Mammals from the Allen Formation, Late Cretaceous, Argentina

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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 mamifero del Cretacico Argentino, Campaniano-Maastrichtiano, (Condylarthra). Ameghiniana 21, 177–183] leads to a reassessment of mesungulatid 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 epiric 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 1800’s (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; Gello and Pascual, 2001; Rougier et al., 2000, 2001, 2007a,b; Rauhut et al., 2002; Martin and Rauhut, 2005; Gurovich, 2006; Pascual and Ortiz-Jaureguizar, 2007).
Los Alamos has had an unparalleled impact on our appreciation of Cretaceous South American faunas. It was not until Pascual and collaborators explored the 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 (Casadio, 1999; Wilson and Arens, 2001; Casadio et al., 2005). This unit, widely distributed in northern Patagonia, 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 ferugliotheriids and sudamericts (Bonaparte, 1986a,b, 1990; Bonaparte et al., 1989; Sigogneau-Russell, et al., 1991; Krause et al., 1992; Kielen-Jaworowska and Bonaparte, 1996; Kielen-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 Ortiz-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 Pallado (Cañadón Asfalito) (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 Volaticotherium (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; Kielen-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 Ortiz-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 sudamericts, 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 Ortiz-Jaureguizar, 2007).

Therians are dominant in the South American Early Paleogene record. However, survival of lineages with an old Mesozoic pre-therian ancestry occur in the Paleocene of Salamanca Formation, where dryolestoids and the enigmatic gondwanatherians are still important components, coexisting side by side with monotremes, didelphid 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 Gulsano, 1990). During the Late Campanian and Early Maastrichtian, the Neuquen 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–Cenomanian Neuquen 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 Neuquen 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 (Casadio 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, Neuquen 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 $37^\circ$S by marginal marine facies. Legarreta et al. (1989) suggested that this event reached northwards into the Malargüe area about $36^\circ$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 (Casadio, 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 (Casadio, 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 $37^\circ$S. This can be inferred from the thickness of the evaporites recorded in the Auca Mahuida, Lago Pellegrini and Aguara areas.

The upper beds of the Allen Formation exposed at Barda Baya show evidence of an important sub-aereal exposure event (Casadio, 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.*, *Biomorphicaria* *sp.* and *Paleoanculosa sp.*), dinosaur eggshells, coprolites (Parras et al., 2004), and the mammal remains studied herein, as well as fish, snake vertebrae (*Apesteguia* and Rougier, 2007; Gómez et al., 2008), and chelid turtles. The turtles are similar to those described from the Los Alamitos Formation (Brock, 1987; Brock 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, 1993; Martinelli and Forasiepi, 2004a, b; Gómez et al., 2008) and we believe they are all close in age. La Colonia Formation has large size mesungulatids (Rougier et al., 2001a, b, 2002; 2) that seem to correspond with later large sized dryolestoids from the Paleocene Salamanca Formation (i.e. *Pelgromotherium*). We believe that it is possible to argue for a slightly younger age for La Colonia Formation with respect to either Allen or Los Alamitos formations, with the latter two closer to each other in age. The Los Alamitos 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) ($39^\circ 47^\prime 02.1^\prime S; 66^\circ 42^\prime 17.9^\prime W$) soaked in water, and then screen washed either at the local museum in Lamarque or at “El Matuasto” ranch (GPS) ($39^\circ 46^\prime 53.65^\prime S; 66^\circ 33^\prime 44.5^\prime W$) 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
Family: Mesungulatidae Bonaparte, 1986a

Genus *Mesungulatum* Bonaparte and Soria, 1985

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

*Mesungulatum lamarquensis* sp. nov.

Figs. 2-4f

Derivation of the specific name. *lamarquensis*, a latinized version of Lamarque, the largest city in the area, and home of the Museo.
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. Mesungulatid 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 taps lingually, having a more distinct triangular outline. The mesial and distal cingula culminate lingually in robust and distinct cuspsules in M. lamarquensis, but they are not as developed as 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 species 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 mesungulatids (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 mesungulatids. 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 mesungulatids, the stylocone occupies a mid-way position between the mesial and distal stylar 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 paraconal apex. The preparacrista (preparacrista) extends labially in the direction of the paracone, 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 paracone. The paracone is conical and moderately procumbent, somewhat buccolingually compressed, and forming a rudimentary parastylar hook that projects medially from the line determined by the preparacrista. There is no distinct metacone in mesungulatids 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 cup. The metacone is fully separated from the postparacrista, and closely abuts the stylocone. The buccal aspects of all the stylar cusps are rather vertical and do not bulge much buccally; an ectoflexus is lacking. Large cingula are present medially 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 paracone, whereas the distal one does not extend past the distal cingular cup. 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 adorned by numerous cuspsules. 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 mesungulatid; 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
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:** *Groebbletherium* Bonaparte, 1986

**Type species.** *Groebbletherium 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.** *Groebbletherium 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 parastylar forms a small hook. A centrocrista is poorly defined and, if at all 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 *Groebbletherium* 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 meso-crista climbs the buccal surface of the paracone, but it is barely distinguishable. No metacone is present as individual cusp, and
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 two species become objective synonyms. The specimens found at Allen Formation share with G. stipanicicii 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 stylar area, 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
There are, however, a few differences between the lower specimen and the upper molar of *Brandonia intermedia* size to *Brandonia* commonly seen in Laurasian dyolestoids. The talonid cusp is interlocked with cusps developed than its mesial counterparts and slightly posteriorly (perhaps homologous of the hypoconulid of later therians; Crompton, 1971; Bonaparte, 1990). This distal cingular cusp is more extended. The talonid cusp is interlocked with cusps lingualmost extension of the metacristid, and thus they 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 cingular 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 dyolestoids.  

**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 metastyle, 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.

**Horizon and locality.** Microvertebrate layer, Cerro Tortuga, Allen Formation, 38 m below the top of the Allen Formation.
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 mesiobuccally 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 paracone, 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 paracone, ending distal to it. The paracone 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 paraconid. The paraconid hook is relatively small, much smaller than in the similar Barberenia araujoae (Bonaparte, 1990). The cingulum extending distolingually from the paracone 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 paracone 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; Kielen-Jaworowska et al., 2004). This supposition is mainly based on the similarity between Barberenini 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 paracone 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; Kielen-Jaworowska et al., 2004) raised the possibility that the molars of Barberenia were molariform premolars, perhaps deciduous ones, of other Los Alamitos 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 Groebertherium, and we agree that they might represent deciduous teeth, or alternative molariform positions of other dryolestoids from Los Alamitos, 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 para-

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 decid-

uous 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 euitherians such as zalambdalestids and to a lesser degree asiotheres.

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. Ferugliotheriidi similar in size to Ferugliotherium, differs from species of the Los Alamitos 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 ferugliotheriidi 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 buc-

codistal 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

Fig. 9. Stereo SEM photographs in occlusal view of the type specimen of Trapalco-

therium matuastensis MML-Pv 16, left lower first molar (A) and B interpretative drawing. The arrows point anterior and lingually.
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 anterior 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 the interpreted homologue 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 pronoucnedly 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 windhaueani: (1) the mesial triangle in MML-Pv 16 is narrow in contrast to the big and open one from F. windhaueani; (2) the second furrow (first one behind the mesial triangle) is almost transverse in MML-Pv 16 and oblique in F. windhaueani; (3) the second lingual cusp in MML-Pv 16 has two ridges that form a rather triangular shape, not seen in F. windhaueani; (4) the molar in MML-Pv16 is proportionately shorter and wider than that of F. windhaueani, (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. windhaueani. There is, therefore, place for a bulging platform mesial and lingually in T. matuastensis, which is poorly developed in F. windhaueani MACN-RN 253 or in the well worn MACN-RN 174 (originally assigned to “Vucetichia gracilis,” now considered junior synonym from F. windhaueani 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 sudamericans, 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 sudamericans should be present in both Late Cretaceous localities from Río Negro Province. Recently, Kielen-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 ferugliotheriids are either multituberculates or closely related taxa and would support the earlier interpretation by Kielen-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 ferugliotheriids.

**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 titanosaurids, large and advanced non-saltasaurine eutitanosaurs, highly derived and large carnosaurs abelisaurid theropods, ornithure and non-ornithure ornithorhynchus birds, hadrosaurid and ankylosaurian ornithischians, “Madssoidae” snakes, non-eiloenodontinae splendodontids, chelid and meiolaniid turtles, pterids and lepadodactylids anurans, and chordrichthyes 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; Alaminian 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; Kieilen-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 triposphenic 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 Rocaense sea in southern South America (Andreas et al., 1989; Casadio, 1998; Casadio 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 Rio 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 Apesteguia, 2004). The record of Australosphenidian mammals in the Jurassic Cañadón Asfalto Formation (Rauhut et al., 2002; Martin and Rauhut, 2005; Forasiepi et al., 2004a; 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 australosphenidians 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, 1992) and the new fauna is paralleled in the Late Cretaceous-Paleocene turnover, might not be as primitive as it was once thought to be, and this assignation is quit uncertain; Goin et al., 2006) and dryolestoids worldwide; they are represented in this fauna by highly autapomorphic taxa. The monorophytes are uncertain members of the South American Mesozoic radiation. They might be a link to the Jurassic australosphenidian diaspora (Luo et al., 2002; Kielen-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 Peli- grenas 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 Mesungulatid Diversity

In addition to Mesungulatidae (Bonaparte, 1986a), monotypic families were coined to include Reigitherium from the Cretaceous of Los Alamitos and Peligrotherium from the Paleocene of Punta Peligro (Reigitheridae Bonaparte, 1990; and Peligrotheridae Bonaparte et al., 1993 respectively). All three families share many derived features that unequivocally cluster them in a monophyletic group (Rougier and Pérez Arango, 2007). Among these features are the presence of well-developed cingula on upper and lower molars, which also had bunodontid dentitions. The conspicuous hypercrown of the last premolar/first molar position of mesungulatids seems problematic at present for Gondwana, let alone for 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 (see Stihle 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, in the paleoecogeographic it is 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 flambouyant as it is more practical and accurate nomenclature. The Paleocene Punta Peligro fauna (Peligrene SALMA sensu Pascual and Ortíz Jaureguizar, 1990) is formed by a mixture of condylarths and metatherians with gondwanatherians, mesungulatid (peligoritheriids) dryolestoids and monotremes. The Paleogene constitutes the youngest undoubted record for the gondwanatherians (a mandible assigned to Gondwanantheria was recovered from the Eocene from Antarctica but because it has no teeth in it, this assignation is quite 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 australosphenidian diaspora (Luo et al., 2002; Kielen-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 Peligre makes also possible that they are an extra-South American
The similarities extend now to the mammalian components. The presence of ferugliothériids, mesungulatids, Goebertherium, 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 Alamos 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 bioestratigraphy 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 Alamos and Cerro Tortuga. The La Colonia fauna is also the result of the Late Cretaceous marine transgression that segmented 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 Alamos and Cerro Tortuga and appear to be more derived, suggesting that La Colonia deposits are slightly younger than those from Los Alamos 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 Alamos 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 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 Alamos and Cerro Tortuga. The poor mammalian diversity in La Colonia is probably artificial because of preservation bias, while that from Los Alamos 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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References


