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New mammalian remains from the Late Cretaceous La Colonia Formation, Patagonia, Argentina

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Knowledge of the latest Late Cretaceous mammalian fauna in the South America was, until now, mostly based on dentally known taxa recovered at Los Alamitos (Río Negro, Argentina). Here we describe new mammalian remains collected in outcrops of the La Colonia Formation (Campanian–Maastrichtian) exposed in Chubut Province, Argentina, warranting the recognition of a new mesungulatid: *Coloniatherium cilinskii* gen. et sp. nov. The mammalian high-level taxonomic compositions of the localities in the La Colonia Formation and at Los Alamitos are roughly similar (Reigitheriidae, Mesungulatidae, and Ferugliotheridae are represented in both localities), but gondwanatheriids and the more plesiomorphic dryolestoids from Los Alamitos are missing from La Colonia. The most abundant mammalian remains collected at La Colonia correspond to large-sized mesungulatids. *Coloniatherium cilinskii* is recognized by the dentition and lower jaw, and we assign five isolated petrosal bones, focusing our study primarily on the analysis of the ear regions. The morphology of the petrosals suggests a phylogenetic position similar to *Vincelestes*, but sharing some derived features, possibly convergent, with therians. Attribution of the petrosals to the mesungulatid *Coloniatherium cilinskii* is supported by overall morphology, size, and relative abundance among the mammalian remains from La Colonia.

Key words: Mammalia, Mesungulatidae, Campanian–Maastrichtian, Cretaceous, La Colonia Formation, Argentina.

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Introduction

The late Mesozoic South American fauna has gained notoriety over the last 30 years thanks to an impressive array of well-preserved vertebrates, dinosaurs in particular, discovered in Patagonia, Argentina (e.g., Bonaparte 1979, 1985, 1986a, 1991, 1999; Bonaparte et al. 1984, 1990; Bonaparte and Novas 1985; Bonaparte and Rougier 1987a; Calvo and Bonaparte 1991; Salgado and Bonaparte 1991; Bonaparte and Coria 1993; Chiappe and Calvo 1994; Calvo and Salgado 1995; Coria and Salgado 1995; Chiappe 1996; Novas 1997; Rauhut et al. 2003; Rauhut 2005; Makovicky et al. 2005; Novas et al. 2008; Paulina Carbajal et al. 2008; Gonzales Riga et al. 2009). Despite the relative abundance of dinosaurs and assorted vertebrates (including some of small size such as anurans, snakes, and fishes), mammals, however, remained elusive until the discovery of the Late Cretaceous Los Alamitos fauna in 1983 (Bonaparte and Soria 1985; Bonaparte 1986b, 1990, 1992, 1994, 2002; Bonaparte and Pascual 1987). Over ten years of intensive work ensued at Los Alamitos, resulting in the discovery of a moderately diverse fauna of highly autapomorphic dryolestoids, multituberculates, and groups of controversial affinities such as reigitherids and gondwanatherians (Bonaparte 1986b, 1987, 1990, 1992, 1994, 2002; Krause and Bonaparte 1990, 1993; Pascual et al. 1993, 1999, 2000; Krause et al. 1992; Pascual and Goin 2001). In addition to Los Alamitos, the Cretaceous of Patagonia has also provided one exquisitely preserved mammal, *Vincelestes neuquenianus*, discovered and reported from the older Hauterivian–Barremian La Amarga Formation (Bonaparte 1986b; Bonaparte and Rougier 1987b; Rougier et al 1992; Bonaparte, 2008), and a fragmentary lower jaw of the Campanian Anacleto Formation (Goin et al. 1986) of problematic affinities (Martinelli and Forasiepi 2004). More recently a modest Late Cretaceous mammalian fauna from the Allen Formation, in Northern Patagonia, Argentina, was described by some of us (Rougier et al. 2009); this new fauna consist of a handful of isolated teeth repre-

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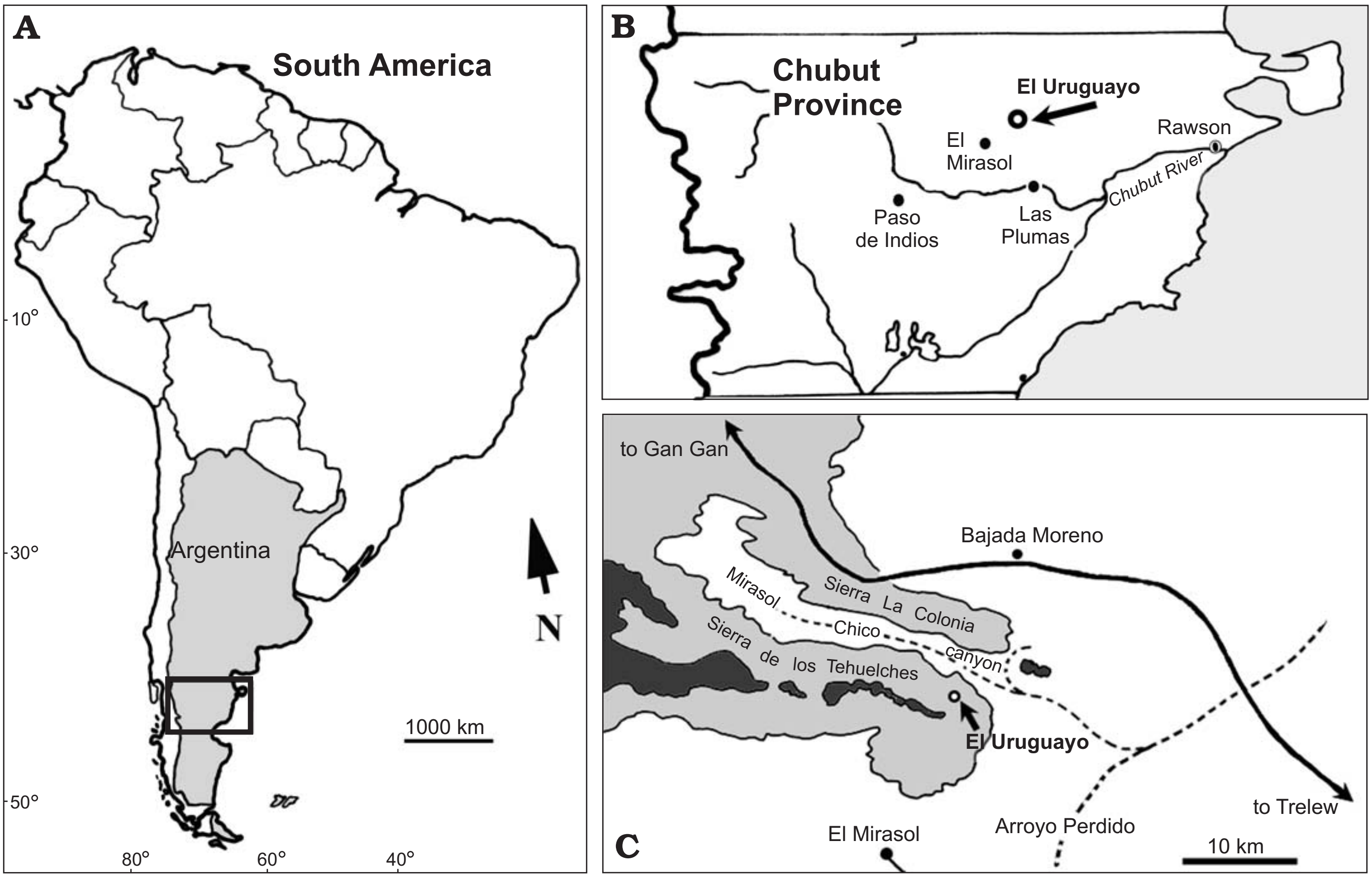

Fig. 1. Map of Chubut province, Patagonia, Argentina (**A**) showing the location of El Uruguayo (**B**), the locality in the La Colonia Formation (**C**), that provided most of the specimens described here.

senting higher level taxa described from Los Alamitos, including some common genera and some distinct taxa but all of them closely related to those from Los Alamitos.

Two extra-Patagonian localities, one in Peru (Gayet et al. 2001) and another in Brazil (Bertini et al. 1993), have provided a few teeth; some of the Peruvian specimens appear to be similar to the dryolestoids from Patagonia, but the material is poor.

New taxa have recently been reported from the Middle–Late Jurassic Cañadón Asfalto Formation. The first Jurassic record was described by Rauhut and colleagues (Rauhut et al. 2002; Martin and Rauhut 2005) who reported on a partial jaw, the type of *Asfaltomylos patagonicus*. A second mammalian species, *Henosferus molus*, was recently recognized from the same locality and age as *Asfaltomylos* (Rougier et al. 2007a); both Jurassic mammals are closely related to each other, and are possibly more distantly related to monotremes and other Mesozoic Australian taxa (i.e., Australosphenida; Luo et al. 2001, 2002; Kielan-Jaworowska et al. 2004; Rougier et al. 2007a). Finally, a third taxon, a triconodont with highly compressed dentition, was described from the Jurassic of Cañadón Asfalto Formation (Rougier et al. 2007b). None of these pre-late Cretaceous taxa: *Vincelestes*, Australosphenida, or the triconodont, show any clear relationships with the forms commonly found in the Campanian–Maastrichtian Los Alamitos, Allen or La Colonia Formations (Pascual et al. 2000; Rougier et al. 2001, 2002, 2003; Kielan-Jaworowska et al. 2007; Rougier et al. 2008). Several higher level taxa are common to both the highly derived Los Alamitos fauna and the more recently discovered localities of La Colonia, but it is unlikely that the same species are represented in both faunas. This suggests temporal and /or geographical differences between the two formations and their respective faunas. Reigitheriidae (Pascual et al. 2000; GWR personal observation), Mesungulatidae, and ferugliotheriids (or multituberculates depending on the ultimate interpretation of their affinities) are represented in both La Colonia and Los Alamitos (Pascual et al. 2000; Rougier et al. 2001, 2002, 2003; Kielan-Jaworowska et al. 2007). Nevertheless, gondwanatheriids and the putative symmetrodonts from Los Alamitos are missing in La Colonia (Rougier et al. 2001, 2002), and the multituberculate record (Kielan-Jaworowska et al. 2007) is problematic if *Ferugliotherium* and allies are not considered to be multituberculates (Pascual et al. 1999; Kielan-Jaworowska et al. 2007). A few fragmentary molars from La Colonia, not described here, may represent Dryolestidae sensu stricto, but this attribution is uncertain because all the specimens show a variable development of the anterior and posterior cingula, making them more reminiscent of mesungulatids. Of the taxa present in La Colonia, the mesungulatids are by far the most abundant, including taxa of several sizes that share a common morphology.

The La Colonia Formation is exposed over wide areas of the southern slopes of the North Patagonian Massif ("Comarca Norpatagonica") in northern central Chubut Province (Ardolino and Franchi 1996; Pascual et al. 2000; Albino 2000; Gandolfo and Cúneo 2003, 2005). The sediments represent a variety of paleoenvironments including fluvial, deep marine, and albupheric/near-shore deposits (Ardolino and Franchi 1996; Albino 2000; Pascual et al. 2000; Gandolfo and Cúneo 2005). The fossils reported here were collected on small outcrops south of the right margin of the Mirasol Chico Canyon. These outcrops are small in comparison to the expansive exposures present on the left margin of the Mirasol Chico Valley and their N-NE continuation (Ardolino and Franchi 1996; Pascual et al. 2000). In the area of study, La Colonia Formation is deposited above the Cerro Barcino Formation (Cenomanian age) (Ardolino and Delpino 1987) and below the pyroclastic Sarmiento Group (Eocene–Miocene; Ardolino and Franchi 1996; Archangelsky and Zamaloa 2003; Muzzopappa and Baez 2004). The La Colonia Formation is mainly composed of a relatively homogeneous series of upward-fining sediments: sandstones, siltstones, and claystones. The recognized facies represent continental to marginal marine depositional settings (Pascual et al. 2000). The facies that yielded the mammal remains has been interpreted as an estuary, tidal flat or coastal plain environment, influenced by occasional fresh water upland streams and tidal currents from the sea (Pascual et al. 2000). The deposition of La Colonia sediments may encompass the Campanian and Maastrichtian ages, probably beginning later than the Campanian and extending later than the Maastrichtian in some areas (Pascual et al. 2000). The more derived nature of the mammals from La Colonia suggests that they may be slightly younger than those from Los Alamitos (Rougier et al. 2009).

The main purpose of this contribution is to describe some isolated petrosals from the La Colonia Formation, one of which (MPEF-PV 600) was collected several years ago by joint expeditions of Museo de La Plata led by Dr. Rosendo Pascual and the Museo Paleontológico "Egidio Feruglio" (Pascual et al. 2000). During the intervening time, a new series of expeditions was led by the senior author as part of the project "Paleontological exploration of Patagonia" jointly developed by the American Museum of Natural History, the Museo Paleontológico "Egidio Feruglio", and the University of Louisville. This new series of expeditions resulted in the discovery of an extremely rich locality, El Uruguayo, on the right margin of the Mirasol Chico Canyon (Rougier et al. 2001, 2002). A few petrosals, all apparently representing the same taxon, were recovered at El Uruguayo or in its immediate vicinity. Additionally, these new expeditions recovered several hundred assorted mammalian remains including fragmentary jaws, isolated teeth, and several postcranial elements (Rougier et al. 2001, 2002). Here, we describe the petrosal bones and assign them to a new genus and species that represents the largest and most abundant mammalian taxon found at La Colonia.

Institutional abbreviations.—MACN-RN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina, Río Negro collection; MPEF-PV, Museo Paleontológico Egidio Feruglio, Chubut, Argentina, Paleontología de Vertebrados.

Other abbreviations.—CTPP, caudal tympanic process of the petrosal; IAM, internal acoustic meatus; ICA, internal carotid artery.

Systematic paleontology

Legion Cladotheria McKenna, 1975

Superorder Dryolestoidea Butler, 1939

Family Mesungulatidae Bonaparte, 1986b

Genus *Coloniatherium* nov.

Etymology: Colonia, after Sierra de La Colonia Chubut Province, Patagonia Argentina and the homonymous Formation, where the fossils where found; *therium*, from Greek therion meaning beast or animal, a common suffix for mammalian taxa.

Type species: *Coloniatherium cilinskii* sp. nov.

Diagnosis.—As for type and only known species.

Coloniatherium cilinskii sp. nov.

Figs. 2–6.

Etymology: After Mr. Juan Cilinski, a local rancher who provided great support to our field efforts while working at El Uruguayo.

Holotype: MPEF-PV 2087, fragmentary right lower jaw with complete p3, root fragments of p2, m1–m3, and alveoli for p1 and double rooted canine (Fig. 2A).

Type locality: El Uruguayo (43°06'18.8'' S; 67°41'45.3" W), Estancia El Pino, belonging to the Avila family.

Type horizon: Upper part of La Colonia Formation, Campanian–Maastrichtian, Upper Cretaceous.

Material.—MPEF-PV 2085, fragmentary right lower jaw with very worn remnants of m1–m3 in situ, and alveolus for p3 (Fig. 2B); MPEF-PV 2104, fragmentary lower jaw with worn down p1 and p2; MPEF-PV 2192, fragmentary jaw with partial canine; MPEF-PV 2070 left C; MPEF-PV 2223 P1; MPEF-PV 2066 P1; MPEF-PV 2088 right P2; MPEF-PV 2100 right P2; MPEF-PV 2103 left P2; MPEF-PV 2081 right P3; MPEF-PV 2079 left P3; MPEF-PV 2142 right P3; MPEF-PV 2260 right M1; MPEF-PV 2078 left M1 (Fig. 3A); MPEF-PV 2301 right M1; MPEF-PV 2183 left M2; MPEF-PV 2163 right M3; MPEF-PV 2300 right M3; MPEF-PV 2059 right p2; MPEF-PV 2090 right p2; MPEF-PV 2148 right p2; MPEF-PV 2078 right p3; MPEF-PV 2073 left p3; MPEF-PV 2064 left m1; MPEF-PV 2011 left m1; MPEF-PV 2063 right m2; MPEF-PV 2299 right m2; MPEF-PV 2091 left m2 (Fig. 3B); MPEF-PV 2092 left m3; MPEF-PV 2137 left m3; MPEF-PV 2203 left m3.

Diagnosis.—Large mesungulatid with a dental formula of I?C1P3M3. Length of the postcanine dental series 230 mm (average of three specimens); p1 small and implanted

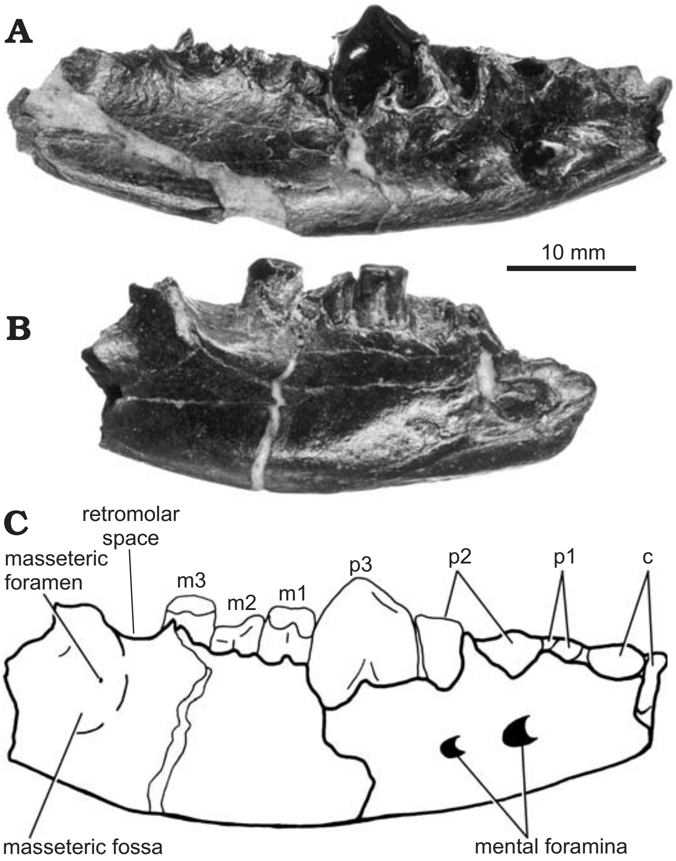

Fig. 2. Right dentaries of cladotherid mammal *Coloniatherium cilinskii* gen. et sp. nov., from the Upper Cretaceous La Colonia Formation, Chubut, Argentina. **A**. Specimen MPEF-PV 2087. **B**. Specimen MPEF-PV 2085. **C**. Reconstruction of the dentary based on the two previous specimens. The fracture line posterior to the p3 indicates the junction of the two different elements.

obliquely without diastema behind a double rooted canine; p2 with a broad posterior cingulid absent mesially; m1 possessing inflated crown with small mesial and distal cingulids and a variable number of small roots between the two principal ones; p3 trigonid proportionately smaller than in more posterior molars. Differs from *Mesungulatum* by its larger size, more bunoid appearance, proportionately broader molars, and a greater posterior reduction of the lower molars (assuming MACN-RN 6 represents m1–m2). The cingula of the upper and lower molars are broader, and more elevated into the crown; the cingular cusps are not as well-defined as in *Mesungulatum*. The lingual crest of the paracone that would contribute to the "Medianer Grat", very distinct in *Mesungulatum*, is less conspicuous in *Coloniatherium*. The mesial cingulum in *Coloniatherium* extends to the base of the parastyle, while it lies mesial to the parastyle in *Mesungulatum*. The parastyle and metastyle are similar in size in *Coloniatherium*, while the parastyle is proportionately higher in *Mesungulatum*; the stylocone is relatively higher in *Coloniatherium*. In some specimens of *Coloniatherium* the upper molars have a small labial rugosity or cingulum, which is absent in *Mesungulatum* (Fig. 3A). The M3 is more mesiodistally compressed in the taxon from La Colonia than in that from Los Alamitos, with the stylocone more distally located directly connected to the metacrista.

Attributed specimens.—MPEF-PV 600, an incomplete right petrosal missing the back half of the promontorium exposing the broken cochlea and part of the vestibular apparatus (Figs. 4, 5); MPEF-PV 2130, a fragmentary right petrosal, missing most of the pars canalicularis and having the promontorium broken open; MPEF-PV 2273, an incomplete left petrosal missing the postpromontorial portion but well preserved otherwise (Fig. 6); MPEF-PV 2280, a heavily weathered and fragmentary right petrosal; MPEF-PV 2281, an incomplete and moderately worn right petrosal, broken to expose cochlear and vestibular cavities. All the above mentioned specimens are referred to *Coloniatherium cilinskii*.

Locality and age of attributed specimens.—All petrosals were collected in La Colonia Formation. MPEF-PV 600 comes from stake 002 Estancia Baibián (in the vicinity of 43°00'25.4" S; 67°38'02.5" W), left margin of the Mirasol Chico Canyon; MPEF-PV 2130, MPEF-PV 2281, and MPEF-PV 2273 come from El Uruguayo Quarry, and MPEF-PV 2280 comes from the locality "Ulna" also on the left margin of the Mirasol Chico Canyon (38°52'27.0" S; 69°28'21.7" W).

Mandibular and dental description.—The jaws of *Coloniatherium* are very robust and proportionately short. The ventral border of the dentary forms a smooth convex curve. The buccal side of the alveolar border is much lower than the lingual side; this feature, related to the lingual shift of the posterior molar positions, results in a large retromolar space. In lateral view, the edges of the alveoli converge ventrally from both the front and back of the jaw towards the p2–m1 area. Two large mental foramina are located below the roots of the p2. The more anterior of these foramina is larger and determines a deep groove extending mesially to the level of the canine. The coronoid process is incomplete in all the jaws but their broken bases suggest that the coronoid ridge was close to vertical, forming almost a right angle with the alveolar process, a feature also seen in the close relatives *Peligrotherium* and *Reigitherium*. The masseteric fossa is delimited by a sharp coronoid crest and a more rounded ventral edge. A small masseteric foramen is present in some of the specimens, but absent in others. On the medial aspect of the dentary there is no clear evidence of either a coronoid bone or a Meckelian groove. The symphysis is well-preserved in MPEF-PV 2087; it is oval, relatively smooth, and extends posteriorly to the level of the anterior root of p2. A small genial tubercle is recognized immediately behind the symphysis.

The dental formula as presented in the diagnosis is obtained from several specimens. The total count of incisors is unknown but the likely number is 2 or 3 (based on MPEF-PV 2087), with the two more distal incisors somewhat transversely set. The lower canine is large, birradiculated and procumbent, and less bulging posteriorly than the upper ca-

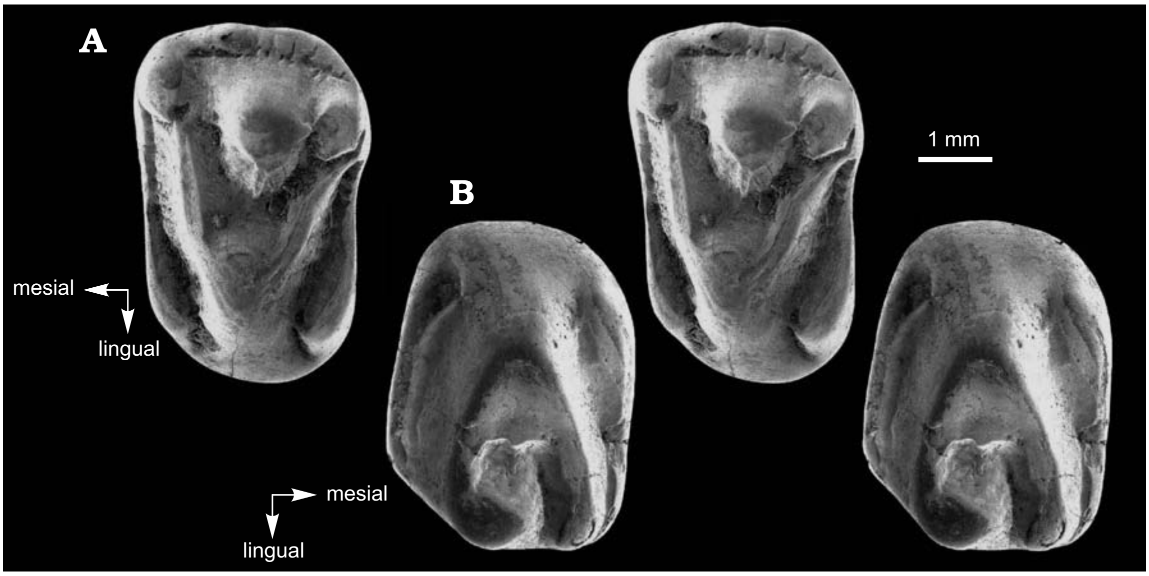

Fig. 3. Stereophotograph of the upper (**A**) and lower (**B**) molar of cladotherid mammal *Coloniatherium cilinskii* gen. et sp. nov., from the Upper Cretaceous La Colonia Formation, Chubut, Argentina; specimens MPEF-PV 2078 and 2091, respectively.

nine. The p1 is small, double rooted and obliquely inset in the jaw, but as preserved in MPEF-PV 2104 the crown characters are obliterated by wear. The p2 is the largest lower tooth, and has a molar-like appearance. This tooth has two stout roots, the mesial one anteriorly directed and the distal one vertical. The crown is dominated by a centrally-located protoconid. A large and distinct anterior accessory cusp (paraconid) and the rudiments of a cingulid give the mesial half of the tooth a triangular aspect. The lingual metaconid is low and small, connected to the protoconid by a blunt crest that is rapidly removed by wear; the trigonid angle is approximately 140°. The distal half of the tooth is broad and dominated by a transverse posterior cingulum that culminates on a distinct labial cusp. The p3 is a large, bulbous tooth, with a poorly developed trigonid located centrally and two broad and expansive mesial and distal cingula. Typically the p3 has three or more roots; the smaller ones are located lingually, between the lager mesiolabial and distal roots. The larger roots are mesiodistally compressed. The molars (Fig. 3B) uniformly diminish in size and all have a similar pattern to the p3, retaining the compressed mesial and distal roots, but without accessory roots. In the molars (m1–m3) the trigonid is formed by a tall protoconid located on the distolingual corner of the tooth, a distinct, anteriorly displaced paraconid, and a large metaconid aligned transversely with the protoconid and lingually with the paraconid. From the mesial and distolingual edges of the protoconid descend blunt, well-developed cristae: the paracristid and metacristid respectively, forming an angle of 45–50° to each other. In some specimens, a feeble crest extends labially from the labial slope of the metaconid towards the protoconid subdividing the basin of the trigonid. Mesial and distal cingula are broad, well developed, and relatively higher in the crown (elevated cingula), less distant from the occlusal surfaces than in *Mesungulatum*. Cingular cusps (cusps e, f, and d) are not present, unless the cuspules present in both mesial and distal cingulids are regarded as homologous of such structures. The cuspules in the cingula are not as distinct as those in *Mesungulatum*, and there is not a cristid obliqua as in Los Alamitos mesungulatids (Bonaparte 1986b, 1987, 1990, 1994), differing from some Laurasian dryolestoids (Prothero 1981). The m3 is a much reduced and simplified version of the mesial molars.

The upper incisor count is unknown. The upper canine is taller and more robust than the lower, with a prominent bulge of the base of the posterior root determining a sigmoid posterior outline, similar to the condition seen in *Vincelestes* and *Peligrotherium*. Three upper premolars are recognized based on morphology. The P1 is relatively small, double-rooted, with a mesially located paracone, and two distinct but small cingular cusps. The posterior cingular cusp is connected to the paracone by a crest that descends posteriorly from the tip of the paracone. Midway along this crest, and over the distal slope of the paracone, there is typically a conspicuous cusp or swelling but this is effaced by wear in many specimens. The posterior accessory cusp is also contacted by buccal and lingual cingula.

The P2 is a large, complex tooth with a small, cylindrical mesial root and a large, transverse, distal root. The crown is dominated by a centrally located, conical paracone. The paracone is loosely connected to the metastyle by a crest. A large, broad cingulum occupies the distal margin of the tooth, which culminates lingually in a thickening, or cuspule, similar to the condition seen in the molars. A small parastyle determines a high platform, which is supported by the small anterior root, hanging from the mesial slope of the massive paracone. The parastyle is connected to the lingual and buccal aspects of the paracone by distinct crests.

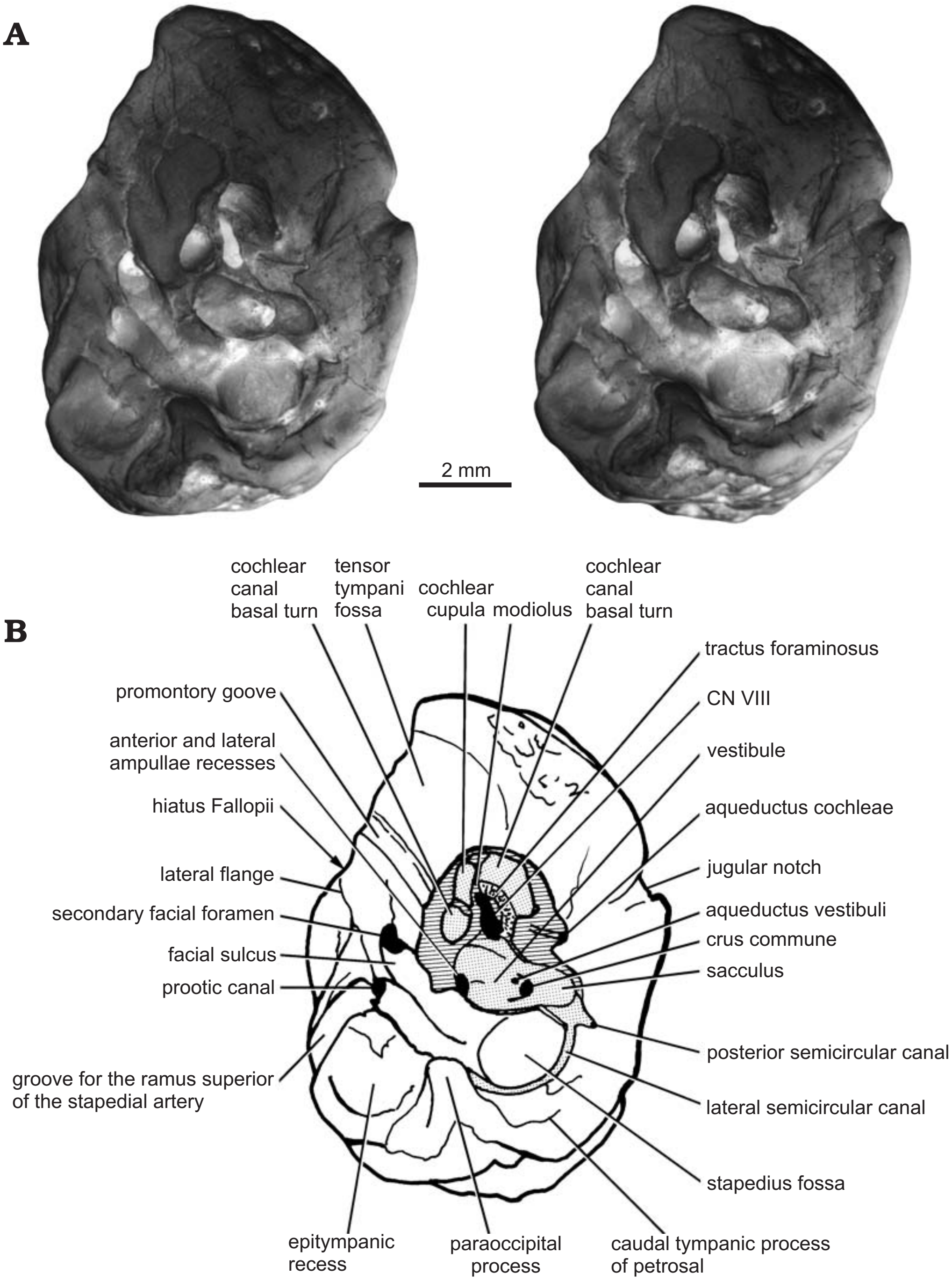

Fig. 4. **A**. SEM stereophotograph of the fragmentary right petrosal of cladotherid mammal *Coloniatherium cilinskii* gen. et sp. nov., from the Upper Cretaceous La Colonia Formation, Chubut, Argentina, specimen MPEF-PV 600. **B**. Diagrammatic outline of the right petrosal of *Coloniatherium cilinskii* gen. et sp. nov., specimen MPEF-PV 600. Hatching indicates broken bone surfaces; the stipple pattern represents inner ear cavities or canals exposed by breakage of the petrosal.

The last upper premolar (P3) is molarized; the trigons of the four last postcanines (P3–M1–3) resemble an isosceles triangle, wider labiolingually, and formed by the lingual paracone and the labial stylar cusps (Fig. 3A). The overall shape of the crowns is subrectangular because of the more pronounced lingual development of the cingula and cingular cusps, which diminish in size posteriorly. As in the lower dentition, the P3 is massive and bunoid with a proportionately small trigon. The M1 is a nearly symmetrical molar dominated by a large paracone and stylocone that divide the tooth in mesial and distal halves (Fig. 3A). The paracone is connected to the parastyle by a broad paracrista. The parastyle is a robust conical cusp that connects to the labial end of the broad mesial cingulum. A second large crest, the metacrista, rises labiodistally from the paracone and ends on the buccal margin of the tooth without contacting a pro-

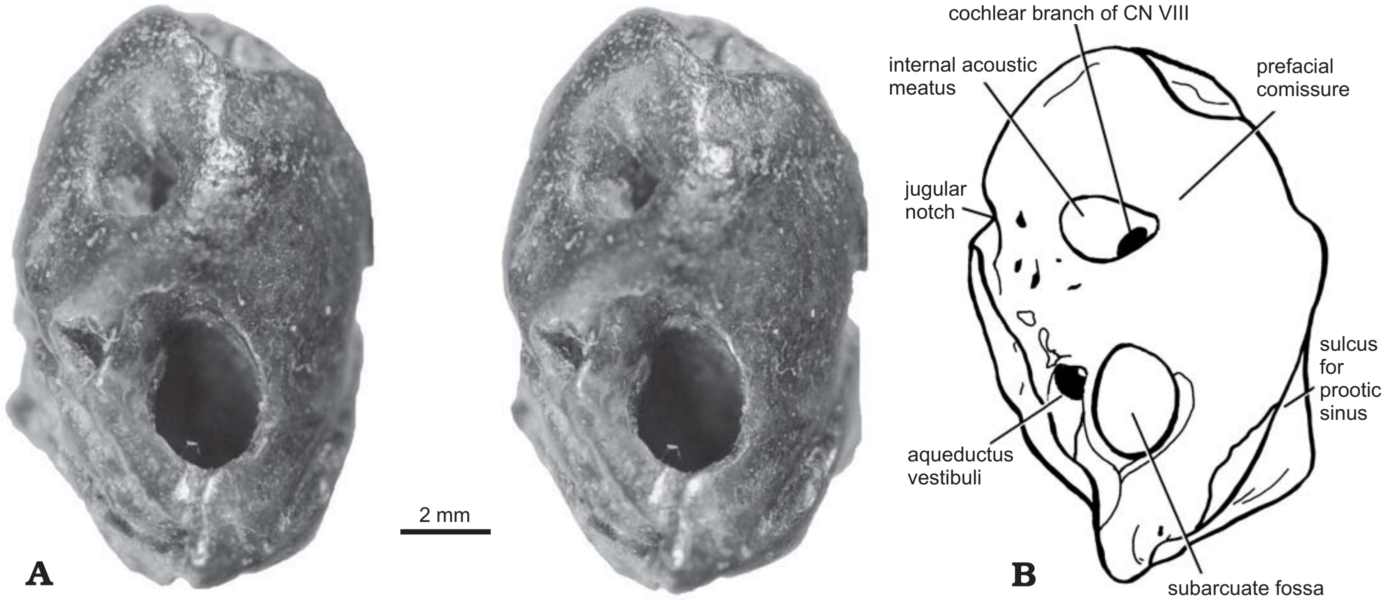

Fig. 5. Stereophotograph (**A**) and interpretative diagram (**B**) of the endocranial view of the fragmentary right petrosal of cladotherid mammal *Coloniatherium cilinskii* gen. et sp. nov., from the Upper Cretaceous La Colonia Formation, Chubut, Argentina, specimen MPEF-PV 600.

portionately large metastyle. The metastyle is conical and in close contact with the stylocone. No metacone swelling or cusp is present, a condition similar to that observed in certain mesungulatids (e.g., *Mesungulatum*, Bonaparte 1986b, 1987), but differing from the Laurasian dryolestoids (Simpson 1927; Prothero 1981). Both mesial and distal cingula are broad and contribute a semi-quadrangular occlusal outline to the molar. Both cingula end lingually in a swelling, but do not form a cusp as seen in *Mesungulatum*. The stylocone is high; the lingual slope of this cusp bears a distinct mesocrista (Medianer Grat; Martin 1999) that does not reach the buccal aspect of the paracone. There is a variously developed lingual cingulum (e.g., MPEF-PV 2065, 2301, 2078, Fig. 3A) between the parastyle and the buccal surface of the metastyle, indicating what we believe is intraspecific variability. In the M2-M3, the metastylar portion of the molars is reduced (more so in the M3) to accommodate a sharp inturned distal portion of the alveolar line, a feature also seen in *Mesungulatum* (MACN-RN 05, Bonaparte 1986b), and therefore both M2 and M3 acquire the typical "last molar morphology". The M3 lacks a metastyle, and the metacrista connects the stylocone, which in turn is relatively lower than the anterior molars (only slightly taller than the parastyle).

Justification of postcanine identification.—Among Recent mammals identification of premolar/molars is based on the observation of a developmental process, the replacement of a tooth by another, or the lack of such event (Clemens and Lillegraven 1986). In fossils this information is seldom available (Kielan-Jaworowska et al. 2004) and the specimens described here are no exception. Morphology is traditionally used as a proxy to determine the boundary between premolar and molars. In the case of *Coloniatherium* and all the other known Mesungulatidae and *Mesungulatum*-like taxa (*Reigitherium* and *Peligrotherium*), the identification of the boundary between premolars and molars is challenging. The first two postcanines in *Coloniatherium* are simple and semi-trenchant teeth; we feel quite comfortable calling them premolars. The third element, however, has all three of the main cusps forming a small trigon/trigonid high up in the crown, the tooth is the largest of the postcanine series, and is very bulbous and massive. This is unlike the three following teeth, which are not bulbous, except for the somewhat bunodont cusps, and subequal to each other in morphology. The P/p2 and the teeth here identified as P/p3 have supernumerary roots not known in the more posterior elements. Additionally, the roots of the premolars (P/p1–P/p3) are of cylindrical or oblong section while those of the last three postcanines are mesiodistally compressed and broad buccolingually. Despite the molarized nature of the third postcanine, we believe the differences outlined above suggest a tooth formula of P/p3–M/m3.

Further support for this interpretation is provided by the closely related *Peligrotherium*, which has a similar number of teeth and morphology, but because some of the specimens are very well preserved it is possible to note that the third postcanine is far less worn than the fourth. This, in turn, indicates that the third postcanine erupted after the fourth, a pattern consistent with replacement of the third position (Rougier and Paez 2007; Paez 2008). Taking everything into consideration, we believe a postcanine formula of P/p3–M/m3 is the best supported.

Petrosal description.—All of the petrosals are heavily weathered and broken. The exposure to watery media has resulted in a polished surface patina on the fossils that can usually be distinguished from the relatively unpolished surfaces of recent breaks. In some instances, however, all the break-

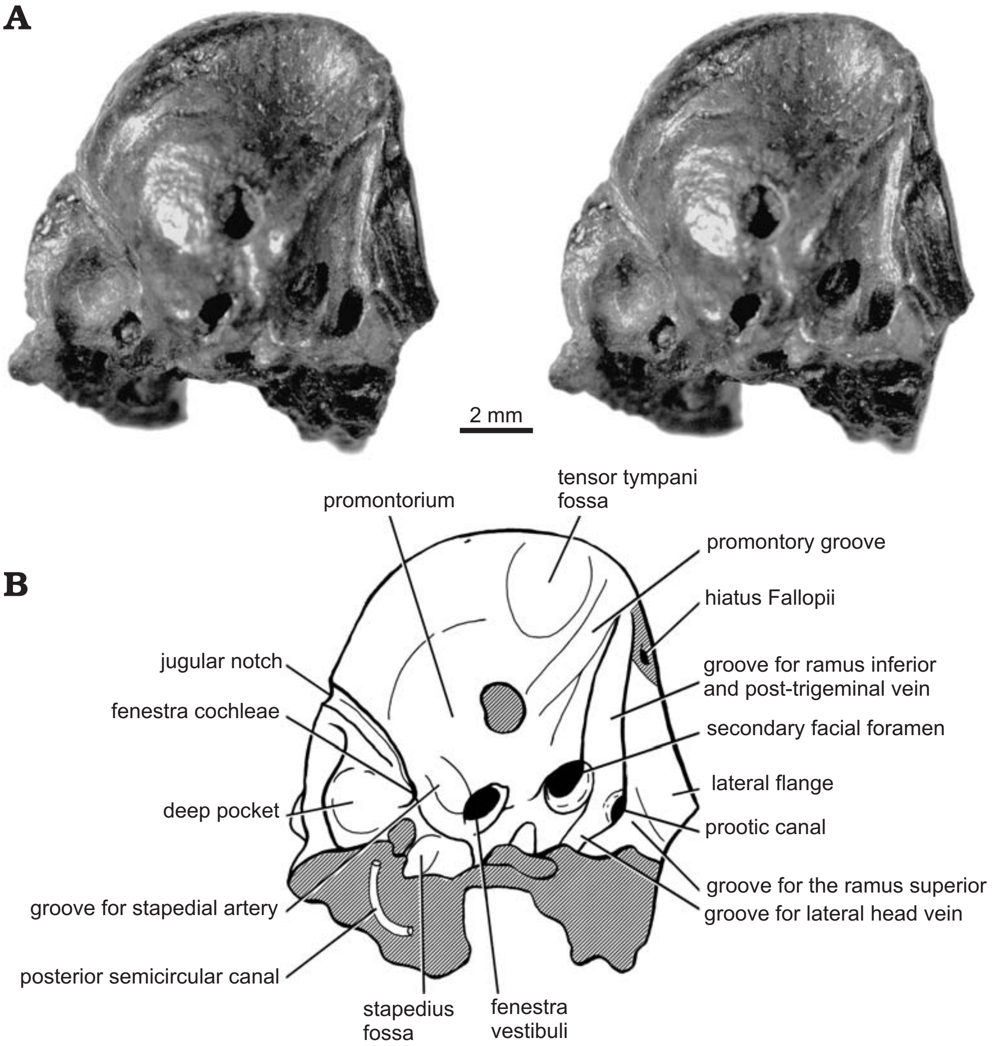

Fig. 6 Stereophotograph (**A**) and interpretative diagram (**B**) of the fragmentary left petrosal of cladotherid mammal *Coloniatherium cilinskii* gen. et sp. nov., from the Upper Cretaceous La Colonia Formation, Chubut, Argentina; specimen MPEF-PV 2273 in tympanic view. Line pattern indicates broken bone surfaces.

age can be repolished by the elements and rendered indistinguishable from the normal bone surface. This introduces a degree of uncertainty on the interpretation of the petrosal morphology. Because MPEF-PV 600 is one of the better preserved petrosals, the description is mostly based on this specimen and completed with information provided by the other specimens.

The petrosals are large by comparison to those of other Mesozoic mammals (MPEF-PV 600: 12.6 mm long in ventral view; Figs. 4, 5; perhaps a little longer when complete). The skull length is estimated at 87.5 mm based on the proportions of the prototribosphenidan *Vincelestes* (Bonaparte and Rougier 1987b; Rougier et al. 1992); 161.5 mm based on *Didelphis*; or 148.3 mm based on *Leptictis*. These differences in estimated skull length (based alternatively on comparisons with *Vincelestes* or therian mammals) reflect the progressive proportional reduction of petrosal length during mammaliaform evolution (Rougier et al. 1996a; Rougier and Wible 2006). The smaller predicted skull length (based on *Vincelestes* proportions) agrees closely with the predicted skull length based on the jaws of *Coloniatherium*.

Mammalian petrosals comprise two major portions; the pars cochlearis, housing the auditory portion of the inner ear, and the pars canalicularis, housing the organs of equilibrium (Klaauw 1931; MacIntyre 1972). In most Mesozoic mammals the pars cochlearis comprises (in addition to the cochlea and its bony enclosure) the promontorium and other posterior and lateral structures such as the rostral tympanic process, lateral trough, facial canal, and lateral flange (Rougier and Wible 2006). The pars canalicularis is represented by the semicircular canals and the vestibule (in life occupied by the utriculus and sacculus), which would have been filled with endolymph and connected to the endocranial space (see below). The osteological features of the pars canalicularis are dominated by the subarcuate fossa which is circumscribed by the semicircular canals. The anterior semicircular canal forms the rim of the fossa, the lateral canal is located in the floor of the fossa. The posterior semicircular canal is located in the medial wall of the subarcuate fossa and the mastoid exposure of the petrosal (De Beer 1937; MacPhee 1981; Meng and Fox 1995a, b; Wible et al. 2001). The vestibule occupies the central part of the osseous labyrinth, and communicates with the cochlear canal anteriorly and the semicircular canals posteriorly (Meng and Fox 1995a, b; Wible et al. 2001).

The pars cochlearis is represented in MPEF-PV 600 by a low promontorium, which has been broken open, exposing the coiled cochlea and the vestibule (Fig. 4). The promontorium is almost complete in MPEF-PV 2273 (Fig. 6) except for the presence of one erosive hole developed at the most ventral projection of the promontorium where the bone is the thinnest because of the underlying cochlea. The surface of the promontorium is broad and slightly convex, and projects only moderately ventrally. The anterior pole of the promontorium is flat and has a fossa located anterolaterally that can be interpreted as an attachment site for the tensor tympani muscle. This fossa is shallow, although better pronounced than in therians, and similar to that found in *Vincelestes* (Rougier et al. 1992; Rougier et al. 1996a). In the MEPV-PV 2273, lateral to the tensor tympani fossa, there is a broad, shallow sulcus that runs anteroposteriorly from the anterolateral corner of the promontorium to the fenestra vestibuli. This sulcus, the promontorial groove, is better developed anteriorly and fainter in the proximity of the fenestra vestibuli (Fig. 6). The internal carotid (ICA) artery was the likely occupant of this groove, indicating a transpromontorial course for the vessel (Wible 1986). Medial to the fossa for the tensor tympani, the petrosal is very thick with a deep medial margin, but despite the ossification of the anterior half of the petrosal, a rostral tympanic process is absent. In extant mammals the promontorium closely matches the size of the enclosed cochlea. In the petrosals from La Colonia and in most Mesozoic taxa, the promontorium encloses a proportionally small cochlea leaving a substantial part of the promontorium unoccupied by any inner ear structure. This anterior portion of the promontorium is remarkably stout and developed in the petrosals from La Colonia. The anterior border of the promontorium is eroded in all the specimens, exposing the trabecular structure of the bone. Based on the thickness of the preserved base, however, it is probable that this border protruded anteriorly forming a shelf, as in *Vincelestes* and some therians (Rougier et al. 1992; Wible et al. 2001, in press; Wible 2003.

The back portion of the promontorium in MPEF-PV 600 is badly damaged, revealing the structures of the inner ear in ventral view (Fig. 4). The cochlea is broken through the modiolar axis exposing the medial and lateral portions of the basal turn, and the impression of the cochlear cupula ventral to the modiolar axis. What is preserved of the petrosal suggests that the cochlea had at least one and a half turns arranged in a tight spiral. There are no remnants of the primary spiral lamina in the MPEF-PV 600, but in the more complete MPEF-PV 2273, a small portion of the primary spiral lamina can be seen through the fenestra cochleae. In MPEF-PV 600 there is only a faint ridge in the basalmost portion of the cochlea, which reflects the presence of a short secondary spiral lamina. Evidence of this structure in other petrosals (MPEF-PV 2281) is equally poor. In life, the primary and secondary spiral laminae separate the cochlear canal into the scala vestibuli and scala tympani. The space between the laminae contains the basilar membrane that supports the organ of Corti (MacIntyre 1972; Meng and Fox 1975a, b). The modiolus is obliquely sectioned in MPEF-PV 600 and 2281.

In both specimens numerous minute openings can be clearly seen forming the tractus foraminosus, which would transmit branches of the cochlear nerve (CN VIII) into the primary spiral lamina. The edges forming the dorsal and ventral limits of the tractus foraminosus are smooth and seem to have finished edges. In specimen MPEF-PV 600 (Fig. 4), behind the cochlea there is an elongated, deep depression that constitutes the vestibule. In the medial side of the roof of the vestibule are two openings, the larger of which corresponds to the vestibular opening of the crus commune (formed by the anterior and posterior semicircular canals). The second, tiny foramen, lateral to the crus commune, represents the internal opening of the vestibular aqueduct, which would have transmitted the endolymphatic duct. At the posterolateral corner of the vestibule, the anterior and lateral semicircular canals merge in a single rounded space that likely lodged their respective ampullae. Portions of the posterior and lateral semicircular canals are partially visible in ventral view of MPEF-PV 600 and 2281 due to breakage in the vestibular and postpromontorial area. In MPEF-PV 600 the lateral semicircular canal encircles the stapedial fossa (Fig. 4), however most of its medial extension is damaged, exposing the broken canal. The posterior semicircular canal can be seen in the vicinity of the opening of the lateral semicircular canal as a small foramen directed laterodorsally towards the vestibule. In this area there is an expansion that likely lodged both part of the ampulla of the posterior semicircular canal and the saccular portion of the vestibule. The nearly vertical posterior semicircular canal is clearly visible in the medial wall of the subarcuate fossa of MPEF-PV 2273, opening immediately lateral to the connection of the lateral semicircular canal with the vestibule.

Between the vestibule and the cochlea in MPEF-PV 600 and 2281, there is a narrow sulcus limited posteriorly by a low, somewhat damaged, broad crest. This sulcus is the inner ear opening of the aqueductus cochleae that would have transmitted the perilymphatic duct. The aqueductus cochleae is long, so that the medial opening in the jugular notch is removed from the lateral aperture in the inner ear (Figs. 4, 5). In medial view, the external opening of the aqueductus cochleae is a small, dorsoventrally compressed fissure located dorsal to the jugular notch. The processus recessus, which floors the aqueductus cochleae (De Beer 1937; MacPhee 1981), is relatively thin and horizontal. It is less extensively developed than in Recent mammals, because the medial aperture of the perilimphatic duct (in the inner ear) can be seen in posterior view through the fenestra cochleae.

The promontorium of petrosal MPEF-PV 2273 (Fig. 6) is very well preserved and there are three major apertures around its posterior perimeter. From lateral to medial these are the secondary facial foramen, fenestra vestibuli, and fenestra cochleae. The fenestra cochleae is located in the posteromedial corner of the promontorium. It is narrow, elongated, and well-separated from the postpromontorial tympanic sinus by a low crest. It is also intimately connected with a groove that marks the contact between the processus recessus and the tympanic roof. The fenestra would have been, in life, closed by the secondary tympanic membrane, as in all living mammals. The fenestra cochleae sits in a relatively shallow fossula fenestra cochleae. Two weak ridges extend from the posteromedial margin of the fenestra cochleae to the edge of the jugular notch, forming a groove that continues a short distance inside the endocranial surface. The occupant of this groove is unknown.

The morphology seen in the petrosals, in particular that of MPEF-PV 2273, indicates that two structures are connecting the inner ear and the area in the vicinity of the jugular foramen. One is the occupant of the bony canal that we have called here aqueductus cochleae; the other is the occupant of the groove that runs along the processus recessus. To our knowledge, there is no model among Recent mammals for a morphology like this. It is known, however, that among some forms (e.g., *Ornithorhynchus*; Zeller 1989, 1991) a small vein accompanies the perilymphatic duct. It is therefore conceivable that the smaller osseous canal carries the vein and the duct is left exposed to the middle ear cavity and the postpromontorial tympanic sinus. If this were to be the case, a true fenestra cochleae would be absent among mesungulatids. Until additional information in support of this possibility is gathered, we will continue to interpret the osseous canal in La Colonia mesungulatids as the aqueductus cochleae, and the fenestra in the rear of the promontorium as a true fenestra cochleae.

Immediately posteromedial to the fenestra cochleae and the processus recessus there is a deep, rounded excavation of the roof of the postpromontorial tympanic sinus (clearly seen in MPEF-PV 2273; Fig. 6). The area is partially circumscribed laterally by the crest indicating the posterior semicircular canal, and medially by the thickened edge of the petrosal. This depression is reminiscent of the "deep pocket medial to the paroccipital process" (Rougier et al. 1996b). In the La Colonia petrosals, this depression seems to be simply an excavated portion of the postpromontorial sinus of the tympanic cavity.

The fenestra vestibuli, which in life accommodates the footplate of the stapes, is elongated with its major axis oriented anterolateral-posteromedial. It opens into a deep and elongated fossula fenestra vestibuli (Fig. 6). The stapedial ratio (Segall 1970) is approximately 1.5, that is, slightly oval, but with a smaller ratio than that of most eutherians (Wible et al. 2001). A circular or slightly elliptical fenestra vestibuli, as seen in La Colonia petrosals, is the primitive morphology shared among basal mammals and retained in some therians (Archibald 1979). The anteromedial margin of the fossula fenestra vestibuli is notched by a shallow sulcus that represents the pre-stapes portion of the stapedial artery. Slightly posterolateral to the fossula fenestra vestibuli, the subtle continuation of the stapedial artery can be observed, directed toward the groove interpreted here as for the ramus superior.

In most Mesozoic groups, a well-developed lateral flange partially delimits the lateral trough. Monotremes are the only Recent mammals that possess a lateral flange, which in turn is continuous dorsally with an intramembranous ossification, the anterior lamina (Griffiths 1978; Kuhn and Zeller 1987; Hopson and Rougier 1993). In the petrosals MPEF 600 (Fig. 4) and 2273 (Fig. 6) there is a portion of the lateral flange preserved immediately anterior to the groove for the ramus superior of the stapedial artery (see below). This surface is concave and low, projecting ventrally in a less pronounced way than in *Vincelestes*. The dorsal broken surface of the lateral flange faces dorsolaterally, and therefore it is probable that at least a portion of the lateral flange, when complete, was exposed on lateral view of the skull. We are uncertain if there were dorsal and anterodorsal continuations of this surface resulting in an anterior lamina, but we regard this as likely. A slight roughness suggests a possible broken surface. Regardless of the extension of the connections of a putative anterior lamina, what remains of the lateral flange contributed to form part of the enclosure of the cavum epiptericum and cavum supracochleare.

The pars canalicularis is well preserved in MPEF-PV 2273 (Fig. 6) and 600 (Fig. 4). The facial sulcus is proportionally broad, with the hiatus Fallopii placed at the anterior edge of the petrosal. The hiatus Fallopii is a relatively small aperture and given its position on the anterior margin of the petrosal floor of the cavum epiptericum, it probably transmitted an intracranial palatine branch of the facial nerve. In MPEF-PV 2273 the large secondary facial foramen opens posterolateral to the promontorium. The primary facial foramen and the cavum supracochleare are visible through the somewhat damaged promontorium and secondary facial foramen in MPEF-PV 600 (Fig. 4) and MPEF-PV 2281. The structures associated with the facial nerve are proportionally large, with a spacious cavum supracochleare and large foramina for the nerves branching off from the geniculate ganglion. The floor of the ganglion is extensive; this, in turn, determines that the hiatus Fallopii and the secondary facial foramen are far apart from each other.

Posterolateral to the secondary facial foramen there is a broad, shallow groove that probably housed the ramus superior of the stapedial artery (Figs. 4, 6). The area around the groove for the ramus superior is somewhat eroded in all the specimens, and despite the fact that the groove is open ventrally in MPEF PV 600 and 2273, it is possible that the artery was enclosed in a canal like that of *Vincelestes* (Rougier et al. 1992), which has been eroded. The groove for the ramus superior connects with another sulcus on the vertical posterior face of the petrosal (MPEF-PV 600 and 2281), which presumably was occupied by the arteria diploëtica magna. Yet another shallow but distinct groove runs anteroposteriorly on the tympanic roof, ventral to the floor of the cavum supracochleare and along the lateral trough. The likely occupants of this groove are the ramus inferior of the stapedial artery and postrigeminal vein (see also below). The position of the stapedial artery is indicated by a faint groove posterolateral to the fossula fenestra vestibuli. This groove and the more substantial one leading to it, anteromedial to the fossula, strongly suggests that the artery perforated the stapes as predicted for *Vincelestes*, some multituberculates, and some eutherians (Kielan-Jaworowska et al. 1986; Rougier et al. 1996a, 2002; Wible et al. 2001). The exact position of the bifurcation of the stapedial artery into the rami superior and inferior is not clearly indicated in any of the specimens but likely occurred in the midst of the lateral trough. A similarly developed stapedial-internal carotid system is purported to be primitive for Mammalia (Wible 1986; Rougier et al. 1992; Wible and Hopson 1995; Rougier and Wible 2006). A large horizontal canal, completely enclosed in the petrosal, runs dorsal to the shelf of bone that roofs the groove for the ramus superior. This canal continues in a deep sulcus on the lateral surface of the petrosal and in a broadly open sulcus running parallel to the facial nerve on the ventral surface. The close association of this canal with the facial nerve and the connection with a large sub-vertical sulcus on the lateral side of the petrosal indicates the presence of a prootic sinus and lateral head vein (Wible 1990; Wible and Hopson 1995; Rougier and Wible 2006). The canal, therefore, is identified as the prootic canal. The aperture of the prootic canal is relatively large, at least as large as the secondary facial foramen. Anteriorly to the ventral opening of the prootic canal, there is a broad groove that forms the bulk of the lateral trough. This sizable groove enters the prootic canal, indicating the presence of a robust post-trigeminal vein. A post-trigeminal vein is a primitive amniote feature retained among adult extant mammals only in monotremes, but predicted in a variety of fossil mammaliaforms (Wible and Hopson 1995; Wible et al. 1995; Rougier et al. 1996b; Rougier and Wible 2006).

Behind the groove for the ramus superior of the stapedial artery is the epitympanic recess (Figs. 4–6), the portion of the tympanic cavity dorsal to the incudo-malleolar articulation (Klaauw 1931). The recess is deep and approximately oval, with raised posterior and medial walls formed by the lateral extension of the damaged paroccipital process and the small, anteriorly directed crista parotica, respectively. A deep pocket on the posteromedial portion of the fossa likely represents the fossa incudis, for the articulation of the crus brevis of the incus (Klaauw 1931). A low, anteroposteriorly directed crest marks the lateral limit of the fossa incudis.

The caudal tympanic process of the petrosal (CTPP) is somewhat damaged and extends medially from the paroccipital process as a ridge that becomes progressively low (Fig. 4). The CTPP forms the posterolateral wall of the enormous stapedial fossa, which would have housed the stapedius muscle. The stapedial fossa is deep, subcircular, and positioned posteromedial to the fenestra vestibuli. The lateral semicircular canal curves around the stapedial fossa and is exposed in ventral view due to partial loss of the tympanic floor. Medial to the stapedial fossa, there is an extensive surface, slightly concave dorsally. This portion of the petrosal is homologous to the mastoid exposure of the eutherian petrosals described by MacIntyre (1972) and Wible (1990) from the Late Cretaceous Lance Formation, Wyoming. On the medial edge of the Patagonian petrosals, behind the promontorium and in front of the surface for the articulation with the exoccipital, the jugular notch is recognized (Figs. 4–6). Judging from the size of the notch, the jugular foramen was small, a common condition among the petrosals of many Mesozoic cladotheres such as *Vincelestes* and the "symmetrodont" Khoobur (Wible et al. 1995; Rougier et al. 1996b).

In medial view, the La Colonia petrosals each have a rugose, triangular facet for articulation with the exoccipital. No evidence of an inferior petrosal sinus is found, though the appropriate areas of the petrosal are reasonably well preserved in most specimens. The anterior pole of the promontorium and its medial surface are highly trabeculated and were likely filled by a venous sinus, as in monotremes (Zeller 1989), that was fed and drained by small foramina that riddle the petrosal. In lateral view, the most distinctive feature is the deep groove for the prootic sinus, which is almost vertical and positioned very posteriorly, behind the posterior edge of the subarcuate fossa. This feature can be clearly seen in MPEF PV 2273 (Fig. 6), 2283, and 600 (Fig. 5). At the level of the lateral flange, the groove for the prootic sinus curves sharply medially into the large, semi-horizontal prootic canal. The similar size of the prootic sinus groove and prootic canal, in addition to the absence of a groove continuing ventrally to the groove of the prootic sinus, suggest that a postglenoid vein was absent in the La Colonia petrosals, as in most Mesozoic groups (Wible and Hopson 1995; Rougier and Wible 2006).

In endocranial, or dorsal view (Fig. 5), the dominant features are the subarcuate fossa and the internal auditory meatus (IAM). The subarcuate fossa, which lodged the paraflocculus of the cerebellum, is deep, narrow, and more tubular than spherical, in contrast to the usual mammalian condition (MacIntyre 1972; Wible 1990, 2003; Wible et al. 1995, 2001; Rougier et al. 1996b; Sánchez-Villagra 2002). On the ventromedial edge of the fossa, there is a narrow, elongated foramen interpreted as the aqueductus vestibuli, the internal aperture of the endolymphatic canal. The internal auditory meatus (IAM) is separated from the subarcuate fossa by a broad bony bridge. The morphology of the IAM varies among the specimens; in MPEF-PV 600 the IAM is subequal in size to the subarcuate fossa, it is deep and not very broad (Fig. 5B); in MPEF-PV 2273, 2130, and 2281 the IAM is considerably smaller and rounded in shape, even accounting for some erosion due to transport. The internal division inside the IAM of cranial nerve (CN) VII, vestibular branch of CN VIII, and cochlear branch of CN VIII is seen in MPEF PV 600. As preserved, all of these branches leave the IAM through relatively large foramina, but due to the rough preservation, this feature may be artificial. The foramen for the facial nerve leaves the IAM anterolaterally, piercing the thick commissura prefacialis. This structure is best preserved in MPEF-PV 600 (Fig. 5B).

The abundant cancellous bone on the medial and anterior pole of the promontorium coalesces in small sized canals and canaliculi in the substance of the petrosal; a particularly large one is exposed along a portion of the medial boundary of the petrosal MPEF-PV 2281 by breakage. This canal is, however, not an inferior petrosal sinus (contra Rougier and Wible 2006: 292) because it lacks an exit on the vicinity of the jugular foramen, but it might have been connected to it via foramina leading from the cancellous promontorium to the sinus.

The petrosals from La Colonia had a very small, subrectangular occipital exposure. Covering the lateral portion of the occipital exposure and forming the lateral wall of the canal for the substantial arteria diploëtica magna was the squamosal (not preserved in any of the available specimens but deduced from articular surfaces). The arteria diploëtica magna was directed anterolaterally as in *Vincelestes*, and, judging from the size of the grooves, it was of similar size to the ramus superior.

Stratigraphic and geographic range.—Upper Cretaceous La Colonia Formation in Chubut Province, Argentina.

Discussion

The petrosals of La Colonia show a unique combination of primitive and derived features, making a preliminary assessment of their relationships a challenging, but enticing task. Several papers have recently tried, with at least partial success, to employ petrosal and basicranial characters either solely or in combination with other character systems in broad comparative studies of Mammaliaformes (Wible 1990; Rougier et al 1992, 1996a, b, 1998, 2004, 2007a; Crompton and Luo 1993; Wible and Hopson 1993, 1995; Wible et al. 1995, 2001; Luo et al. 2001, 2002; 2003; Luo and Wible 2005; Ji et al. 2006; Li and Luo 2006; Rougier and Wible 2006). The characters employed in these studies cover a wide array of forms mostly representing the Mesozoic radiation of mammaliaforms. These contributions and some comparative summaries (Kielan-Jaworowska et al. 2004; Rougier and Wible 2006) provide the base for the comparisons developed here; however, most of these morphological transformations pertain to basal members and are not relevant in discussing the affinities of the petrosals from La Colonia.

In attempting to attribute these petrosals to a given mammalian taxon, the first candidates are obviously those that can be recognized by dental remains in the same quarry from which the petrosals were collected. All of the fossils come from lenses that preserve reworked material, resulting in a high concentration of mammals. It is therefore likely that dental remains of the same taxon are present in those lenses. The mesungulatids are the only forms with dental and mandibular remains in the appropriate size range to match the predicted skull size based on the isolated petrosals. Moreover, based on previous studies of petrosal and basicranial evolution (Wible et al. 1995; Rougier et al. 1996b; Rougier and Wible 2006), the petrosal morphology matches the expected stem position to the therian lineage deduced from their dental remains (Bonaparte 1987, 1990, 1992, 1994, 2002). This suggests that our comparisons should focus on therians and their immediate outgroups.

Vincelestes neuquenianus (Bonaparte 1986b; Bonaparte and Rougier 1987b; Rougier et al. 1992) from the Early Cretaceous of Argentina is the best known non-tribosphenic mammal with a position close to therians (see, however, Bonaparte 2008 for an alternative interpretation). The petrosals from La Colonia possess some primitive features with regard to *Vincelestes*, among them (i) the extensive groove for a post-trigeminal vein, (ii) the very small portion of the promontorium occupied by the cochlea (though this may result from the lesser coiling of the cochlea in *Vincelestes*), and (iii) the presence of a deep pocket on the postpromontorial tympanic sinus, medial to the paroccipital process. The isolated petrosals share with *Vincelestes* many primitive mammalian features, including (i) an extensive lateral flange with a lateral exposure in the braincase wall, (ii) large lateral trough, (iii) prootic canal, (iv) distinct tensor tympani fossa, (v) transpromontorial groove for the ICA, (vi) a circular or slightly oval fenestra vestibuli, and (vii) large epitympanic recess excavated at the rear of the lateral flange. It is likely that the petrosals described here also had, as in *Vincelestes* and all non-therian mammals, an extensive anterior lamina that formed part of the braincase wall, but support for this feature is equivocal.

Several characters, however, suggest that the petrosals from La Colonia Formation could be more derived than *Vincelestes* (Bonaparte and Rougier 1987b; Rougier et al. 1992) and similar to therians. They include (i) a fully coiled cochlea, (ii) ramus superior lodged in a groove and not in an intrapetrosal canal, (iii) inferior petrosal sinus not intrapetrosal, (iv) a hiatus Fallopii that does not open into the tympanic cavity, but in the anterior edge of the petrosal, (v) cavum supracochleare fully enclosed by bone, and probably, (vi) horizontally positioned prootic canal. The microstructural details of the cochlea in MPEF-PV 600 and 2273 are identical to those described for tribosphenic therians by Meng and Fox (1995a, b; see also Vater et al. 2004) with regard to the coiled cochlea and primary and secondary spiral laminae. Developed primary and secondary lamina have been preliminary reported for *Henkelotherium* (Ruf et al. 2007).

The Patagonian petrosals share with metatherian petrosals from the Late Cretaceous of North America the intracranial aperture for the hiatus Fallopii at the tip of the promontorium (Clemens 1966; Archibald 1979; Wible 1990; Sánchez-Villagra and Wible 2002). An intracranial aperture of the hiatus Fallopii is also present in some basal eutherians, including Lipotyphla (with the exception of *Solenodon*) and some Erinaceidae. In contrast, primitive members of Metatheria, such as the deltatheridian *Delta-*

theridium, have a hiatus Fallopii that opens ventrally into the middle ear (Rougier et al. 1998), although the petrosals available are juvenile and the floor of the geniculate ganglion is not fully ossified. This condition is, however, not generalized because in at least some of the petrosals described by Ladevèze (2004, 2007) from the Paleocene of Itaboraí, Brazil (Type I and Type II) the hiatus Fallopii opens intracranially, on the dorsal side of the petrosal, not at the anterior pole of the promontorium.

Wible (1990) identified four synapomorphies for Metatheria, all of them related to circulatory features: (i) absence of stapedial artery, (i) prootic canal reduced in length and with an intramural opening, (iii) continuation of prootic sinus in a canal between petrosal and squamosal, and (iv) sphenoparietal emissary vein present. Judging from the transpromontorial groove for the internal carotid artery and broad groove for the ramus superior, the stapedial artery was probably present in the petrosals from La Colonia, indicating the retention of a primitive condition in these specimens. Character 4 is also likely to show the primitive condition in the petrosals attributed to *Coloniatherium*, because a postglenoid foramen is regarded as absent. Character 2 is present in the La Colonia petrosals but character 3 as worded by Wible (1990) is not. The prootic sinus, however, is very close to the articular surface for the squamosal and the sinus may have been ultimately encased in a composite structure.

The short intramural prootic canal present in many basal metatherians may be, as proposed by Wible (1990), diagnostic of Metatheria or some less inclusive groups of marsupials. This character, however, has not been recovered as diagnostic by Rougier et al. (1998; character 124) nor by Luo et al. (2003; character 282). Nevertheless, the prootic canal, generally absent in placentals (Rowe 1988; Wible 1991; but see Wible 2008 for an exception), has been convincingly identified in *Prokennalestes* (Wible et al. 2001, see below) and zhelestids (Ekdale et al. 2004). It is therefore difficult to argue that the condition displayed by marsupials was not also ancestrally present in eutherians (Rougier and Wible 2006). It would be expected that the prootic canal became reduced in length and diameter before completely disappearing; the recent observation of such a canal in *Solenodon* (Wible 2008) supports this scenario.

Ladevèze 2004, 2007, and Ladevèze and Muizon, 2007 have recognized an anterior lamina in the petrosals from Itaboraí, Brazil and those of *Pucadelphys* and *Andinodelpys*. We disagree with this interpretation, which has been discussed elsewhere (Rougier and Wible 2006).

Eutherian petrosals and the petrosals from La Colonia, on the other hand, have broader and lower promontories than metatherians and retain several primitive features present in *Vincelestes* (Rougier et al. 1992; Rougier 1993) but absent in metatherians. These characters include, among others, (i) the presence of a transpromontorial internal carotid artery, (ii) a stapedial artery and its major branches (ramus superior, ramus inferior, and arteria diploëtica magna; Wible 1987), (iii) a proportionally small, unexpanded, subarcuate fossa, and (iv) a deep IAM with a thick prefacial commissure. The petrosals from La Colonia also have a medially low CTPP that does not reach the jugular area, and a moderate exposure of bone lateral to the jugular notch confluent with the stapedial fossa that is probably equivalent to what Wible (1990) called the mastoid exposure in an isolated Late Cretaceous eutherian petrosal. The medial reduction of the CTPP is very poorly developed or absent in metatherian and therian outgroups, but widespread among basal eutherians. However, the relatively extensive lateral flange, the likely presence of an anterior lamina, the well developed groove for the post-trigeminal vein and the large prootic canal argue for a position basal to both marsupials and placentals for the La Colonia petrosals.

Wible et al. (2001) described an isolated petrosal from the Early Cretaceous of Mongolia and attributed it to *Prokennalestes*, a very basal eutherian (Kielan-Jaworowska and Dashzeveg 1989; Sigogneau-Russell et al. 1992; Rougier et al. 1998; Luo et al. 2002). The petrosal of *Prokennalestes* exhibits several primitive features such as (i) a short, vertical prootic canal, (ii) the remnants of an anterior lamina, (iii) a fully closed canal in the petrosal for the ramus superior, (iv) a slightly elliptical fenestra vestibuli, and probably (v) an incompletely ossified cavum supracochleare (Wible et al. 2001).

Ekdale et al. (2004) described petrosals referred to the enigmatic zhelestids, which could either be basal ungulatomorphs (Nessov et al. 1998; Archibald 1996, 1999, 2003; Archibald et al. 2001; Archibald and Averianov 2001, 2003, 2005) or more generalized eutherians, possibly closely related to Mongolian stem eutherians (asioryctitheres and zalambdalestids; Novacek et al. 2001, 2002; Wible et al. 2004; Asher et al. 2005). As in *Prokennalestes*, the zhelestid petrosals are primitive, retaining a large prootic sinus canal and remnants of a lateral flange. If we accept the attribution of these petrosals to *Prokennalestes* (Wible et al. 2001) and zhelestids (Ekdale et al. 2004), and both *Prokennalestes* and zhelestids are eutherians (as up to now uncontroversially affirmed; Kielan-Jaworowska and Dashzeveg 1989; Nessov et al. 1998; Cifelli 1999; Rougier et al. 1998; Archibald 1996; Archibald et al. 2001; Archibald and Averianov 2005; Luo et al. 2002), the petrosals from La Colonia would approximate several of the features expected in basal eutherians. Notable among these characters are the combination of (i) a fully spiral cochlea, (ii) a medially diminished CTPP, and (iii) the retention of a fully developed stapedial arterial system. Crown-group eutherians and eutherian petrosals from the Late Cretaceous Lance Formation (MacIntyre 1972; Clemens 1973) are more derived than the Patagonian petrosals and *Prokennalestes* in having no trace of a prootic sinus canal, lateral flange, and post-trigeminal vein groove.

To date, no unequivocal cranial or dental remains of therian mammals are known from the Late Cretaceous of South America. Fragmentary mammalian remains from the Late Cretaceous of Brazil and Bolivia were tentatively assigned to therians, but this assignment remains problematic (Bertini et al. 1993; Gayet et al. 2001). In La Colonia, where over 300 mammalian specimens have been collected, there is no evidence that therians were ever present. Based on the relative abundance of teeth in the mammalian sample, their size, and the overall morphology discussed above, it seems likely that the isolated petrosals can be referred to the new species *Coloniatherium cilinskii*. The dental remains suggest close phylogenetic relationships between the new species and the already known *Mesungulatum houssayi* from Los Alamitos Formation and the newly described *Mesungulatum lamarquensis* (Rougier et al. 2009). The assignment of these teeth to the Dryolestida is apparently well supported (Bonaparte 1987, 1990, 1992, 1994, 2002) and we concur that, although they are highly autapomorphic, mesungulatids are members of a cladothere radiation that appears to have dominated the Late Cretaceous mammalian assemblages in South America.

In the most recent phylogenetic analyses of the major Mesozoic lineages, dryolestoids are placed at the base of Cladotheria (Prothero 1981; Hu et al. 1997; Rougier et al. 1998; 2007a; Luo et al. 2001, 2002, Kielan-Jaworowska et al. 2004; Luo and Wible 2005; Martin and Rauhut 2005), or as a relatively derived member of Holotheria (Hopson 1994). If dryolestoids are basal to *Vincelestes*, and the attribution of the petrosals of La Colonia to *Coloniatherium* is correct, all the derived characters observed in the ear region are convergent with those of prototribosphenians and later therians. Most notable among these are the reduction of the lateral flange and the achievement of a fully spiral cochlea, which would have been acquired convergently, a point stressed by the cochleas of *Henkelotherium* and *Vincelestes*, both of which are curved roughly 270°.

Mesungulatids and their relatives, *Reigitherium* and *Peligrotherium* (Bonaparte 1990, Bonaparte et al. 1993; Pascual et al. 1999; Rougier et al. 2000, 2009; Gelfo and Pascual 2001; Rougier and Paez 2007), are known from other Late Cretaceous and Paleocene localities, but no relevant cranial remains have so far been described that aid in resolving the conflict between the apparently basal dental anatomy and the progressive petrosal morphology of the La Colonia mesungulatids. The seemingly dissimilar dental and basicranial morphology illustrates once more the uniqueness and distinctiveness of the Late Cretaceous South American mammals with respect to their Holarctic counterparts. The highly derived dentition of the mesungulatids with bunodont cusps, robust cingula development, and increase in the height of the crown, coupled with extensive tooth-on-tooth occlusion are all characters that differentiate mesungulatids from more generalized dryolestoids. The root system of mesungulatids with two mesiodistally compressed roots that support the whole width of the crown differ from the typical dryolestoid condition of an extremely reduced posterior root (Butler 1939; Martin 1999). These differences, among others, like the dental formula, could be used to argue for the recognition of a separate lineage of mammals for mesungulatids. However, we agree with Bonaparte (1985), that some of the forms from Los Alamitos can be linked to Holarctic dryolestids and these in turn root mesungulatids within Dryolestoidea. Mesungulatids, and in a greater degree the closely related *Peligrotherium* and *Reigitherium,* achieve a dentition reflecting omnivorous and herbivorous habits with a progressive reduction of the orthal component during mastication culminating finally with the acquisition of an almost lophodont dentition in *Peligrotherium.* The enlargement of the posterior premolars also occurs among periptychid condylarths which have an almost exclusive North American Paleocene record (Rose 2006), suggesting that the specialized dentition of mesungulatids and relatives responds to a global event. The Late Cretaceous radiation of angiosperms with its abundance of hard fruits is a prime suspect. If mesungulatids are dryolestoids their specialized dentitions and ear regions makes them one of the most distinctive groups of Dryolestoidea underscoring the endemic nature of the Mesozoic mammalian fauna in South America.

The prospecting and collecting of different Late Cretaceous Patagonian Formations is at an early stage. Field work being conducted at present is likely to provide in the near future dental or cranial elements to refine or refute the tentative systematic allocation we propose here for the isolated petrosals.

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