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FIRST DRYOLESTOID (MAMMALIA, DRYOLESTOIDEA, MERIDIOLESTIDA) FROM THE CONIACIAN OF PATAGONIA AND NEW EVIDENCE ON THEIR EARLY RADIATION IN SOUTH AMERICA

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Abstract. We report on a new dryolestoid (Mammalia, Dryolestoidea, Meridiolestida) from the Los Bastos Formation (Coniacian), Neuquén Province, Patagonia, Argentina, consisting of an edentulous left dentary (MCF-PVPH 412). The alveoli preserved suggest the presence of three incisors, one double-rooted canine, and six double-rooted postcanines (probably three premolars and three molars). Based on comparisons with previously known dentaries and isolated teeth, MCF-PVPH 412 would have been about the same size as *Reigitherium* Bonaparte. Among Dryolestoidea, MCF-PVPH 412 is assigned to Meridiolestida because there were probably three molars, the roots of the posterior molars are anteroposteriorly compressed, and there is no Meckelian groove. In addition, the penultimate lower premolar would be the largest in the tooth series, which is also true in other meridiolestidans. The position of the mandibular foramen, the probable presence of three premolars, and the outline of the posteroventral part of the jaw suggest affinities with the Mesungulatoidea (*e.g.*, *Coloniatherium* Rougier, Forasiepi, Hill and Novaceck; *Peligrotherium* Bonaparte, Van Valen and Kramarz; and *Reigitherium*). The Coniacian specimen represents the oldest Mesungulatoidea and fills the gap in the record between the oldest South American dryolestoid (*i.e.*, Cenomanian) and the better known Campanian–Maastrichtian taxa. The discovery of MCF-PVPH 412 in the Coniacian of Patagonia is consistent with the dryolestoid diversification during the Late Cretaceous that makes them the most abundant mammals during that period in South America.

Key words. Mammalia. Mesozoic. Late Cretaceous. Patagonia. South America.

Resumen. PRIMER DRIOLESTOIDEO (MAMMALIA, DRYOLESTOIDEA, MERIDIOLESTIDA) DEL CONIACIANO DE PATAGONIA Y NUEVAS EVIDENCIAS SOBRE SU RADIACIÓN TEMPRANA EN AMÉRICA DEL SUR. Se describe un nuevo driolestoideo (Mammalia, Dryolestoidea, Meridiolestida) hallado en la Formación Los Bastos (Coniaciano), provincia del Neuquén, Patagonia, Argentina; el espécimen consiste en un dentario izquierdo edéntulo (MCF-PVPH 412). Los alvéolos preservados sugieren la presencia de tres incisivos, un canino birradiculado y seis postcaninos birradiculados (probablemente tres premolares y tres molares). Comparado con otros restos de dentarios fragmentarios y dientes aislados previamente conocidos, MCF-PVPH 412 habría sido de una talla similar a *Reigitherium* Bonaparte. Entre los Dryolestoidea, MCF-PVPH 412 es asignado a los Meridiolestida porque habría tenido tres molares, las raíces de los molares posteriores están anteroposteriormente comprimidas y no hay surco Meckeliano en las formas adultas. Además, el penúltimo premolar inferior habría sido el mayor de la serie, lo cual también sucede en otros meridioléstidos. La posición del foramen mandibular, la probable presencia de tres premolares y la morfología de la parte posteroventral del dentario sugieren afinidades con los Mesungulatoidea (*e.g.*, *Coloniatherium* Rougier, Forasiepi, Hill y Novacek; *Peligrotherium* Bonaparte, Van Valen y Kramarz; y *Reigitherium*). El espécimen coniaciano representa el Mesungulatoidea más antiguo y completa el intervalo entre el registro más antiguo de driolestoideos en América del Sur (*i.e.*, Cenomaniano) y los taxones mejor conocidos del Campaniano–Maastrichtiano. El hallazgo de MCF-PVPH 412 en el Coniaciano de Patagonia es consistente con la diversificación de los driolestoideos durante el Cretácico Tardío, convirtiéndose en el grupo más abundante de mamíferos durante ese período en América del Sur.

Palabras clave. Mammalia. Mesozoico. Cretácico Tardío. Patagonia. América del Sur.

THE record of Gondwanan Mesozoic mammals is scarce compared to Laurasia (Kielan-Jaworowska *et al.*, 2004; Rougier *et al.*, 2010). In South America, Jurassic trackways attributed to a mammal-like form (Casamiquela, 1964; de Valais, 2009) have been known since the mid sixties, but the first dental fossil bone remains were collected by Bonaparte and colleagues in the nineteen eighties (Bonaparte and Soria, 1985) in Patagonia, Argentina. In recent years, systematic explorations of Mesozoic continental outcrops have steadily increased the number of discoveries (*e.g.*, Rauhut *et al.*, 2002; Rougier

et al., 2007a,b, 2009a,b, 2011). South American Mesozoic mammals are represented by Australosphenida, Dryolestoidea, Gondwanatheria, Multituberculata, Triconodonta, and a basal stem therian. Pascual *et al.* (2000) claimed the occurrence of Docodonta; however, subsequent papers place the taxon in question (*i.e.*, *Reigitherium* Bonaparte, 1990) among the Dryolestoidea (Rougier *et al.*, 2011). The South American Mesozoic taxa come from the Callovian–Oxfordian Cañadón Asfalto Formation, the Barremian–Aptian La Amarga Formation, the Cenomanian Candeleros Formation, the Turonian–Santonian Adamantina Formation and several (Allen, Anacleto, El Molino, La Colonia, and Los Alamitos) formations of the Late Cretaceous Campanian–Maastrichtian (Bonaparte, 1986, 1987, 1990, 1992, 1994, 2002; Goin *et al.*, 1986; Bertini *et al.*, 1993; Pascual *et al.*, 2000; Gayet *et al.*, 2001; Rauhut *et al.*, 2002; Candeiro *et al.*, 2006; Rougier *et al.*, 2007a,b, 2009a,b, 2010, 2011; Bonaparte and Migale, 2010). Some lineages are likely endemic from Gondwana (Australosphenida, Gondwanatheria), while others have a broader distribution. Dryolestoids are known in beds of Laurasia and Gondwana (Simpson, 1928, 1929; Krebs, 1971, 1991; Martin, 1999, 2001; Kielan-Jaworowska *et al.*, 2004) from the Middle Jurassic (Late Bathonian; Freeman, 1976) to the late Paleocene (Selandian; Gelfo and Pascual, 2001). When present, they are more abundant than any other mammalian group (*e.g.*, the Late Jurassic Guimarota fauna — Martin, 2001— and the Late Cretaceous Los Alamitos and La Colonia associations —Bonaparte, 1990; Rougier *et al.*, 2009b). In South America, dryolestoids are known from the Cenomanian, followed by a gap in their record, and appear again from the Campanian–Maastrichtian to the late Paleocene (Gelfo and Pascual, 2001; Rougier *et al.*, 2011). Here we communicate the discovery of a dryolestoid edentulous lower jaw (MCF-PVPH 412) from Coniacian deposits, which partially fills that gap.

The specimen was collected north of Barreales Lake, Neuquén Province, Argentina (Fig. 1.1). The outcrops were originally regarded as the Plottier Formation (Danderfer and Vera, 1992), but have been recently identified as belonging to a new unit, the Los Bastos Formation from the Río Neuquén Subgroup, Neuquén Group (Garrido, 2010, 2011). MCF-PVPH 412 was found in a thin bed of medium to large grained sandstones (Fig. 1.2) that would correspond with an ephemeral fluvial channel developed over a flood plain. Fossils are scarce in the Los Bastos Formation compared to other units of the Río Neuquén Subgroup and consist of fresh-water mollusks, plants, turtle shell fragments, fragmentary dinosaur bones, and the mammal studied here (Coria *et al.*, 2001; Garrido, 2010). The age of the Los Bastos Formation was estimated by its stratigraphic relationships and was considered to be early to middle Coniacian, Late Cretaceous (Garrido, 2010, 2011).

MATERIALS AND METHODS

Nomenclature for the description follows the *Nomina Anatomica Veterinaria* (Schaller, 1992) and specific papers (Krebs, 1971). Dryolestoidea taxa used for comparisons are listed in the Appendix 1, supplementary information. Systematics follows Rougier *et al.* (2011).

Institutional abbreviations. **MACN-PV RN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Río Negro collection, Buenos Aires, Argentina; **MCF-PVPH**, Museo Carmen Funes, vertebrate paleontology collection, Plaza Huincul, Argentina.

Anatomical abbreviations. **c**, canine; **i**, incisor (from 1 to 3); **m**, molar; **p**, premolar; **pc**, postcanine (from 1 to 6).

SYSTEMATIC PALEONTOLOGY

Class Mammalia Linnaeus, 1758

Superorder Dryolestoidea Butler, 1939

Order Meridiolestida Rougier, Apesteguía and Gaetano, 2011

Genus and species indet.

(Figure 2.1–4; Table 1)

Referred specimen. MCF-PVPH 412, edentulous left dentary (Fig. 2).

Locality and stratigraphy. Los Bastos Formation, Neuquén Group, early to middle Coniacian, Late Cretaceous (Garrido, 2010, 2011). The specimen comes from the north slope of the Los Barreales Lake (GPS coordinates provided upon request), Neuquén Province, Argentina (Fig. 1).

Table 1 - Measurements in millimeters of the dentary of the Dryolestoidea gen et sp. indet. MCF-PVPH 412/ **medidas en milímetros del dentario del Dryolestoidea gen. et sp. indet. MCF-PVPH 412.**

Maximum length of dentary (from the tip of the body to the posterior border of the angular process)	*34.3*
Depth of dentary below the anterior root of p1 (lingual view)	*4.6*
Depth of dentary below the posterior root of m3 (labial view)	*4.1*
Depth of dentary below the posterior root of m3 (lingual view)	*5.5*
Length of retromolar space	*1.7*
Length c–m3	*19.9*

Description and comparisons

The specimen MCF-PVPH 412 is assigned to the Dryolestoidea by the combination of the following features (*sensu* Kielan-Jaworowska *et al.*, 2004): ramus of the dentary broad and high, with a steeply inclined coronoid process; labial alveolar margin lower than the lingual at the level of molars; condyle positioned above the occlusal level of the teeth; angular process prominent with an angular notch, and reduction of the posterior molar root at least in the posteriormost molars. Comparisons in the description are focused on the Dryolestoidea.

The body of the dentary is low and slender. The labial surface is broken away from the tip to the level of the antepenultimate alveolus (Fig. 2.1–3). In cross section, the labial face is convex, at least at the level of the last two teeth, and the lingual face is flat. As can be seen at the level of the posterior postcanines, the labial alveolar border is lower than the lingual (Fig. 2.2; Tab. 1). The coronoid process is broken dorsally, although the preserved portion is more than twice as high as the body of the jaw. The anterior border of the coronoid process forms a nearly right angle with the alveolar border, as in dryolestids (Martin, 1999), *Coloniatherium* Rougier, Forasiepi, Hill and Novacek, 2009b, and *Peligrotherium* Bonaparte, Van Valen and Kramarz, 1993. It is reclined in *Reigitherium* and *Cronopio* Rougier, Apesteguía and Gaetano, 2011 (Rougier *et al.*, 2011). The coronoid crest (Fig. 2.2) is thick and distinct. The posterior border of the coronoid process parallels the anterior. The masseteric fossa is shallow and broad, occupying most of the labial surface of the coronoid process (Fig. 2.2). The masseteric crest is blunt and low and is directed towards the angular process. There is a short crest framing the masseteric fossa posteroventrally that extends obliquely from the condylar process to the level of the posterior border of the coronoid process (the condyloid crest in Fig. 2.2). The condyloid and masseteric crests are not in contact. The Coniacian specimen, as well as most meridiolestidans and Laurasian dryolestoids, lacks the steeply inclined masseteric process of *Cronopio* that rises from the ventral border of the jaw (Rougier *et al.*, 2011). There is no masseteric foramen. The occurrence of this opening apparently varies among meridiolestidans; it is present in some specimens of *Coloniatherium* (Rougier *et al.*, 2009b), but is absent in *Cronopio* and *Peligrotherium* (Páez Arango, 2008; Rougier *et al.*, 2011). The condylar process is broken at its base. It is directed upward, suggesting that the condyle was positioned well above the level of the occlusal surfaces of the teeth, as in other dryolestoids (Simpson, 1928, 1929; Martin, 1999; Páez Arango, 2008; Rougier *et al.*, 2011).

The angular process is thick, posteriorly directed, and in the same plane as the ramus, similar to *Coloniatherium* and *Peligrotherium*, but differing from *Cronopio* in which the process is inflected (Rougier *et al.*, 2011). The angular notch between the angular and the condylar processes is shallow (Fig. 2.2). *Cronopio* lacks a notch (the condyle is continuous with the semicircular posterior margin of the dentary; Rougier *et al.*, 2011) whereas Laurasian dryolestoids have

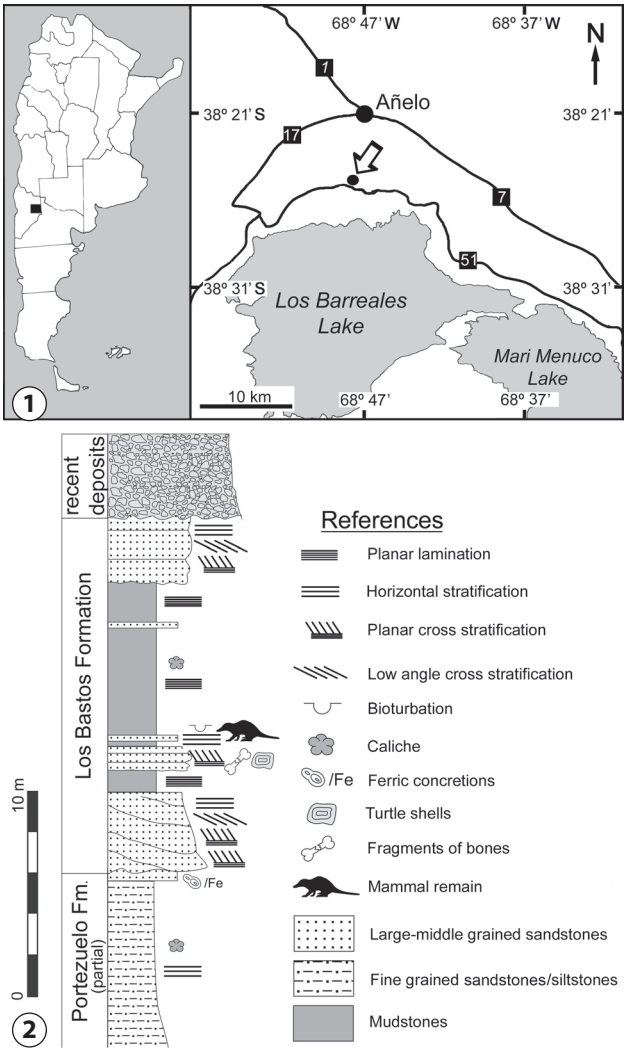

Figure 1. Map and stratigraphic profile of the locality where the **Dryolestoidea gen. et sp. indet.** MCF-PVPH 412 was found/ *Mapa y perfil estratigráfico de la localidad donde fue hallado el* ***Dryolestoidea gen. et sp. indet.*** *MCF-PVPH 412*. **1**, fossiliferous site (arrow) north of Los Barreales Lake, Neuquén Province, Patagonia, Argentina/ *sitio fosilífero (flecha), al norte del Lago Los Barreales, provincia del Neuquén, Patagonia, Argentina*; **2**, stratigraphic section of the Los Bastos Formation, Coniacian (Upper Cretaceous) showing the level where MCF-PVPH 412 was found (modified from Garrido, 2010)/ *sección estratigráfica de la Formación Los Bastos, Coniaciano (Cretácico Superior) mostrando el nivel donde fue hallado MCF-PVPH 412 (modificado de Garrido, 2010).*

deeper notches associated with more protruded angular processes (Simpson, 1929; Martin, 1999). On the ventral border of the dentary, the Coniacian jaw has another notch at the base of the angular process (the ventral notch in Fig. 2.2) that is also present in *Peligrotherium* and probably in *Coloniatherium* (Páez Arango, 2008; Rougier *et al*., 2009b), but is absent in *Cronopio* (Rougier *et al*., 2011) and the Laurasian dryolestoids (Simpson, 1929; Martin, 1999). A similar notch is seen in amphitheriids, peramurids, and other Zatheria and is associated with the downturned angular process (*e.g*., Simpson, 1928).

In lingual view (Fig. 2.4), the symphysis is smooth, oval, and nearly horizontal. The posterior border of the symphysis is not clearly seen; it extends at least to the level of the posterior root of the first postcanine. In *Coloniatherium*, the symphysis extends to the level of the anterior root of p2, whereas in *Peligrotherium* it ends at the level of the interradicular process of p2 (Páez Arango, 2008; Rougier *et al*., 2009b). It is probable that the symphysis of MCF-PVPH 412 was slightly longer than it appears to be on the specimen. Dorsal to the symphysis and at the level of the anterior root of the canine, there is a minute nutrient foramen (Fig. 2.1), as observed in the dentary of *Peligrotherium* (Páez Arango, 2008).

A Meckelian groove is not seen in the Coniacian specimen or in other South American dryolestoids (*Coloniatherium*, *Cronopio*, *Leonardus* Bonaparte, 1990, *Peligrotherium*, *Reigitherium*, and another fragmentary edentulous dentary from the Los Alamitos Formation: Appendix 1, supplementary information; Páez Arango, 2008; Rougier *et al*., 2009b, 2011; Chornogubsky, 2011). Although weakly developed, a Meckelian groove is present in Laurasian dryolestoids like *Crusafontia* Henkel and Krebs, 1969 (Simpson, 1928, 1929; Krebs, 1969, 1971; Martin, 1999, but see Prothero, 1981).

In lingual view (Fig. 2.4), the coronoid process is nearly flat and has shallow scars for the attachment of the temporal musculature. There is no evidence of either coronoid or splenial bones or the sutural surfaces for their attachment, which is also true in other South American taxa (Páez Arango, 2008; Rougier *et al*., 2009b, 2011) and *Crusafontia* among Laurasian dryolestoids (Krebs 1969, 1971). The bones (or

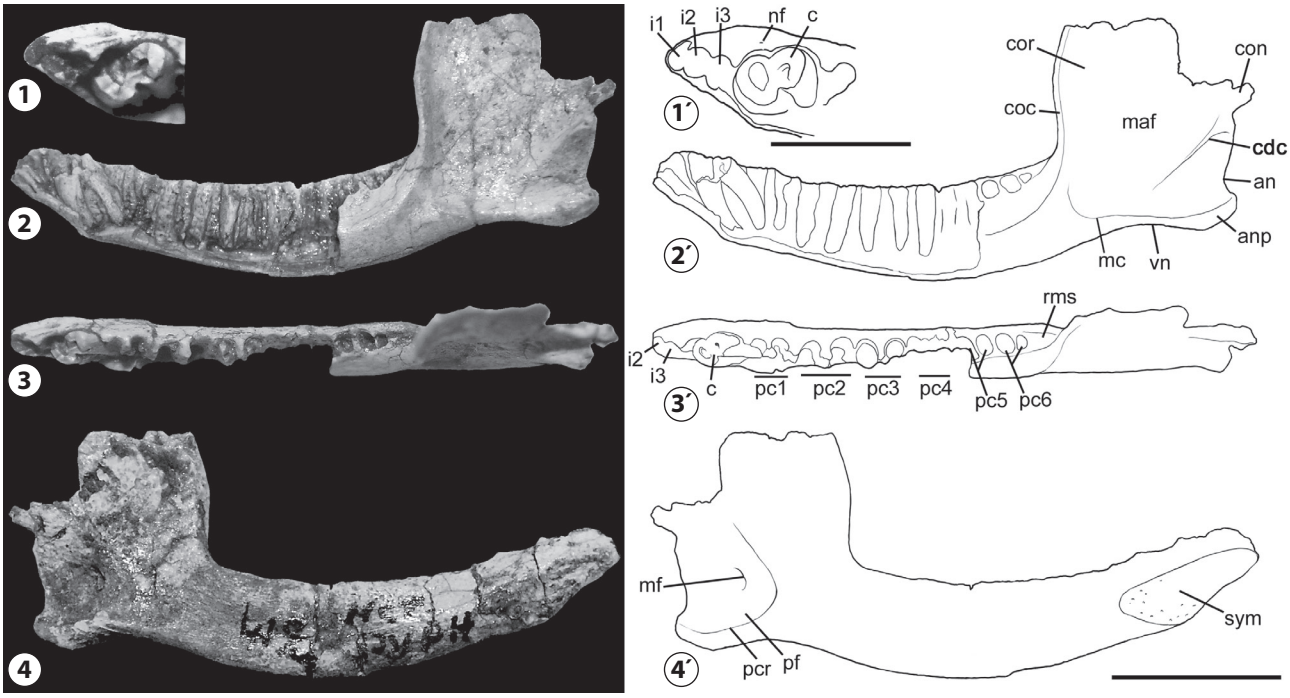

Figure 2. Photographs and line drawings of the left dentary of **Dryolestoidea gen et sp. indet**. MCF-PVPH 412/ *fotografías y dibujos lineales del dentario izquierdo del* ***Dryolestoidea gen. et sp. indet****. MCF-PVPH 412*. **1–1'**, close-up of the tip of the dentary in antero-oclussal view/ *detalle del extremo anterior del dentario en vista antero-oclusal*; **2–2'**, labial view/ *vista labial*; **3–3'**, occlusal view/ *vista oclusal*; **4–4'**, lingual view/ *vista lingual*. Abbreviations/ *abreviaturas*: **an**, angular notch/ *muesca angular*; **anp**, angular process/ *proceso angular*; **c**, canine/ *canino*; **cdc**, condyloid crest/ cresta condilar**; coc**, coronoid crest/ *cresta coronoidea*; **con**, condylar process/ *proceso condilar*; **cor**, coronoid process/ *proceso coronoides*; **i**, incisor (from first to third)/ *incisivo (del primero al tercero)*; **maf**, masseteric fossa/ *fosa masetérica*; **mc**, masseteric crest/ *cresta masetérica*; **mf**, mandibular foramen/ *foramen mandibular*; **nf**, nutrient foramen/ *foramen nutricio*; **pc**, postcanine (from first to sixth)/ *postcanino (del primero al sexto)*; **pcr**, pterygoid crest/ *cresta pterigoidea*; **pf**, pterygoid fossa/ *fosa pterigoidea*; **rms**, retromolar space/ *espacio retromolar*; **sym**, mandibular symphysis/ *sínfisis mandibular*; **vn**, ventral notch/ *muesca ventral*. Scale bar for/ *escala para* 1= 5 mm; 2–4= 10 mm.

at least the sutural surfaces for them) are present in Jurassic Laurasian dryolestoids (Simpson, 1928, 1929; Krebs, 1969, 1971; Martin, 1999). The pterygoid fossa is shallow and is limited ventrally by a blunt pterygoid crest that is directed towards the angular process. The mandibular foramen is oval in section, bordered by a sharp edge, and opens almost at the level of the posterior border of the coronoid process. This position is even more posterior than in *Cronopio, Peligrotherium* —in which it opens anterior to the posterior border of the coronoid process (Páez Arango, 2008)— and some Laurasian dryolestoids (*Dryolestes* Marsh, 1878, *Henkelotherium* Krebs, 1991, *Laolestes* Simpson, 1927; Prothero, 1981; Martin, 1999; Rougier *et al.*, 2011), in which it opens below or near the base of the anterior border of the coronoid process. The posterior position of the mandibular foramen is commonly interpreted as a derived feature present in therians and close relatives (*e.g.*, Rougier *et al.*, 2007b, 2011).

In occlusal view (Fig. 2.3), the roots of the canine and the roots of pc3 are seen in their sockets, as well as 13 additional alveoli, which together suggest the presence of three incisors, one biradiculate canine, and six biradiculate postcanines (Fig. 2.1–3). The sockets for the incisors are crowded at the anterior tip of the dentary (Fig. 2.3). The alveolus for i1 is circular in cross section and separated from i2 by a thin interdental process. The remaining alveoli are partially preserved, lacking part of the lateral wall. The last incisor socket is limited posteriorly by the interdental bone that separates it from the canine. There is no diastema between them. An extra incisor in the dental formula is unlikely. As indicated by the diameters of the alveoli, the three incisors were similar in size (Fig. 2.1). There is no data about the lower incisor number or shape for any other South American dryolestoid.

The roots of the canine are obliquely oriented in the jaw (Fig. 2.2), suggesting a procumbent tooth. The anterior root is larger and oval in section with a longer transverse axis. The posterior root is circular in section and extends posteriorly beneath the adjacent alveoli. A biradiculate canine is present in other Dryolestoidea (Prothero, 1981), including the highly specialized *Coloniatherium* and *Peligrotherium* (Páez Arango, 2008; Rougier *et al.*, 2009b). *Cronopio* instead has single-rooted canines, at least in the upper dentition (Rougier *et al.*, 2011, figs. 2–3).

Twelve postcanine alveoli are present in MCF-PVPH 412. The first to ninth postcanine alveoli only preserve their lingual walls, whereas the last three sockets are complete (Fig. 2.3). The alveoli are tightly packed. The sockets are deep and extend almost to the ventral border of the jaw (Fig. 2.2). This suggests that the roots were long, occupying almost the entire height of the body of the dentary, as in Laurasian dryolestids like *Dryolestes* (Martin, 1999). The first socket in the Coniacian jaw is separated from the second by a tall process that presumably nestled between the two roots of the pc1. The anterior root was the smallest, as in the p1 of other South American dryolestoids (Páez Arango, 2008; Rougier *et al.*, 2009b). The third and fourth alveoli are the largest amongst the sockets of the jaw. Both are similar in size and separated by a thick and tall interradicular process. This morphology suggests that the locus housed one double-rooted tooth that was the largest amongst the postcanines, such as the penultimate premolar of meridiolestidans (Páez Arango, 2008; Rougier *et al.*, 2009b, 2011). The fifth and sixth postcanine alveoli are similar in size and contain fragments of roots. The anterior root is oval in section. The two following alveoli (seventh and eight) are badly damaged. Only the most anterior part of the medial border of the seventh alveolus is preserved. The space occupied by the sockets is roughly similar to that of the previous element, suggesting a tooth of about the same length. The ninth alveolus lacks its anterolateral wall and the tenth alveolus is complete. The ninth socket is larger and apparently oval in cross section, while the tenth is smaller and circular. The eleventh alveolus is slightly compressed anteroposteriorly and larger than the tenth and the twelfth. The last (twelfth) alveolus is the smallest of the series and circular in cross section. It is probable that the last four alveoli lodged two birradiculate molars, with their anterior roots slightly compressed anteroposteriorly and larger than the posterior ones. Moreover, the small size of the last alveolus suggests that the root of the last molar and the corresponding part of the crown was reduced, as in *Coloniatherium* and *Peligrotherium* (Páez Arango, 2008; Rougier *et al.*, 2009b), but less than in Laurasian dryolestoids (Simpson, 1929).

There is a concave retromolar space, between the last molar and the coronoid process. It is more than half the length of the last tooth, similar to other South American drylestoids and paurodontids, and differing from dryolestids in which the space is shorter (Rougier *et al.*, 2011).

DISCUSSION AND CONCLUSIONS

Number of postcanines. The morphology of the twelve postcanine alveoli and processes suggest that MCF-PVPH 412 likely had six double-rooted postcanines as in mesungulatoideans, which would possibly correspond to three premolars and three molars. Three biradiculate premolars have been

recognized in *Coloniatherium* and *Peligrotherium*, whereas there are three biradiculate molars in these two taxa and *Mesungulatum* Bonaparte and Soria, 1985 (Páez Arango, 2008; Rougier *et al*., 2009b). In contrast, *Cronopio* has probably four biradiculate premolars and three single-rooted molars (Rougier *et al*., 2011). Laurasian Dryolestidae have more postcanines and can number as many as 13 elements (Simpson, 1928, 1929; Martin, 1999). The sizes and shapes of the sockets of MCF-PVPH 412 suggest that the first four alveoli would lodge a small double-rooted p1 and a large double-rooted p2 (the largest tooth of the series), and that the last four loci would house the penultimate and the ultimate double-rooted molars, which diminish in size posteriorly. Similar characteristics in the dentition occur in *Coloniatherium* and *Peligrotherium* (Páez Arango, 2008; Rougier *et al*., 2009b). There is no particular morphological feature to indicate the identity of the occupants of the third and fourth loci. It is assumed, by comparison with other mesungulatoideans, that they were for the p3 and m1, respectively.

Accessory roots are present in p2 and p3 of *Coloniatherium* and *Peligrotherium*, at least in one premolar of *Reigitherium* (Pascual *et al*., 2000), and one molar of *Leonardus* (Chornogubsky, 2011; Appendix 1, supplementary information). Apparently, there were no accessory roots in the first three alveoli of MCF-PVPH 412, where most of the septa are preserved, nor are they present in the fifth and sixth alveoli, in which fragments of the roots are still lodged. Accessory roots are also absent in the last three alveoli, which are complete. However, the presence of extra roots in the fourth alveolus (possible p2), and in the eighth to tenth alveoli (possible m1 and m2) cannot be confirmed, or denied, because of the damage. The presence of single-rooted molars, as reported in *Cronopio* (Rougier *et al*., 2011) is ruled out for the last four loci of the Coniacian dryolestoid. The differences in alveolar sizes are characteristic of teeth with paired roots of dissimilar sizes. There is no basis for interpreting the seventh and eighth loci, although it is unlikely that they were occupied by two single-rooted teeth; the sockets probably housed a double-rooted molar, as in *Coloniatherium*, *Leonardus*, *Mesungulatum*, and *Peligrotherium* (Páez Arango, 2008; Rougier *et al*., 2009b; Chornogubsky, 2011).

Comparisons with taxa from the Campanian–Maastrichtian Patagonian assemblages. Other than *Coloniatherium* and *Peligrotherium*, most Late Cretaceous Patagonian mammalian assemblages (Los Alamitos, Allen, and La Colonia formations) are known by fragmentary jaw material (*Leonardus, Reigitherium*; Pascual *et al*., 2000; Chornogubsky, 2011) or by isolated teeth. Up to now, the Los Alamitos assemblage has yielded the richest dryolestoid diversity known from South America with eleven genera (Bonaparte, 1986, 1987, 1990, 1992, 1994, 2002; Chornogubsky, 2003; Bonaparte and Migale, 2010) some of which might be synonyms of each other (see Rougier *et al*., 2011 for the discussion about the synonymy of *Barberenia* Bonaparte, 1990 and *Quirogatherium* Bonaparte, 1990). The Allen assemblage has provided four dryolestoid genera already recognized in the Los Alamitos (Rougier *et al*., 2009a), whereas the La Colonia assemblage has only two, *Coloniatherium* and *Reigitherium,* although the dryolestoid diversity is higher than that (Rougier *et al*., 2009b).

The dentary of *Reigitherium* is about the same size as MCF-PVPH 412 and both share the presence of tightly packed teeth with subequal roots in the postcanines at mid-length of the dentary. It differs, however, in the coronoid process that is less than vertical in *Reigitherium* (about 115º and 125º) and in the presence of supernumerary roots in the ultimate premolar (Rougier *et al*., 2011). The dentary of *Leonardus* (height is 6.5 mm; other measurements in Chornogubsky, 2011) is larger than MCF-PVPH 412. The teeth preserved (probably the ultimate premolar and two molars; Appendix 1, supplementary information) are separated by a short diastema, and the teeth are supported by dissimilar, anteroposteriorly compressed roots. In addition, one of the teeth (the probable second molar; Appendix 1, supplementary information) has supernumerary roots (Chornogubsky, 2011). Other dentary fragment from Los Alamitos (MACN-PV RN 1141; Appendix 1, supplementary information) that could be assigned to a dryolestoid is similar to *Leonardus* because of the slightly larger size, the postcanines placed at the middle of the dentary have dissimilar roots, and the larger root (the posterior one in *Leonardus*; Chornogubsky, 2011) is conspicuously compressed.

The fragmentary lower jaw recovered from the Campanian Anacleto Formation (Goin *et al*., 1986) tentatively assigned to the Dryolestoidea (Martinelli and Forasiepi, 2004) is slightly smaller than the Coniacian jaw (height of the dentary at the level of last molar is 2.3 mm, according to Goin *et al*., 1986). It shares with the MCF-PVPH 412 features that are also seen in other dryolestoids (labial alveolar margin lower than the lingual and reduction of the posterior molar root) and meridiolestidans (slight anteroposterior compression of the alveoli of the last molars) (Goin *et al*., 1986).

In summary, compared with previously known dentary fragments, and based on tooth dimensions, MCF-PVPH

412 would have been about the same size as *Brandonia* Bonaparte, 1990, *Groebertherium* Bonaparte, 1986, and *Reigitherium*. MCF-PVPH 412 is larger than the fragmentary edentulous jaw from the Anacleto Formation, and is smaller than *Leonardus* and the remaining taxa known from Los Alamitos, Allen, and La Colonia assemblages.

The Coniacian jaw (MCF-PVPH 412) shares with the Meridiolestida (Rougier *et al*., 2011) the likely presence of three molars, the posterior molars with anteroposteriorly compressed roots, and the lack of the Meckelian groove in adults. In addition, the penultimate lower premolar is the largest of tooth series, which is also true in other meridiolestidans. It shares with Mesungulatoidea (Rougier *et al*., 2011) the presence of a mandibular foramen far removed from the level of the anterior edge of the coronoid process, presence of a ventral notch, blunt pterygoid crest, and the probable presence of three premolars. The only putative synapomorphy of the Mesungulatoidea in the lower jaw (following Rougier *et al*., 2011) is the presence of supernumerary roots on the penultimate lower premolar, which could not be evaluated in MCF-PVPH 412 because of damage.

Concluding remarks. MCF-PVPH 412 is similar in size and shape to the dentary of *Reigitherium* from the Los Alamitos (Campanian–Maastrichtian) and La Colonia (Maastrichtian) assemblages (Bonaparte, 1990; Pascual *et al*., 2000), although the differences in the tilting of the coronoid process and the extra-roots in the ultimate premolar (Rougier *et al*., 2011) prevent the allocation of the new specimen to that taxon. Because most South American dryolestoid taxa are based on isolated teeth, it is not possible to compare them with MCF-PVPH 412. With all these caveats, the derived features observed in the dentary suggest affinity between MCF-PVPH 412 and the Mesungulatoidea (the group that contains *Coloniatherium*, *Mesungulatum*, *Peligrotherium*, *Reigitherium,* and all its descendants). Therefore, the Coniacian specimen represents the oldest record of the Mesungulatoidea. This group diversifies during the Late Cretaceous, producing large body sizes plus unique and specialized cranial and dental features (Páez Arango, 2008; Rougier *et al*., 2009b) and survives the Cretaceous/Paleogene extinction, at least in the Patagonian ecosystems (Gelfo and Pascual, 2001). Dryolestoids are the most abundant mammals known from the Late Cretaceous in South America. The new discovery is not inconsistent with this scenario, although MCF-PVPH 412 is the only mammalian fossil collected from the Los Bastos Formation, and so far, one of the few fossils known from the locality and stratigraphic unit.

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REFERENCES

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

Bonaparte, J.F. 1986. Sobre *Musungulatum housayi* y nuevos mamíferos cretácicos de Patagonia, Argentina. *4º Congreso Argentino de Paleontología y Estratigrafía* (Mendoza), *Actas* 2: 63–95.

Bonaparte, J.F. 1987. The Late Cretaceous fauna of Los Alamitos, Patagonia, Argentina. Part VIII- The mammals. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Paleontología* 3: 163–169.

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

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

Bonaparte, J.F. 1994. Approach to the significance of the Late Cretaceous mammals of South America. *Berliner Geowissenchaftliche* 13: 31–44.

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

Bonaparte, J.F. and Migale, L.A. 2010. *Protomamíferos y mamíferos Mesozoicos de América del Sur*. Museo de Ciencias Naturales Carlos Ameghino, Mercedes, 442 p.

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

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

Candeiro, C.R.A., Martinelli, A.G., Avilla, L.S., and Rich, T. 2006. Tetrapods from the Upper Cretaceous (Turonian Maastrichtian) Bauru Group of Brazil: a reappraisal. *Cretaceous Research* 27: 923–946.

Casamiquela, R.M. 1964. *Estudios icnológicos*. Imprenta del Colegio Industrial Pío X, Buenos Aires, 229 p.

Chornogubsky, L. 2003. [*Revisión preliminar de los mamíferos de la Formación Los Alamitos (Campaniano-Maastrichtiano, provincia de Río Negro, Argentina*. M.S. Thesis, UBA, 160 p., Unpublished.].

Chornogubsky, L. 2011. New remains of the dryolestoid mammal *Leonardus cuspidatus* from the Los Alamitos Formation (Late Cretaceous, Argentina). *Paläontologische Zeitschrif* 85: 345–350.

Coria, R.A., Currie, P.J., Eberth, D., Garrido, A.C., and Koppelhus, E. 2001. Nuevos vertebrados fósiles del Cretácico Superior de Neuquén. *Ameghiniana, Suplemento Resúmenes* 38: 6R.

Danderfer, J.C. and Vera, P. 1992. Cartas Geológicas y de Recursos Minerales de la provincia del Neuquén. Geología y Recursos Minerales del Departamento Confluencia. *Dirección Provincial de Minería,* Zapala, Boletín 1: 1–91.

de Valais, S. 2009. Ichnotaxonomic revision of *Ameghinichnus*, a mammalian ichnogenus from the Middle Jurassic La Matilde Formation, Santa Cruz province, Argentina. *Zootaxa* 2203: 1–21.

Freeman, E.F. 1976. Mammal teeth from the Forest Marble (Middle Jurassic) of Oxfordshire, England. *Science* 194: 1053–1055.

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

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

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

Gelfo, J.N. and Pascual, R. 2001. *Peligrotherium tropicalis* (Mammalia, Dryolestida) from the early Paleocene of Patagonia, a survival from a Mesozoic Gondwanan radiation. *Geodiversitas* 23: 369–379.

Goin, F.J., Carlini, A.A., and Pascual, R. 1986. Un probable marsupial del Cretácico Tardío del norte de Patagonia, Argentina. *4º Congreso Argentino de Paleontología y Bioestratigrafía* (Mendoza), *Actas* 2: 401–410.

Henkel, S. and Krebs, B. 1969. Zwei Säugetier-Unterkiefer aus der Unteren Kreide von Uña (Prov. Cuenca, Spanien). *Neues Jahrbuch für Geologie und Paläontologie* 8: 449–463.

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

Krebs, B. 1969. Nachweis eines rudimentären Coronoids im Unterkiefer der Pantotheria (Mammalia). *Paläontologische Zeitschrift* 43: 57–63.

Krebs, B. 1971. Evolution of the mandible and lower dentition in dryolestids. In: D.M. Kermack and K.A. Kermack (Eds.), Early Mammals, *Zoological Journal of the Linnean Society* 50, supplement 1: 89–102.

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

Marsh, O.C. 1878. Fossil mammal from the Jurassic of the Rocky Mountains. *American Journal of Science, serie 3,* 15: 459.

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

Martin, T. 2001. Mammalian fauna of the Late Jurassic Guimarota ecosystem. *Asociación Paleontológica Argentina, Publicación Especial* 7: 123–126.

Martinelli, A.G. and Forasiepi, A.M. 2004. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Río Negro Province, Patagonia (Argentina). *Revista del Museo Argentino de Ciencias Naturales, nueva serie* 6: 257–305.

Páez Arango, A.N. 2008. [*Dental and craniomandibular anatomy of* Peligrotherium tropicalis: *the evolutionary radiation of South American dryolestoid mammals*. M.S. Thesis, University of Louisville, 105 p., Unpublished.].

Pascual, R., Goin, F.J., González, P., Ardolino, A., and Puerta, P.F. 2000. A highly derived docodont from the Patagonian Late Cretaceous: evolutionary implications for Gondwanan mammals. *Geodiversitas* 22: 395–414.

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.

Rauhut, O.W.M., Martin, T., and Ortiz Jaureguizar, E. 2002. The first Jurassic mammal from South America. *Nature* 416: 165–168.

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

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

Rougier, G.W., Forasiepi A.M., Hill R.V., and Novacek M. 2009b. New mammalian remains from the Late Cretaceous La Colonia Formation, Patagonia, Argentina. *Acta Palaeontologica Polonica* 54: 195–21.

Rougier, G.W. Gaetano, L., Drury, B.R., Colella, R., Gómez, R.O., and Páez Arango, N. 2010. A review of the Mesozoic mammalian record of South America. In: J. Calvo, J. Porfiri, B. González Riga and D. Dos Santos (Eds.), *Dinosaurios y Paleontología desde América Latina*, Editorial de la Universidad Nacional de Cuyo, Mendoza, p. 195–214.

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

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

Schaller, O. 1992. *Illustrated veterinary anatomical nomenclature.* Ferdinand Enke Verlag, Stuttgart, 575 p.

Simpson, G.G. 1927. Mesozoic Mammalia. VI. Genera of Morrison pantotheres. *American Journal of Science, serie 5,* 13: 411–416.

Simpson, G.G. 1928. *A catalogue of the Mesozoic Mammalia in the Geological Department of the British Museum*. Trustees of the British Museum, London, 215 p.

Simpson, G.G. 1929. American Mesozoic Mammalia. *Memoirs of the Peabody Museum of Natural History* 3: 1–235.

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