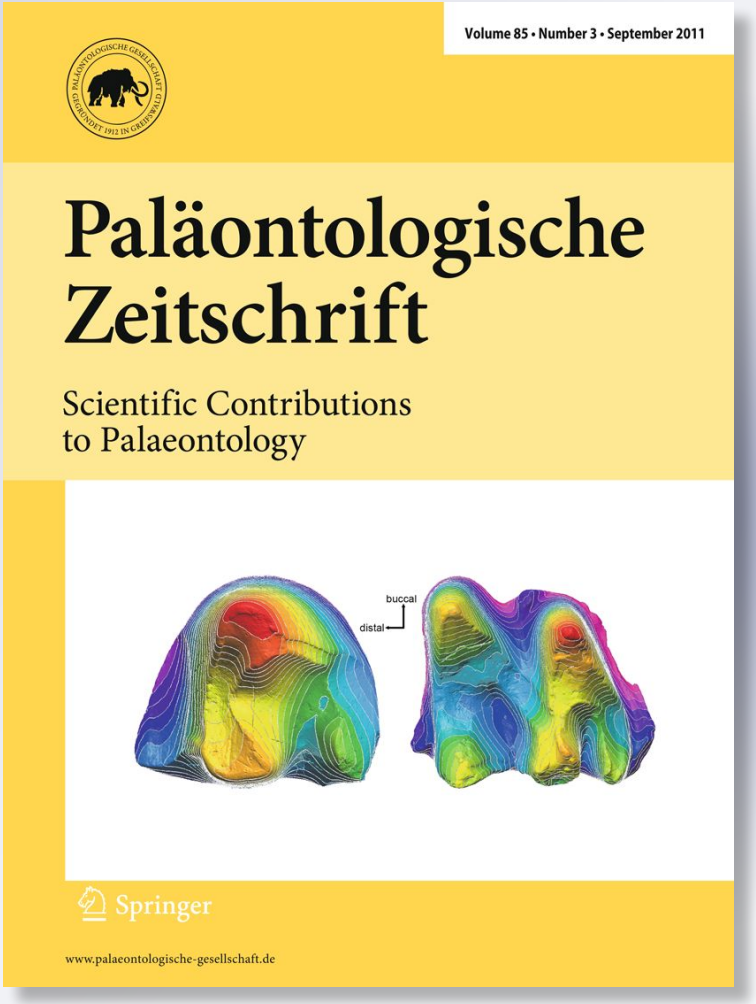
New remains of the dryolestoid mammal Leonardus cuspidatus *from the Los Alamitos Formation (Late Cretaceous, Argentina)*

Laura Chornogubsky

Paläontologische Zeitschrift
Scientific Contributions to Palaeontology

ISSN 0031-0220
Volume 85
Number 3

Paläontol Z (2011) 85:343-350
DOI 10.1007/s12542-010-0095-4



Springer

Paläontol Z (2011) 85:343–350
DOI 10.1007/s12542-010-0095-4

SHORT COMMUNICATION

New remains of the dryolestoid mammal *Leonardus cuspidatus* from the Los Alamitos Formation (Late Cretaceous, Argentina)

Laura Chornogubsky

Received: 8 September 2010 / Accepted: 21 December 2010 / Published online: 27 January 2011

Abstract The great diversity of mammals from the Los Alamitos Formation (Campanian–Maastrichtian) in Río Negro Province, Argentina has provided significant information about the evolution of South American dryolestoids. Among these mammals the alleged dryolestid *Leonardus cuspidatus* Bonaparte was described based on a fragment of maxilla with four molariforms. A right mandibular fragment with two molariforms from the same site as the maxilla is here assigned to *L. cuspidatus*. The lower molariforms are compatible in the expected morphology with those from the holotype. Even though referred to Dryolestidae, *Leonardus* shows unique features: (1) the presence of a huge and dome-like stylocone, disconnected and more centrally placed from the other cusps than in other dryolestoids such as *Groebertherium*, but contacting the preparacrista in the first preserved molar; (2) the absence of cingulae in both upper and lower molars, the latter being similar in shape to the former; (3) the presence of three roots in at least one of the lower molars, which has only been documented in the mesungulatid *Coloniatherium* for the m1. These characters confirm the diversity and uniqueness of the South American Mesozoic mammals.

Keywords Dyolestoidea · South America · Patagonia · Late Cretaceous

Kurzfassung Die große Säugetiervielfalt der Los Alamitos-Formation (Campanium–Maastrichtium, Río Negro Provinz, Argentinien) leistet einen erheblichen Beitrag zum Verständnis der Evolution der südamerikanischen Dryolestoiden. Basierend auf einem Oberkieferfragment mit vier Molaren, wurde auch der angebliche Dryolestidae *Leonardus cuspidatus* Bonaparte aus dieser Lokalität beschrieben. Ein weiteres Kieferfragment mit zwei Zähnen wird ebenfalls *L. cuspidatus* zu geordnet. Die unteren Molaren zeigen die nach dem Holotypus zu erwartende Morphologie. Obwohl *Leonardus* den Dryolestidae zugeschrieben wird, weist dieser einige einzigartige Merkmale auf: (1) das Vorhandensein eines prominenten und kuppelförmigen Stylocon, der, verglichen mit dem anderer Dryolestoiden wie beispielsweise *Groebertherium*, stärker von den anderen Höckern isoliert ist und zentraler liegt, obwohl dennoch beim ersten erhaltenen Molaren ein Kontakt des Stylocon mit der Präparacrista auftritt; (2) das Fehlen der Cingulide sowohl in den oberen als auch in den unteren Molaren, wodurch letztere in der Form den oberen Molaren ähneln; (3) das Vorhandensein von drei Wurzeln bei mindestens einem der unteren Molaren, was bisher nur für den m1 des mesungulatiden Dryolestoiden *Coloniatherium* beschrieben wurde. Diese besonderen Merkmale unterstreichen die Diversität und Einzigartigkeit der mesozoischen Säugetierfauna Südamerikas.

Schlüsselwörter Dyolestoidea · Südamerika · Patagonien · Spätkreide

L. Chornogubsky (✉)
CONICET. Sección Paleontología de Vertebrados,
Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av. Ángel Gallardo 470,
C1405DRJ Buenos Aires, Argentina
e-mail: lchorno@macn.gov.ar

Introduction

Among the Cretaceous mammalian faunas from South America, the one from the Los Alamitos Formation (Río

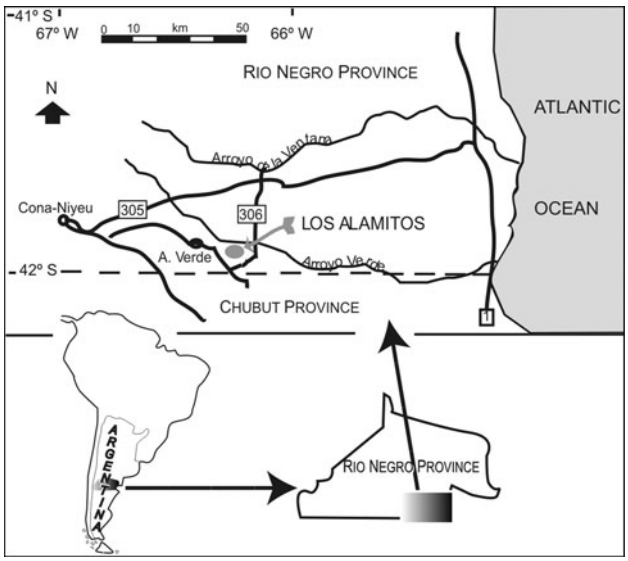


Fig. 1 Map of Río Negro Province showing the location of the Los Alamitos Formation

Negro Province, Argentina; Andreis 1987) (Fig. 1) provides significant information about mammalian evolution and diversity (Bonaparte and Soria 1985; Bonaparte 1986, 1987, 1990, 1992, 1994, 2002). That evolution was significantly different from what took place in the Northern Hemisphere, which shows the existence of dissimilar patterns in both Northern and Southern landmasses and, at the same time, indicates a strong biogeographic isolation that may have conditioned this differential evolution (Bonaparte 1996).

Some of the mammalian taxa represented in the Los Alamitos Formation may be a derived stock of a larger Pangean radiation, which had already disappeared in Laurasia by the beginning of the Late Cretaceous (e.g., Dryolestida Prothero 1981; Symmetrodonta Simpson 1925). However, the interpretation of this fauna has been discussed by several authors through time (see Bonaparte 1986, 1987, 1990, 1994, 2002; Martin 1999; Sigogneau-Russell and Ensom 1998, among others), because the 17 species that have been currently recognized from this locality were based primarily on isolated upper molariforms.

Even though other localities with mammals were found later in the latest Cretaceous of Argentina (Rougier et al. 2009a, b) and Bolivia (Gayet et al. 2001), the diversity shown at Los Alamitos is still the highest.

Among the mammals from Los Alamitos, one particular species is the focus of this paper: *Leonardus cuspidatus*, which was originally represented by a fragment of maxilla including four molariforms, and was attributed to the family Dryolestidae (Bonaparte 1990).

Materials and methods

The material belonging to *Leonardus cuspidatus* was collected in the fieldtrips to Patagonia carried out by a crew of the Museo Argentino de Ciencias Naturales, Buenos Aires, between the years 1982 and 1986, with the financial help of CONICET and a National Geographic Society grant. All of them were lead by Dr. J.F. Bonaparte.

The cusp nomenclature follows Rougier et al. (2009a, Figs. 2, 6). In this work, the trigon basin refers to the "primary trigon," not homologous with the true trigon basin of tribosphenic molars (see Kielan-Jaworowska et al. 2004; p. 374 and literature cited).

Abbreviations: L: length; W: width.

Institutional abbreviations: MACN-RN: material housed at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Río Negro Province collection.

Systematic paleontology

Mammalia Linnaeus 1758
Holotheria Wible et al. 1995
Cladotheria McKenna 1975
Dryolestoidea Butler 1939
?Dryolestidae Marsh 1879
Leonardus Bonaparte 1990
Leonardus cuspidatus Bonaparte 1990

Holotype MACN-RN 172, a fragment of a left maxilla with four molariforms, and parts of two pairs of alveoli (one anterior to the molariforms and the other one posterior) (Fig. 2a–c).

Referred material MACN-RN 1097, a right mandibular fragment with two molariforms (Fig. 3a–d).

Provenance Median section of the Los Alamitos Formation, west slope of the Cerro Cuadrado, Arroyo Verde, Río Negro Province, Argentina (see Andreis 1987).

Measurements See Table 1.

Description

The fragment of left maxilla, the holotype (Fig. 2a–d), has four distinctly separated molariform teeth and alveoli in both the anterior and posterior ends of the maxilla (the posterior preserves part of a root of another tooth). *L. cuspidatus* had at least five upper molariforms. The molariforms are set in a labially convex row. All the molars are affected by wear. The first is more worn than the second, the latter is more worn than the third, and finally the last is the least worn of the row. The main features of the

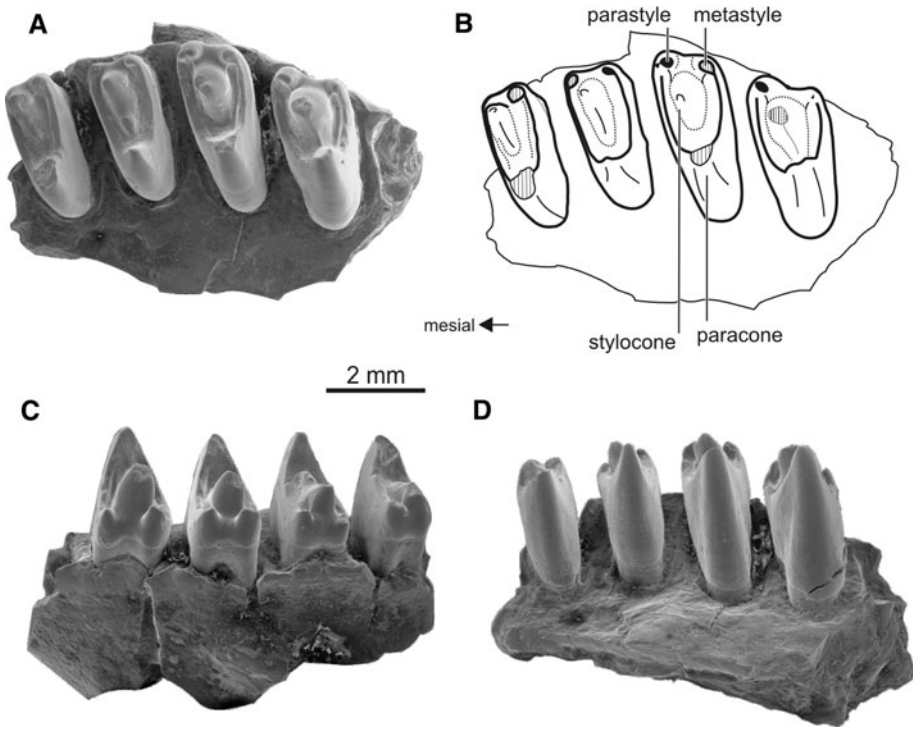


Fig. 2 MACN-RN 172 (holotype of *Leonardus cuspidatus*). **a**, **c–d** SEM photographs in **a** occlusal, **c** labial, and **d** lingual view. **b** *Line drawing* of the occlusal view. *Straight lines* in an area represent breakage

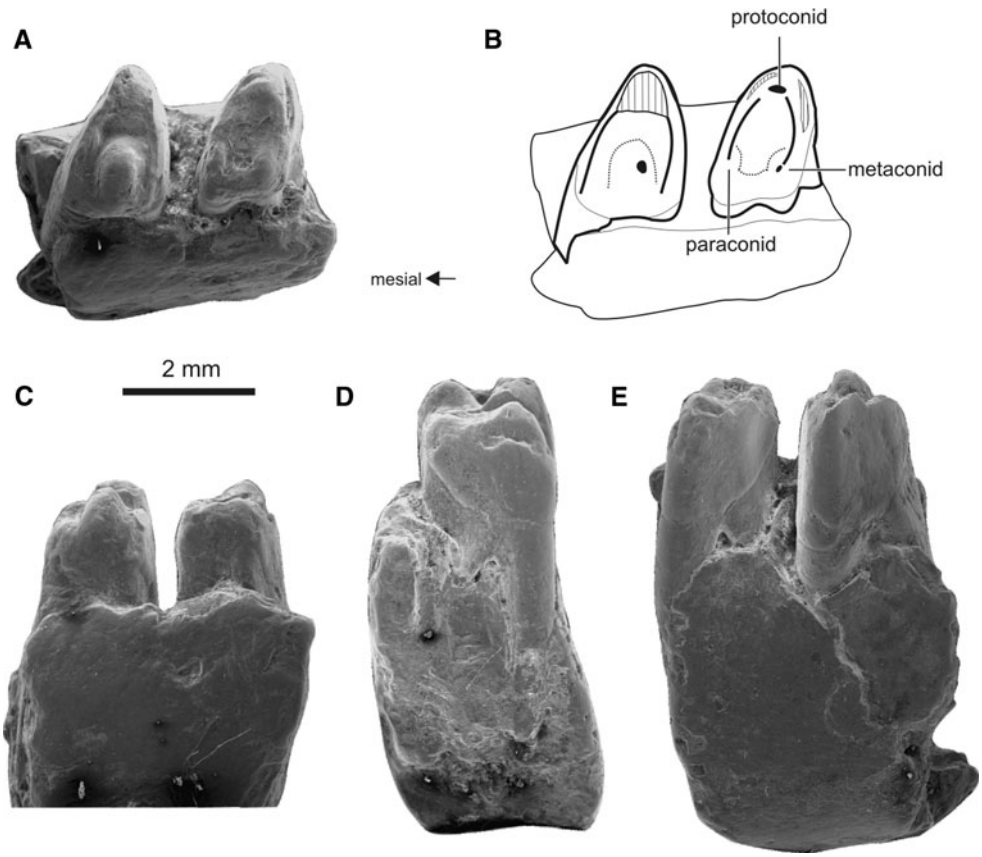


Fig. 3 MACN-RN 1097, referred to *Leonardus cuspidatus* **a**, **c–e** SEM photographs in **a** occlusal, **c** lingual, **d** posterior, and **e** labial view. **b** *Line drawing* of the occlusal view. *Straight lines* in an area represent breakage

molar crowns are that they are mesiodistally compressed, widely separated one from the other, and have a smooth ectoflexus, which is more evident in the last three molars. The anterior edge of the molars is oblique to the axis of the maxilla, and the posterior edge is essentially perpendicular. The molariforms have four cusps, of which the paracone is

Table 1 Teeth measurements

Specimen	Description	*L* (mm)	*W* (mm)
MACN-RN 172	Maxilla w/4 molariforms (holotype)	–	–
	1st molar	1.5	2.15
	2nd molar	1.25	2.5
	3rd molar	1.1	2.1
	4th molar	1	2.3
MACN-RN 1095	Dentary w/2 molariforms	–	–
	1st molar	1.5	2.25
	2nd molar	1.3	2.15

the highest (Fig. 2). The parastyle is in the mesiolabial margin, and the metastyle is distolabial. The parastyle is larger than the metastyle and does not form a parastylar hook as is usually seen in Laurasian dryolestoids. Between the para- and metastyle, and occupying most of the trigon basin, is the large, domelike stylocone (centrocone *sensu* Bonaparte 1990). A smooth median ridge runs from the center of the stylocone to the paracone (Bonaparte 1990). Both the para- and metacrista are sharp and subequal in hight.

The first preserved molariform is the shortest and most strongly affected by wear. It has a small metastyle and a huge, domelike stylocone connected to the preparacrista. A parastyle is not evident, and it could be fused with the stylocone or directly attached to the preparacrista (and removed by wear). Both the preparacrista and the postparacrista are low.

The second preserved molariform in the series is wider than the first one. Its labiolingual length is twice that of the mesiodistal. The metastyle and parastyle are subequal in size. The stylocone is more compressed mesiodistally, but it has, as in the last molar, a median ridge that ends at the base of the paracone. Both the preparacrista and the postparacrista are low.

The third molariform is similar to the second one, but markedly wider. The para- and metastylar regions are subequal in size with the parastyle more lingually placed than the metastyle. The paracone, with its broken tip, is noticeably larger than the paracone of the preceding tooth, and the stylocone is more centrally located in the trigon basin than in the last molariform. It does not have a median ridge.

The last preserved molariform is almost unworn, and is the longest in its mesiodistal diameter. The parastyle is larger and more labially placed than the metastyle. Between them but centrally placed is the stylocone, which has a distinct median ridge.

The new fossil assigned to *Leonardus cuspidatus*, MACN-RN 1097 (Fig. 3a–e), is a fragment of a right mandible preserving two molariforms. Assignment to this taxon is based mainly on the general aspect of the molars, mesiodistally compressed and widely separated from one to the other, and the general size of both molars and mandible, although the lower teeth are slightly larger than those of the holotype. They show no cingulid of any kind, and the crown morphology is similar to those of the upper molars in having a central large cusp (the metaconid) and being almost symmetrical in occlusal view.

The dentary fragment, though broken on its mesial and distal ends, preserves its dorsoventral extension that forms a ventral rounded edge, and lacks foramina or a Meckel′s groove. The first preserved molariform is triangular in occlusal view and somewhat wider than the posterior. It exhibits a large, labially set protoconid. Lingually, the paracristid does not end in a paraconid, but instead reaches the mesioligual corner of the tooth. The dome-like metaconid does not reach the metacristid and is more mesially placed. The metacristid is similar to the paracristid, reaching the distolingual corner of the tooth. The molariform has two roots: a small, mesial one, below the paraconid, and a much larger distal one below the protoconid and metaconid. Both roots are extremely compressed mesiodistally.

The second preserved molariform is more mesiodistally compressed then the mesial. The crown is damaged, but it appears that it has no cusps except for the protoconid, and the cristids do not connect with any cusps lingually. This molar possesses three mesiodistally compressed roots, the largest one being the labial, and two lingually placed, subequal roots.

Comments

The assignment of the mandibular fragment to this taxon is mainly based on the similar occlusal shape of the molariforms, as well as their spaced placement. The lower molariforms, with symmetrical cuspless cristae and a large central cusp, mimic the form of the upper molars. This latter pattern and the short diastema between upper and lower teeth are suggestive of an alternate occlusion. The worn surfaces of the shearing crests of upper and lower molars imply an orthal movement during mastication. The

wear facets on the mesial and distal walls of the upper molariforms suggest tooth-to-tooth shear. The leading edges of the shearing surfaces on both upper and lower molariforms are concave and suggest that this wear is produced by food particles held during molar occlusion. Finally, the mesiodistal compression of the molars and the wide spaces between them suggest the presence of a lateral component of movement as well, and the rest of the crown may contact only food during mastication.

It has been argued that the maxillary fragment of *Leonardus* was originally misinterpreted by Bonaparte (1990) as being from the left side (Chornogubsky 2003; Paez Arango 2008), mainly because of a small fragment of the origin of the zygomatic arch and the orientation of the transverse axes of the teeth. Paez Arango (2008) based her conclusions on three observations. If the maxilla is from the right side, as she pointed out, then: (1) "the major [buccolabial] axis of the molars is directed anteromedially" as in other dryolestoids such as *Henkelotherium* or *Drescheratherium* (Krebs 1991, 1998); (2) "the wear diminishes anteriorly if Bonaparte's interpretation is followed, or posteriorly if the interpretation proposed here is accepted"; (3) "[t]he preserved root of the zygomatic arch is difficult to interpret using Bonaparte's interpretation, but it appears to be directed posteriorly according to my interpretation." Concerning the first observation, the major axes of the teeth are preponderately distally oriented, as Paez Arango argued, however not all four teeth are equally oriented, the first being more perpendicular to the longitudinal axis of the maxilla than the last two (Fig. 2). This character could indicate that the orientation was related to the labial convexity of the maxilla. Nevertheless, the anteromedial orientation of the transverse axes of the molars are not universal, being variable among different groups of mammals (see, for example, specimen MACN-RN 166 of the dryolestoid *Barberenia araujoae* Bonaparte 1990: p. 71, Fig. 6). The second argument of Paez Arango (2008) is mistaken because the wear is exactly opposite to the situation she described (Fig. 2): on the first molar in Bonaparte's interpretation, which is followed here, the tip of the paracone and the stylocone are broken; however, it can be seen that it is more worn than the second, and that the least worn tooth is the last molar of the row. This wear pattern is the expected one following the eruption of the molars if the maxilla is interpreted as a left one. Finally, the location of the zygomatic arch is not conclusive to argue against the original orientation, since only the mesial part of the arch is preserved and the orientation of the distal part of the zygomatic arch cannot be determined from what remains.

Another character cited to falsify the original orientation is related to the mesiodistal length of the teeth. The first is shorter than the last in Bonaparte's interpretation (Chornogubsky 2003). This is, in fact, an exceptional feature of *L. cuspidatus*. However, the compressed first molar shows the common feature of a stylocone that is united to the preparacrista, as expected for a typical dryolestoid.

Finally, in dryolestoids (and other mammals as well) the parastyle is usually more labial than the metastyle (e.g., *Comotherium* Prothero 1981), but these cusps may be aligned on the first molars of the row (as in *Dryolestes leiriensis* Martin 1999). This is the case of *L. cuspidatus* in which the first and the second preserved molariforms have an almost aligned para- and metastyle, but the parastyle is more labially placed in the two last preserved molariforms, particularly in the last one (Fig. 2a). Moreover, in many dryolestoid mammals the last molars have the metastyle in a very lingual position, and it is not present in some (e.g., *Mesungulatum houssayi* Bonaparte and Soria 1985). The last molar preserved in *Leonardus cuspidatus* (even not the last) shows a metastyle more lingually placed, reinforcing the original interpretation of the orientation of the maxilla by Bonaparte (1990).

Discussion

Molar pattern of *Leonardus cuspidatus* as compared with other dryolestidans

Dryolestid upper molars are triangular in occlusal view and mesiodistally compressed. The paracone is placed lingually. The stylar cusps are labial: the parastyle (mesial) generally forms a parastylar hook (Simpson 1929) and the metastyle (distal), which can be doubled (as in *Comotherium* Prothero 1981). The stylocone is located at the buccal end of the preparacrista. The metacrista links the paracone with a small metacone, while the latter is linked with the metastyle. When the metacone is not present (as in *Donodon* Sigogneau-Russell 1991, *Crusafontia* Henkel and Krebs 1969, and the South American dryolestidans except for *Baberenia araujoae*), the crest is, in fact, the postmetacrista. In *Leonardus cuspidatus* there is neither a metacone nor a parastylar hook, and the stylocone is not linked to the preparacrista. This last trait, though not common, is present in other dryolestoids such as *Laolestes* Simpson 1927, *Mesungulatum*, and *Grobertherium* among others (Bonaparte 1986, 2002).

The general pattern of a typical dryolestid lower molar is characterized by three main cusps: the protoconid (labial), and, lingually, the paraconid (mesial) and the metaconid (distal). The metaconid is of about the same hight as the paraconid or is even higher (Prothero 1981), and is in line with the protoconid. This feature and the fact that the paraconid is projecting mesially outlines the characteristic occlusal morphology of dryolestoid lower molars. Another prominent feature in the lower molars is

the strongly reduced talonid, which bears a single cusp. In these molars, two roots are observable; they can be subequal, as in the Paurodontidae (Simpson 1929), or strongly asymmetrical, as in the Dryolestidae, in which the mesial root is considerably larger than the distal (see Prothero 1981; Ensom and Sigogneau-Russell 1998; Martin 1999, among others); in turn, in the Mesungulatidae (Bonaparte 1986), and perhaps Donodontidae (Sigogneau-Russell 1991), the distal root is the largest.

In *Leonardus cuspidatus*, the lower molariforms exhibit a large, rounded metaconid that is not connected to the metacristid, the latter running distal to the former. Moreover, the lower molariform has no trace of a talonid. The roots in the first preserved molariform are uneven, with the anterior one smaller than the posterior one, as in mesungulatids, *Groebertherium*, and perhaps *Donodon*. The distal lower molar of *L. cuspidatus* has three roots; this trait is rare among dryolestoids but also is seen in the m1 of *Coloniatherium cilinskii* Rougier et al. (2009b).

Relationships of Gondwanan Dryolestoids

When Bonaparte (1986) first described *Leonardus cuspidatus*, he assigned it to the Dryolestidae, and initially compared it with *Groebertherium*. He implicitly stated a closer relationship between both of them than with any other dryolestid. Martin (1999) went farther, stating that *Leonardus* was very similar to *Laolestes* in having a large stylocone disconnected from the preparacrista, while also being more derived than the latter because of the relative position of that cusp (more lingual in *Leonardus* than in any other representative of Dryolestidae). He pointed out that, in view of the resemblances between these taxa, the Dryolestidae had a Pangeaic distribution during the Late Jurassic–Early Cretaceous.

Both Martin (1999) and Bonaparte (2002) noted the major role that the African dryolestidan radiation must have played in the South American. No other forms of dryolestidans were known from Gondwana until *Donodon*, from the Lower Cretaceous of Morocco, was described by Sigogneau-Russell (1991). She established some similarities between the former and *Mesungulatum*, in which the stylocone (cusp D according to Sigogneau-Russell 1989) occupied the same relative position, not linked with the preparacrista, and the presence of a well-developed median crest.

Another African form that strongly resembles a dryolestidan from Los Alamitos is *Thereuodon* Sigogneau-Russell 1989, first described as a symmetrodont. This form was compared with "*Barberenia*" because of their similar features: molar proportions and "…the presence of a basin between the parastyle and paracone and another between the paracone and metastyle separated by a crest." (Sigogneau-Russell and Ensom 1998). Although these authors pointed out that one could suggest a relationship between these two forms, they considered these similarities as the product of parallel or convergent evolution, as the Los Alamitos fauna is endemic. Martin (1999) regarded the specimens assigned to both *Thereuodon* and *Barberenia* as deciduous premolars of dryolestidans, a view that was followed by Bonaparte (2002).

Bonaparte (1992, 1994, 2002) also suggested a relationship of *Donodon* with the Los Alamitos *Mesungulatum*, and stated that "…the presence of this species [*Donodon prescriptoris*] in the Early Cretaceous of Morocco…suggests that the Dryolestida of North Africa were related to those from the Late Cretaceous Los Alamitos Formation…" (Bonaparte 1994). He also pointed out that the differences between *Donodon* and *Mesungulatum* (presence of a parastylar hook and absence of cingula in *Donodon*) represent plesiomorphic features in the former (Bonaparte 2002).

Originally, *L. cuspidatus* was assigned to the family Dryolestidae (Bonaparte 1990). This assignment was generally accepted in further papers (see McKenna and Bell 1997; Martin 1999, among others). However, several features unique to *L. cuspidatus* were recognized, such as the absence of a metacone and the presence of widely separated and mesiodistally short molars. Some of these features are only shared with other dryolestids from Los Alamitos, such as the absence of a metacone. Also distinct characters are the absence of a parastylar hook (a feature also observed in *Groebertherium*, *Mesungulatum*, and casamiquelids, where the parastylar region is almost completely reduced) and the presence of a large stylocone, placed between the parastyle and the metastyle, and isolated from the preparacrista. The new mandibular fragment with two molariforms shows differences between *Leonardus* and the Holarctic Dryolestidae. The presence of an anterior root that is smaller than the posterior, both of them mesiodistally compressed, has not been observed in Holarctic Dryolestidae. Instead, it is a character always present in the South American forms (e.g., *Mesungulatum houssayi* Bonaparte and Soria 1985; *Peligrotherium tropicalis* Bonaparte et al. 1993).

Conclusions

Leonardus cuspidatus was originally assigned to Dryolestidae by Bonaparte (1990). However, it has a unique combination of features, some of them comparable to those present in the Holarctic Dryolestidae (e.g., absence of cingula in the upper molars; see above) and others shared with other South American dryolestoids (large stylocone isolated from the preparacrista, absence of parastylar hook

in the upper molars) (Bonaparte 1990). *Leonardus cuspidatus* has also particular characters, such as the position of the stylocone in the upper molars, more centrally placed than in any other dryolestoid, the absence of any kind of cingulid in the lower molars, and the presence of three roots in the second lower molariform preserved in the dentary fragment. The presence of three roots has been only observed in the m1 of *Coloniatherium siliskii* (Rougier et al. 2009b). All these characters make the assignment of *Leonardus cuspidatus* to Dryolestidae doubtful. This mosaic of features linking *L. cuspidatus* to the South American dryolestidan families and also to the Holarctic Dryolestidae may imply a relationship among these two apparently different groups of dryolestoids.

Acknowledgments I want to thank Thomas Martin and an anonymous reviewer whose observations helped to improve the manuscript. I am grateful to José F. Bonaparte, who gave me the opportunity to study the Mesozoic mammals from the Los Alamitos Formation and to Francisco J. Goin. J.F. Bonaparte and Alejandro Kramarz gave me access to the mammal collection of the Museo Argentino de Ciencias Naturales. Guillermo Rougier and Javier N. Gelfo helped me with previous versions of this manuscript. Finally, I wish to thank Simone Hoffmann and Julia Schultz for there help with the German version of the abstract, and to Fabian Tricarico for taking the SEM photographs of the specimens described in this paper.

References

Andreis, R.R. 1987. The late Cretaceous fauna of Los Alamitos, Patagonia, Argentina. Part I- Stratigraphy and Paleoenvironement. In *The Late Cretaceous Fauna of Los Alamitos, Patagonia, Argentina*, ed. José F. Bonaparte, 103–110. Buenos Aires: Revista del Museo Argentino de Ciencias Naturales.

Bonaparte, J.F., and M.F. Soria. 1985. Nota sobre el primer mamífero del Cretácico Argentino, Campaniano-Maastrichtiano, (Condilarthra). *Ameghiniana* 21(2–4): 177–183.

Bonaparte, J.F. 1986. Sobre *Mesungulatum houssayi* y nuevos mamíferos cretácicos de Patagonia, Argentina. *IV congreso Argentino de Paleontología y Bioestratigrafía* 2: 48–61.

Bonaparte, J.F. 1987. The late Cretaceous fauna of Los Alamitos, Patagonia, Argentina. Part VIII- The mammals. In *The Late Cretaceous Fauna of Los Alamitos, Patagonia, Argentina*, ed. José F. Bonaparte, 163–169. Buenos Aires: Revista del Museo Argentino de Ciencias Naturales.

Bonaparte, J.F. 1990. New Late Cretaceous mammals from the Los Alamitos formation, Northern Patagonia. *National Geographic Research* 6(1): 63–93.

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

Bonaparte, J.F. 1994. Approach to the significance of the Late Cretaceous mammals of South America. Berliner geowissenschaftliche Abhandlugen E13. B. Krebs-Festschrift: 31–44.

Bonaparte, J.F. 1996. Cretaceous Tetrapods of Argentina. Münchner geowissenschaftliche, *Abhandlugen (A)* 30: 73–130.

Bonaparte, J.F. 2002. New Dryolestida (Theria) from the Late Cretaceous of Los Alamitos, Argentina, and paleogeographical comments. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 224(3): 339–371.

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

Butler, P. M. 1939. The teeth of the Jurassic mammals. *Proceedings of the Zoological Society of London* 109: 329–356.

Chornogubsky, L. 2003. *Revisión preliminar de los mamíferos de la Formación Los Alamitos* (Campaniano- Maastrichtiano, provincia de Río Negro, Argentina). Tesis de Licenciatura, Universidad de Buenos Aires.

Ensom, P.C. and D. Sigogneau-Russell. 1998. New Dryolestoid mammals from the basal Cretaceous Purbeck Limestone Group of Southern England. *Palaeontology* 41(1): 35–55.

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

Henkel, S. and B. Krebs. 1969. *Zwei Säugetier-Unterkiefer aus der Unteren Kreide von Uña* (Prov. Cuenca, Spanien). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte: 449–463.

Kielan-Jaworowska, Z., Cifelli, R.L., Luo, Z.-X. 2004. Mammals from the age of dinosaurs. In *Origins, evolution, and structure*, 630 pp. New York: Columbia University Press.

Krebs, B. 1991. Das Skelett von *Henkelotherium guimarotae* gen. et sp. nov. (Eupantotheria,Mammalia) aus dem Oberen Jura von Portugal. *Berliner geowissenschafliche Abhandlungen A* 133: 1–110.

Krebs, B. 1998. *Drescheratherium acutum* gen. et sp. nov., ein neuer Eupantotherier (Mammalia) aus dem Oberen Jura von Portugal. *Berliner geowissenschafliche Abhandlungen E* 28: 91–111.

Linnaeus, C. 1758. *Tomus I. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata. Holmiae. (Laurentii Salvii): [1–4], 1–824.

Marsh, O.C. 1879. Notice of new Jurassic mammals. *American Journal of Science* 20: 396–398.

Martin, T. 1999. Dryolestidae (Dryolestoidea, Mammalia) aus dem Oberen Jura von Portugal. *Abhandlungen der senckenbergischen naturforschenden Gesellschaft* 550: 1–119.

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

McKenna, M.C. and S.K. Bell.1997. *Classification of Mammals above the species level*. New York: Columbia University Press.

Paez Arango, N. 2008. Dental and craniomandibular anatomy of Peligrotherium tropicalis: the evolutionary radiation of South American dryolestoid mammals. Thesis for obtaining the degree of Master of Science. Department of Anatomical Sciences and Neurobiology School of Medicine University of Louisville Louisville, Kentucky

Prothero, D.R. 1981. New Jurassic mammals from Como Bluff, Wyoming, and the interrelationships of non-tribosphenic Theria. *Bulletin of the American Museum of Natural History* 167: 277–326.

Rougier, G.W., L. Chornogubsky, S. Casadío, N. Páez Arango, and A. Giallombardo. 2009a. New mammals from the Allen Formation, Late Cretaceous, Argentina. *Cretaceous Research* 30: 223–238.

Rougier, G.W., A.M. Forasiepi, R.V. Hill, and M. Novacek. 2009b. New mammalian remains from the Late Cretaceous La Colonia Formation, Patagonia, Argentina. *Acta Palaeontologica Polonica* 54(2): 195–212.

Sigogneau-Russell, D. 1989. Découverte du premier Symmétrodonte (Mammalia) du continent africain. *Comptes Rendus de l'Académie des Sciences, Paris* 309(2): 921–926.

Sigogneau-Russell, D. 1991. Nouveaux mammifères theriens du Cretacé inférieur du Maroc. *Comptes-Rendus de l'Académie de Sciences de Paris* 313: 279–285.

Sigogneau-Russell, D. and P. Ensom. 1998. *Thereuodon* (Thereia, Symmetrodonta) from the Lower Cretaceous of North Africa and Europe, and a brief review of symmetrodonts. *Cretaceous Research* 19: 445–470.

Simpson, G. G. 1925. Mesozoic Mammalia. III. Preliminary comparison of Jurassic mammals except multituberculates. *American Journal of Sciences* 10: 559–569.

Simpson, G. G. 1927. Mesozoic Mammalia. VI. Genera of Morrison pantotheres. *American Journal of Science* 13: 409–416.

Simpson, G.G. 1929. *American Mesozoic Mammalia*. Memoir of the Peabody Museum, Yale University 3(1): 1–171.

Wible, J. R., G.W. Rougier, M.J. Novacek, M.C. McKenna, and D. Dashzeveg. 1995. A mammalian petrosal from the Early Cretaceous of Mongolia: implications for the evolution of the ear region and mammaliamorph interrelationships. *American Museum Novitates* 3149: 1–19.