs represented by *Barberenia* and *Quirogatherium* are in fact successional positions of other dryolestoids, then the molar we describe here as *B. allenensis* represents a taxon different from any other we have so far in record at the Cerro Tortuga locality. Recent finds in La Colonia Fm. (Rougier et al., in press) suggest, however, that the morphs identified as *Barberenia* and *Quirogatherium* are homologous to the P2 position of mesungulatids and *Peligrotherium*. The South American dryolestoids seem to have retained in the P2 position a morphology similar to that present in deciduous molariforms of typical holarctic dryolestids (Martin, 1997). Because tooth replacement is unknown among the South American dryolestoids, the ultimate nature of the element we identify as P2 in *Peligrotherium* (the only S.A. dryolestoid known by fairly complete dentitions), and by extrapolation on the remaining mesungulatids is uncertain. However, given the high frequency of P2 in the collection from La Colonia, we believe it is highly unlikely that these elements are deciduous. We believe that the simplest explanation for the morphology seen in *Quirogatherium*, *Barberenia* and other molariforms with highly asymmetrical development of the mesial and distal portions of the tooth is to interpret them as premolars located at the root of a narrow rostrum. A very similar morphology can be seen in eutherians such as zalambdalestids and to a lesser degree asioryctitheres.

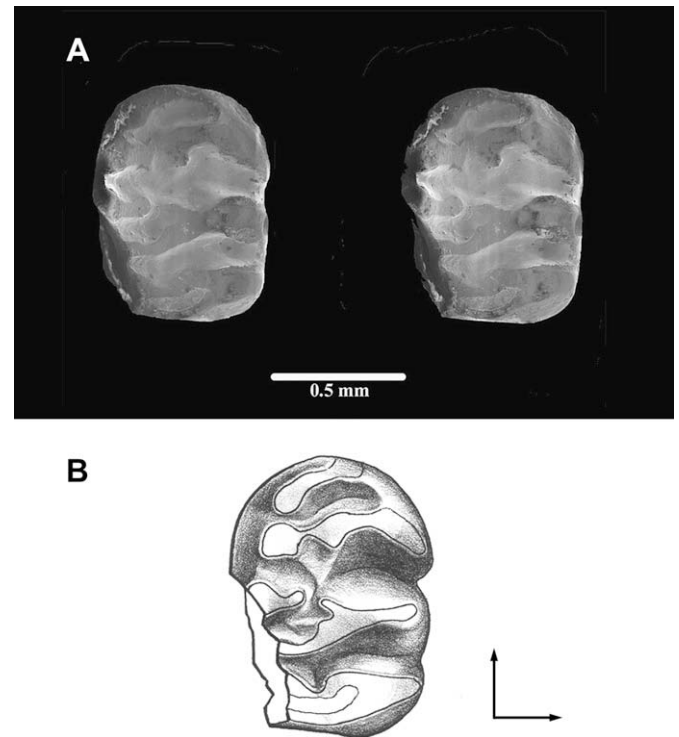


Fig. 9. Stereo SEM photographs in occlusal view of the type specimen of *Trapalcotherium matuastensis* MML-Pv 16, left lower first molar (A) and B interpretative drawing. The arrows point anterior and lingually.

Class: Mammalia Linnaeus, 1758

Infraclass: Allotheria Marsh, 1880

Order: ?Multituberculata Cope, 1884

Family: Ferugliotheriidae Bonaparte, 1986

Genus *Trapalcotherium* nov.

Type and only species. *Trapalcotherium matuastensis* nov.

**Derivation of the name.** *Trapalcotherium* gen. nov. from Bajo Trapalco, the basin where the Cerro Tortuga locality is located; *therium*, from Greek *therion* meaning beast, commonly used in taxonomy as a suffix meaning mammal.

**Diagnosis:** As for the type and only species.

*Trapalcotherium matuastensis* sp. nov. Fig. 9.

**Derivation of the specific name.;** *matuastensis*, after Puesto El Matuasto, a herder's shed facilitated by the Cabaza family for the use of the expedition while prospecting at the Cerro Tortuga locality.

**Holotype.** MML-Pv 16, a left m1.

**Horizon and locality.** Microvertebrate layer, Cerro Tortuga, Allen Formation, 38 m below the top of the Allen Formation.

**Diagnosis.** Ferugliotheriid similar in size to *Ferugliotherium*, differs from species of the Los Alamos Formation in the occlusal figure and cusp proportions. The anterior triangle is more compressed, with a curved anterior crest in the Allen Formation taxon, while it is more open and equilateral in *Ferugliotherium*. The cusp bases are better developed in *Ferugliotherium* than in *Trapalcotherium*, where they become part of the crests and therefore

less differentiated as individual structures. There is a larger degree of height difference between the lingual and buccal cusp rows in *Trapalcotherium* than in *Ferugliotherium*.

**Description.** Following previous interpretations of the orientation of ferugliotheriid molars (Krause et al., 1992; Krause, 1993; Krause and Bonaparte, 1993), the molar to be described here (MML-Pv 16) would be a left m1. The main features bearing on this issue are (1) presence of two rows of cusps which indicates this is a lower molar, (2) higher number of buccal than lingual cusps suggesting this is a left molar, (3) molar longer than wide, which is a widespread feature of multituberculate m1, and finally, (4) the presence of transverse ridges and a triangular wear pattern in the mesial aspect of the tooth, both features diagnostic of *Ferugliotherium* and arguably *Sudamerica* (Krause et al., 1992; Krause and Bonaparte, 1993; von Koenigswald et al., 1999). This molar is missing its buccodistal corner where two cusps were probably present. The tooth is subrectangular with a ratio L/W = 1.20. Two obliquely oriented rows of cusps are present. The lingual row has three main cusps and the buccal at least four but probably five. As in all the known specimens of *Ferugliotherium*, the crown shows deep transverse furrows and ridges uniting labial and lingual cusps. Probably due to the median extension of both labial and lingual cusps in the form of ridges, the individual cusps are not distinctly individualized cones as in most other multituberculates but thickened labial or lingual ends of crests. A single large longitudinal groove runs obliquely, becoming closer to the lingual margin towards the back of the tooth; the groove is, strictly speaking, not a continuous structure because the ridges connecting labial and lingual cusps cut across it.

The cusps are slightly convex mesially and barely concave distally. The three lingual cusps are larger than the labial ones and separated from each other by furrows that open lingually. The labial cusps are not separated by furrows as fully as the lingual ones. The pattern of cusps, crests, and furrows determines a mesial triangle pointing lingually and followed distally by two incompletely developed

transverse ridges. The mesial portion of the tooth is dominated by a triangular arrangement of cusps and crests involving the two more mesial labial cusps and the first lingual cusp. The mesialmost crest is curved following the outline of the crown. This crest is proportionately low and connects the prominent lingual cusp, with the anteriormost of the two labial cusps involved in the formation of the mesial triangle. The distal crest of the triangle connecting the concave distal surface of the first lingual cusp to the second buccal cusp is taller than the mesial one, particularly along its lingual extension. The furrow enclosed between these two crests is slightly arched mesially and not as deep as the furrow that marks the posterior limit of the triangle. This latter furrow is almost horizontal lingually and climbs up the steep wall that connects the second and third buccal cusps; it represents the buccal and lingual limbs of the first “Y-shaped” furrow that Krause (1993) described for *Ferugliotherium* (Krause and Bonaparte, 1993).

The second lingual cusp is also connected with the buccal side by means of two crests. The more anterior one is interrupted at about the midline of the tooth by what, at the wear stage represented by this molar, appears as a notch communicating the groove that forms the distal limit of the mesial triangle with a transverse groove that runs transversely on the buccal half of the tooth and that we interpret as the homolog of the stem of the first “Y” shaped furrow of *Ferugliotherium* (Krause, 1993). The main crest linking the second lingual cusp to the labial surface of the tooth is distal, broader, and taller than the first one. This second ridge of the second lingual cusp probably extended buccally towards a cusp now missing along the buccal edge of the tooth. The almost complete mesial crest and the complete distal crest of the second lingual cusp determine in fact an almost complete triangle that mimics the more mesial triangle. The rear of the second lingual cusp is pronouncedly concave. The furrow between the second and third lingual cusps is shallower than the one between the first and second lingual cusps, corresponding to the smaller size of the cusps involved. There is only a slight embayment midway in the furrow that could correspond to the stem of the “Y” shaped furrow of *Ferugliotherium*.

The third and last lingual cusp also is connected to two crests that encircle a small depression that likely disappeared in more advanced stages of wear. The buccal connections of these two crests are now missing, together with the likely cusps that capped them.

*Measurements.* MML-PV 16 (Lm = 2.48 mm; Wm = 2.07 mm).

*Remarks.* *Trapalcotherium matuastensis* is a ferugliotheriid, but it shows important differences with the *Ferugliotherium windhausenii*: (1) the mesial triangle in MML-Pv 16 is narrow in contrast to the big and open one from *F. windhausenii*; (2) the second furrow (first one behind the mesial triangle) is almost transverse in MML-Pv 16 and oblique in *F. windhausenii*; (3) the second lingual cusp in MML-Pv 16 has two ridges that form a rather triangular shape, not seen in *F. windhausenii*; (4) the molar in MML-Pv16 is proportionately shorter and wider than that of *F. windhausenii*, (5) the “Y’s” formed in the valleys are not well developed in MML-Pv16, and finally, (6) the apices of the first and second lingual cusps are more labially placed in *T. matuastensis* than those of *F. windhausenii*. There is, therefore, place for a bulging platform mesial and lingually in *T. matuastensis*, which is poorly developed in *F. windhausenii* MACN-RN 253 or in the well worn MACN-RN 174 (originally assigned to “*Vucetichia gracilis*,” now considered junior synonym from *F. windhausenii* by Krause et al., 1992 and Krause, 1993).

The ferugliotheriids have been purported to be related to the hypsodont *Gondwanatherium* and *Sudamerica*, which in turn have been linked to multituberculates (Bonaparte, 1990; Krause, 1993; Krause and Bonaparte, 1993) or left as Mammalia incertae sedis (Pascual et al., 2000a). The materials we describe here bear no

additional information for the resolution to this problem. The absence of *Gondwanatherium*, or sudamericids, in the Late Cretaceous localities of Cerro Tortuga and La Colonia is surprising given the robust nature of the teeth. The absence might be just a matter of incomplete record. However, more than 300 mammalian remains have been collected in La Colonia and their absence is conspicuous; more likely the differential record is reflecting the different environmental conditions affecting the deposition of La Colonia and Los Alamitos areas. The scanty mammalian record from Cerro Tortuga and the overall similarity with Los Alamitos (several small-sized dryolestoids absent in La Colonia) suggest that sudamericids should be present in both Late Cretaceous localities from Río Negro Province. Recently, Kielan-Jaworowska et al. (2007) described an isolated p4 from La Colonia Formation as *Argentodites coloniensis* and interpreted it as a cimolodontan multituberculate. Given that we have not recovered a p4, comparisons between *Trapalcotherium* and *Argentodites* are not possible; however, we believe that ferugliotherians are either multituberculates or closely related taxa and would support the earlier interpretation by Kielan-Jaworowska and Bonaparte (1996) of a p4 from Los Alamitos as belonging to *Ferugliotherium*. However, it appears to us simpler to interpret the p4 specimens from both Los Alamitos and *Argentodites* as likely ferugliotherians.

#### 4. Discussion

##### 4.1. Allen's Tetrapods and Faunal Turnover

Before the discoveries presented in this paper, the Allen Formation was already well known by its vertebrate remains, including armored small saltasaurine titanosaurs, large and advanced non-saltasaurine eutitanosaurs, highly derived and large carnosaurine abelisauroid theropods, ornithure and non-ornithure ornithothoracinae birds, hadrosaurid and ankylosaurian ornithischians, “Madtsoidae” snakes, non-eilenodontinae sphenodontians, chelid and meiolanid turtles, pipids and leptodactylids anurans, and chondrichthyes and osteichthyes fishes (Martinelli and Forasiepi, 2004a,b; Leanza et al., 2004: 16 Table 1; Gómez et al., 2008).

Similar vertebrate faunas, although not as diverse, were found in Loncoche and Los Alamitos Formations, both of them also attributed to the Late Cretaceous (Campanian – Maastrichtian; Alamitian vertebrate fauna *sensu* Bonaparte, 1986a,b,c; Allenian *sensu* Leanza et al., 2004) from Patagonia. Of these three formations, Allen, Loncoche, and Los Alamitos, only the latter fauna included mammals prior to this report.

Other South American Late Cretaceous faunas rich in microvertebrates are those from La Colonia Formation (Maastrichtian, Chubut Province, Argentina [Pesce 1979; Pascual et al., 2000b; Kielan-Jaworowska et al., 2007]) and El Molino Formation (Maastrichtian, Southeast of Cochabamba, Bolivia [Gayet et al., 1991]). Both of them are probably younger and have a very rich vertebrate fauna probably including dryolestoid mammals (see Rougier et al., 2001, 2002, 2003; Gayet et al., 2001). Although these faunas share high-level taxa, both faunas differ at the species level from those of Allen and Los Alamitos Formations, particularly those from El Molino Formation, where probable tribosphenic mammals are present (Gayet et al., 2001). The Late Cretaceous mammalian fauna has to be studied against the general backdrop of the Maastrichtian transgression and the dominant role of the Rocanense sea in southern South America (Andreis et al., 1989; Casadío, 1998; Casadío et al., 2005), which produced a fragmentation of the predominantly terrestrial ecosystems that dominated Patagonia during the Early Cretaceous and early Late Cretaceous (Wichmann, 1927; Casamiquela, 1979). The Chubut Group in Chubut Province and the early stages of the Neuquén Group deposition in the Neuquén Basin reflect this continental dominance in the pre-Campanian environments.



The increase in maritime transgressions subdivided the Patagonian environment, with the likely development of archipelagos, insular, and semi isolated communities (Petriella and Archangelsky, 1975; Andreis et al., 1989). The Río Negro Cretaceous distribution of mammals is part of this process of fragmentation and insularity, and it is at present unknown how well they represent the overall composition of the South American mammalian fauna. It is significant that in the Late Cretaceous of Bolivia (Pajcha Pata) the presence of pretribosphenic mammals is scarce and tentative (Gayet et al., 2001), while therians are more confidently recorded, probably manifesting the influence of northern immigrations. This provides evidence that the non-tribosphenic radiation attested in Patagonia extended at least as far as Bolivia; the recurrence of dryolestoids in the early Late Cretaceous La Buitrera locality (Candeleros Formation, Cenomanian-Turonian) indicates that this diversification of non-tribosphenic cladotherians is an event that has its roots in the relatively isolated situation of South America during the Early Cretaceous (Rougier and Apesteguía, 2004). The record of Australosphenidan mammals in the Jurassic Cañadón Asfalto Formation (Rauhut et al., 2002; Martin and Rauhut, 2005; Forasiepi et al., 2004a,b; Rougier et al., 2007a,b) and of specialized cladotherians in the Early Cretaceous La Amarga Formation (Bonaparte, 1986a,b,c; Rougier et al., 1992) indicates that strong and dramatic changes occurred in the mammalian composition at least between the Early Cretaceous and the early Late Cretaceous (see also Pascual and Ortíz-Jaureguizar 2007). The Jurassic australosphenidans might represent a stage on their own without any clear link to those of the Early or Late Cretaceous. Our knowledge on the mammalian succession in the South American area is still too precarious to understand the causes of these seemingly distinct faunas. We are in the early stages of trying to identify the major players. The advent of tribosphenic mammals (i.e., metatherians and eutherians) marks a dramatic change late in the Cretaceous (Bonaparte, 1986c; Bonaparte and Kielan-Jaworowska, 1987; Bonaparte and Pascual, 1987; Pascual et al., 2001) by initiating the decline of non and pre tribosphenic taxa, which would be completed early in the Paleogene; by the Riochican, no remnants of the Mesozoic mammalian fauna are found in South America. This process of faunistic change is what Pascual et al. (2001) called “The First Great Turnover” as a counterpart to “The Second Great Turnover,” which involved those mammals that participated of the “Great American Biotic Interchange” during the Late Cenozoic (see Stehli and Webb, 1989). This is a most unfortunate choice of name because it explicitly states that the Late Cretaceous-Early Tertiary event is the “First.” In the first place, it is philosophically impossible to know if this is the first of such momentous events, particularly when the South American record is so incomplete; second, there is ample emerging evidence that the Jurassic Fauna is at least as distinct from that of the Late Cretaceous as this last one is from that of the Paleocene. Referring these events to the time when they occurred, for example “late Cretaceous-Paleocene turnover,” might not be as flamboyant but is a more practical and accurate nomenclature. The Paleocene Punta Peligro fauna (Peligrense SALMA *sensu* Pascual and Ortíz Jaureguizar, 1990) is formed by a mixture of condylarths and metatherians with gondwanatherians, mesungulatiid (peligrotheriids) dryolestoids and monotremes. The Peligrense constitutes the youngest undoubted record for the gondwanatherians (a mandible assigned to Gondwanatheria was recovered from the Eocene from Antarctica but because it has no teeth in it, this assignment is quit uncertain; Goin et al., 2006) and dryolestoids worldwide; they are represented in this fauna by highly autapomorphic taxa. The monotremes are uncertain members of the South American Mesozoic radiation. They might be a link to the Jurassic australosphenidan diaspora (Luo et al., 2002; Kielan-Jaworowska et al., 2004; Rougier et al., 2007a) or they could have an origin among bizarre dryolestoids (Bonaparte, 1990). However, their sole record in the Paleocene Peligrense makes also possible that they are an extra- South American

faunal elements reaching this continent at the end of the Mesozoic or Early in the Cenozoic. If any weight can be placed on the fossil record, the extra-South American origin of monotremes is supported by the finding of Early Cretaceous basal monotremes in the Australian domains of Gondwana (Rich et al., 2001, 2002, 2005; Rich and Vickers-Rich, 2004). The highly localized monotreme record highlights the provincial distribution of the Gondwana fauna, which by the early Cretaceous was already partitioned in segments with restricted connections. Extrapolating from a few Patagonia localities seems problematic at present for Gondwana, let alone for the South America.

#### 4.2. The Mesungulatiid Diversity

In addition to Mesungulatiidae (Bonaparte, 1986a), monotypic families were coined to include *Reigitherium* from the Cretaceous of Los Alamitos and *Peligrotherium* from the Paleocene of Punta Peligro (Reigitheriidae Bonaparte, 1990; and Peligrotheriidae Bonaparte et al., 1993 respectively). All three families share many derived features that unequivocally cluster them in a monophyletic group (Rougier and Páez Arango, 2007). Among these features are the presence of well developed cingula on upper and lower molari-forms, the presence of anteroposteriorely compressed roots, and presence of supernumerary (more than two) roots on the last premolar position. *Peligrotherium* and *Reigitherium*, in turn, share further derived features to the exclusion of *Mesungulatum*, such as the elevation of the cingula to the level of the occlusal surface, development of relatively high crowns, presence of accessory cusps on the lingual aspect of the lower molars and buccal aspect of the upper molars. As far as it can be reconstructed, the dental formula in *Mesungulatum* and allies, *Peligrotherium* and *Reigitherium*, seems to include two premolars and three molars, in addition to a molarized tooth that could be either an ultimate complex premolar or a molar.

We therefore include *Mesungulatum*, *Reigitherium*, *Peligrotherium*, the taxa from La Colonia Formation, and the material described here under Mesungulatiidae because the creation of redundant monotypic taxonomical categories within a monophyletic group is noninformative and methodologically problematic. In any case, under any view of the diversity of the *Mesungulatum* and allies it is certain that *Mesungulatum* and *Mesungulatum*-like taxa constituted an important group of omnivores-herbivores in the Mesozoic mammalian fauna, represented by taxa that ranged from small to minute (like the late Cretaceous *Reigitherium*), to the relatively large dog-sized *Peligrotherium* in the Paleocene. What is known of the group suggests that mesungulatiids gain in size in the younger strata. *Mesungulatum* from Los Alamitos Formation is a medium sized mammal, those from La Colonia Formation are about 30% larger (Rougier et al., *in press*), and *Peligrotherium* from the Paleocene Salamanca Formation is even larger. *Peligrotherium* is found in association with basal litopterns (Bonaparte and Morales, 1997) and large sized condylarths like *Escribania* and *Raulvaccia* (Bonaparte et al., 1993), which also had bunodontid dentitions. The conspicuous hypertrophy of the last premolar/first molar position of mesungulatiids (as represented by mesungulatiids from La Colonia Formation and *Peligrotherium*) is paralleled in the Late Cretaceous-Paleocene by periprythichid condylarths (Archibald, 1998) and stagodontid metatherians (Clemens, 1966; Fox and Naylor, 1986), probably corresponding to some global change in dietary availability.

#### 4.3. Comparisons among Late Cretaceous mammalian localities from Argentina

Close affinity has been proposed between Allen's and Los Alamito's faunas, based on non-mammalian vertebrates (Martinelli and



Forasiepi, 2004a,b). The similarities extend now to the mammalian components. The presence of ferugliotheriids, mesungulatids, *Groebertherium*, *Brandonia* and *Barberenia* in both localities in addition to the previously known vertebrate remains indicates a probably penecontemporaneous deposition (see Leanza et al., 2004 among other authors). Both Allen and Los Alamitos formations are an expression of an epeiric environment in which marginally more terrestrial facies were deposited, resulting in the mammalian fauna collected in Los Alamitos and Cerro Tortuga. The precise correlation between these two localities is not possible at present; they are, however, part of the same communities that flourished on the shores of the same Rocanense sea. At the time being, the lack of a suitable potential ancestor bars the determination of plesiomorphic states, so the comparison of the mammals from both localities does not allow determining which of these faunas is more generalized than the other. Hence, classic biostratigraphy cannot be applied.

The Late Cretaceous La Colonia Formation (Ardolino and Delpino, 1987) and its equivalents (Puesto Escobar Formation, Ardolino and Franchi, 1996) are widely distributed in Central Chubut province, several hundred kilometers S-SW of both Los Alamitos and Cerro Tortuga. The La Colonia fauna is also the result of the Late Cretaceous marine transgression that fragmented the terrestrial environments of Patagonia. The facies suggest a relatively deep peritidal environment; most fossil vertebrates at La Colonia are found in lenses resulting from the incoming of continental vertebrates into a marine environment. The specimens are transported, in many cases rounded, reflecting a relatively distant source, which would result in a strong preservational bias affecting our sample. Despite the over three hundred mammalian specimens collected the La Colonia, mammalian faunal diversity is relatively poor (Rougier et al., in press): two forms very close to *Mesungulatum*, *Reigitherium*, and a multituberculate (Kielan-Jaworowska et al. 2007) are present. The mesungulatids from La Colonia are larger than those from Los Alamitos and Cerro Tortuga and appear to be more derived, suggesting that La Colonia deposits are slightly younger than those from Los Alamitos or Allen formations. Absolute dates are unknown for all these mammalian Late Cretaceous localities and strict considerations of the age can not resolve the age of these units beyond the Campanian-Maastrichtian interval.

## 5. Conclusions

The mammalian fauna from Cerro Tortuga is similar to that from Los Alamitos at high taxonomical levels, although in most cases, different species are present. The differences involve changes in proportions and relationships of relatively minor morphological features. It is evident that both faunas, Los Alamitos and Cerro Tortuga, about 400 Km apart, are close systematically and temporally. From a paleogeographical point of view it is not surprising to recover similar faunas from two formations that correspond to a penecontemporaneous event occurring in the general framework of the expansion of the epeiric Late Cretaceous Rocanense sea. We suggest here that mesungulatids were major components of Late Cretaceous mammalian fauna occupying a diversity of faunivorous niches. The La Colonia fauna is probably slightly younger than that from Los Alamitos and Cerro Tortuga. The poor mammalian diversity in La Colonia is probably artificial because of preservational bias, while that from Los Alamitos is probably artificially inflated by the recognition of separated species from different dental positions of the same taxa.

The overall composition of the Late Cretaceous fauna can be seen as an extension of a South American, perhaps Gondwanan, radiation manifested at least from the early Late Cretaceous (La Buitrera locality) and concluding in the Paleocene, long after the invasion of tribosphenic mammals in South America, possibly in

the Late Cretaceous. The relationships of these distinctive Late Cretaceous mammalian faunas with those mammals from the Jurassic and Early Cretaceous are at present not evident and might stem from roots of pangeic origin.

The patchy Late Cretaceous South American record, accumulated mostly in Patagonia, cautions against the extrapolation of Patagonian assemblages as a model for South America or West Gondwana.

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