First ?cimolodontan multituberculate mammal from South America

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We describe a Cretaceous ?cimolodontan multituberculate p4 from South America, for which we erect the new genus and species *Argentodites coloniensis*. This new taxon is represented by an isolated ?left p4 from the Upper Cretaceous (?Campanian or Maastrichtian) La Colonia Formation of Patagonia (Fig. 1). It has a strongly convex anterior margin and prismatic enamel, which attest to its cimolodontan nature, while the previously known p4 (MACN-RN 975) from the Late Cretaceous Los Alamitos Formation is roughly rectangular, suggesting "plagiaulacidan" affinity. The presence of normal prismatic enamel in *Argentodites* suggests similarities to Ptilodontoidea. However, it differs from the Late Cretaceous and Paleocene Laurasian cimolodontans (including Ptilodontoidea) in having a long, straight posterior margin, a nearly straight dorsal margin, characteristic of some "Plagiaulacida", and in having the lingual side close to the mirror image of the labial side, the character that poses difficulties in establishing whether it is a right or left tooth. Because of these differences we assign *Argentodites* to ?Cimolodonta, tentatively only, superfamily and family *incertae sedis*.

Key words: Multituberculata, Cimolodonta, Cretaceous, La Colonia Formation, Argentina.

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Introduction

During the Cretaceous the terrestrial vertebrate faunas of North and South America evolved in isolation, resulting in development of different adaptative types on the two continents. While the North American mammalian faunas were dominated by multituberculates and therians, in South America the dominant mammals were Dryolestoidea ("eupantotherians"), accompanied by Gondwanatheria, "triconodontans", "symmetrodontans", and very rare multituberculates (see Kielan-Jaworowska et al. 2004 and references therein). Late Cretaceous South American multituberculates have hitherto been represented by a fragment of the left dentary with alveolus for incisor and a bladelike p4 (MACN-RN 975), and a few isolated upper premolars (see Kielan-Jaworowska et al. 2004: fig. 8.44) all from the Los Alamitos Formation. MACN-RN 975 was originally assigned by Kielan-Jaworowska and Bonaparte (1996) to the gondwanatherian ?*Ferugliotherium*, but subsequently to Multituberculata *incertae sedis* (Kielan-Jaworowska et al. 2004). The second multituberculate p4, which we describe herein differs from (MACN-RN 975) in having rounded anterior margin and we assign it tentatively to Cimolodonta.

Institutional abbreviations.—MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MPEF, Museo Paleontológico "Egidio Feruglio", Trelew, Chubut, Argentina; PMO, Paleontological Museum, University of Oslo, Oslo, Norway.

Systematic paleontology

Subclass Allotheria Marsh, 1880
Order Multituberculata Cope, 1884
Suborder ?Cimolodonta McKenna, 1975
Superfamily and family *incertae sedis*
Genus *Argentodites* nov.

Type and only species: *Argentodites coloniensis* nov.

Derivation of the name: After Argentina (originating from Latin *argentum*, silver), and from Greek *hodites*, a traveler, suggesting its migration from North America.

Diagnosis.—As for the type and only species.

Argentodites coloniensis sp. nov.

Derivation of the name: After the Upper Cretaceous La Colonia Formation, in which the holotype specimen was found.

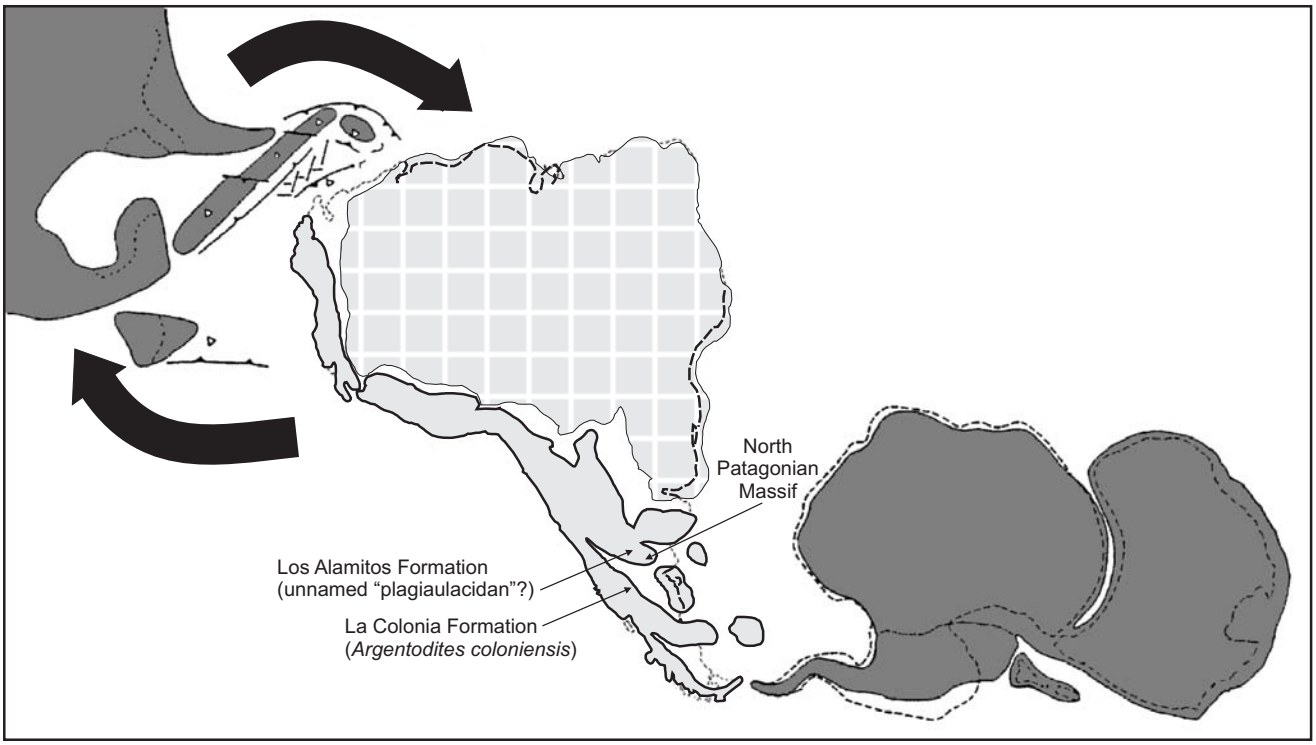

Fig. 1. Position of South America and adjacent lands, 85–63 million years ago, showing location of the formations that yielded Late Cretaceous multituberculates. Black arrows indicate migrations of vertebrates between North and South Americas. Note the division of South America by sea into South Gondwanan Province (light grey) and North Gondwana Province (square hatching). Modified after Pascual (2006).

Holotype and the only known specimen: MPEF 604, nearly complete ?left p4, without roots.

Type horizon and locality: Middle part of the La Colonia Formation (Upper Cretaceous: ?Campanian or Maastrichtian), Arroyo Mirasol Chico Bajada Moreno area, Chubut Province, Patagonia, Argentina (Fig. 1).

Measurements.—The maximum length of the tooth, measured on the lingual side, is 4.15 mm, maximum height on the same side measured above the ventral, medial incurvature of the enamel between the bases of the roots is 2.10 mm, and maximum width in occlusal view (measured in the anterior half of the tooth) is 1.35 mm.

Diagnosis.—The strongly convex anterior margin of the tooth and the normal prismatic enamel with average prism diameter of 3.8 μm suggest affinities of *Argentodites coloniensis* to Cimolodonta. Shares presence of the normal prismatic enamel with members of the Ptilodontoidea, but differs from Laurasian Cimolodonta (including Ptilodontoidea) in having a relatively long and straight posterior margin, and nearly straight dorsal margin (if placed in presumed life position), both features characteristic of some "plagiaulacidans" (i.e., Paulchoffatiidae, Plagiaulacidae, and Allodontidae). Differs from Laurasian cimolodontans with large p4s in having labial side built as nearly a mirror image of the lingual side. Differs from *Paracimexomys* (the only member of the *Paracimexomys* group in which the enamel microstructure is known) in having normal prismatic, rather than gigantoprismatic enamel.

Life position of the ?left p4.—The posterior lower premolar (p4) in "plagiaulacidans" (with exception of Arginbaataridae) is subrectangular, with long anterior and posterior margins directed roughly vertically; in most cimolodontans, in contrast, the p4 is arcuate with convex anterior and posterior margins (Kielan-Jaworowska et al. 2004; Hahn and Hahn 2006a). *Argentodites* is morphologically intermediate between these two patterns, as it has a long, straight posterior margin, but a strongly convex anterior margin. If one places the studied p4 with its posterior margin only slightly turned counterclockwise from a completely vertical position (Fig. 2B) the upper margin of the tooth will appear nearly straight, as characteristic of "Plagiaulacida". We believe that this might have been the life position of the studied p4, as in such a position the middle margins of the roots are symmetrically arranged.

In Fig. 2C, the same tooth is figured from the other side, with straight posterior margin placed obliquely, toward the middle of the tooth. However, in no cimolodontan p4 is the posterior margin as long as in *Argentodites.* In Fig. 2C the dorsal margin is convex upward, as in cimolodontans with large p4s. We believe that the life position in Fig. 2B is more probable than the one in Fig. 2C.

As the lingual side of *Argentodites* p4 is nearly a mirror image of the labial side, it is difficult to demonstrate unequivocally whether the studied tooth is the right or the left one. We tentatively believe that the side illustrated in Fig. 2B is labial, as it is less convex than the opposite side (Fig. 2C), as characteristic of cimolodontans with large p4s. In the upper right corner of the labial side (Fig. 2B) is the postero-labial ridge (or cusp). However, on the lingual side of the tooth (Fig. 2C) there is also

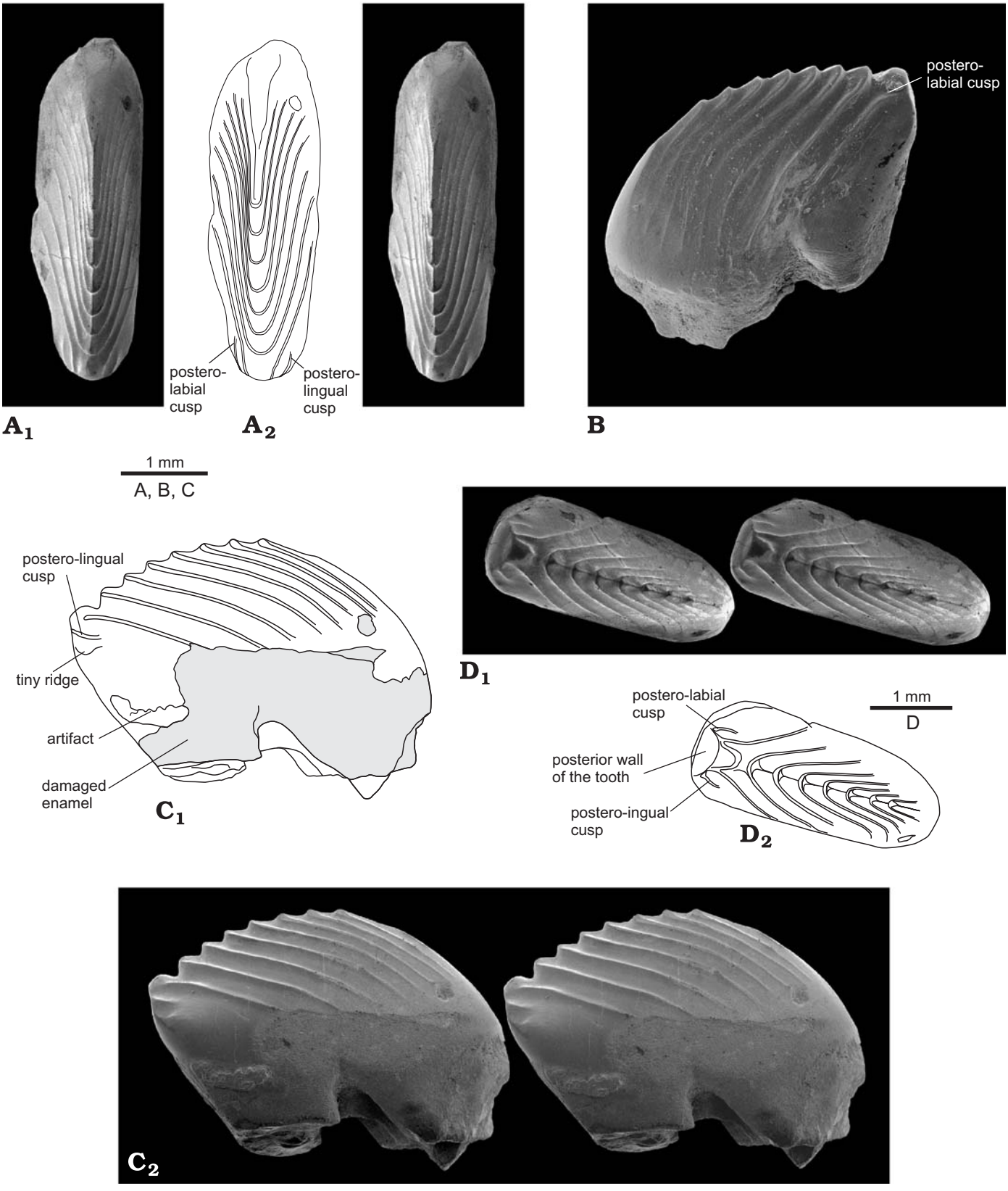

Fig. 2. SEM micrographs of ?left p4 of *Argentodites coloniensis* gen. et sp. nov., MPEF 604 (Upper Cretaceous La Colonia Formation, Chubut Province, Argentina) in different views. **A**. Dorsal view. Stereo-photograph (A_1) and explanatory drawing of the same (A_2). **B**. Labial view of the same, figured in a presumable life position, with posterior margin arranged sub-vertically. **C**. Lingual view of the same, with posterior margin turned counterclockwise from presumable life position. Explanatory drawing (C_1) and stereo-photograph (C_2). **D**. Postero-dorsal view of the same. Stereo-photograph (D_1), and explanatory drawing (D_2).

a ridge, almost identical to that which occurs on the labial side (Fig. 2B). We designate the ridge seen in Fig. 2C the postero-lingual ridge. In spite of this ambiguity and unknown function of the postero-lingual ridge, we identify the more convex side of the tooth as the lingual, and the tooth as the ?left p4.

Description.—The crown of the tooth (Fig. 2) is almost complete, covered with well preserved enamel, which is apparently missing from a large area of the ventral part of the lingual side and from the small antero-ventral strip over the base of the anterior root, on the labial side. The preserved part of the crown shows that the anterior root was more robust (wider) than the posterior one, as is typical for cimolodontan (but not "plagiaulacidan") p4s. The enamel-covered anterior triangular lobe, which in most multituberculates extends over the base of the anterior root on the labial side, is not recognizable, as the root has not been preserved and the crown of the tooth is broken dorsal to it. The crown is also broken over the posterior root.

At the presumed life position of the tooth (Fig. 2B), the dorsal margin is nearly straight; the posterior margin is long and straight, directed downward (and insignificantly medially). At this position the anterior margin is strongly convex anteriorly. The dorsal margin is well preserved, covered with eight apical cusps (serrations), the first seven of which are sharp, indicating a young age for the individual; only the eighth cusp bears insignificant wear. The first cusp is situated at about one third of the tooth length from the front. All the cusps on both sides are provided with ridges, which are more prominent on the labial than on the lingual side. The first seven labial ridges connect to their lingual counterparts at the very edge of the crown. The labial and lingual 8th ridges do not reach the 8th serration and are not connected at the top. The ridges on labial and lingual sides are equally prominent and of comparable length. The apparent differences in prominence of the ridges and their length seen in Figs. 2B and $2C_2$ are caused by different lighting. The first labial (and lingual) ridge extends parallel to the convex anterior margin of the tooth. On the labial side to the rear of the last cusp, there is a very short postero-labial ridge, which reaches the posterior margin of the tooth, below the 8th serration. An identical ridge (postero-lingual) is present on the lingual side of the tooth (Fig. 2C), a feature which does not occur in Laurasian cimolodontans.

Below the postero-lingual ridge there is a tiny ridge, concave upward, hardly discernible (Fig. $2C_1$). We have not discerned such a ridge on the labial side. At the bottom of the preserved lingual side of the crown, there is a structure which could be a poorly preserved row of tiny ?cusps (Fig. $2C_1$), but which we regard as an artifact.

Comparisons

The characteristic feature of most Ptilodontoidea, with which *Argentodites* shares enamel microstructure, is a highly vaulted p4, which protrudes dorsally over the level of the molars (see Kielan-Jaworowska et al. 2004: fig. 8.43). The upper margin of p4 of *Argentodites*, if our identification of its life position in Fig. 2B is correct, would have a more horizontal upper margin than in members of the Ptilodontoidea with lowest crowns such as *Mesodma* and *Mimetodon*.

Argentodites differs from MACN-RN 975, described by Kielan-Jaworowska and Bonaparte (1996) from Los Alamitos Formation of Patagonia. The p4 of MACN-RN 975 is a rectangular tooth with a small number of serrations, recalling p4 or p3 of "plagiaulacidans"; its enamel microstructure has not been studied. *Argentodites*, with convex anterior margin and prismatic enamel, has structure recalling the Cimolodonta. However, its long posterior margin invokes conditions seen in "Plagiaulacida".

Enamel microstructure

Because MPEF 604 is a unique specimen, a non-destructive technique (un-embedded specimen) was used. The specimen was ground at the anterior side, following a plane tangential to the row of cusps to ensure exposure of enamel and dentine. Grinding was done under light microscope using 1000 grit powder. All grit was removed by ultrasonic cleaning and the piece was allowed to air dry. The tooth was etched with 10% hydrochloric acid for three or four seconds to enhance morphological details. Enamel microstructure was studied under Scanning Electron Microscope (SEM) Jeol JSM-6360 LV. The etched enamel zone is shown within the square in Fig. $3A_1$.

The enamel is prismatic. The prisms are small (average diameter 3.8 μm) and fairly well-defined (Fig. 3). Most prisms are clearly surrounded by a prism sheath and could thus be identified as circular, while some sectors have prisms with open sheath (arcade-shaped prisms); both prism types can co-occur (Fig. $3A_2$, A_4). Depending upon the area sampled, prism shape varies considerably from circular (near the dentine, Fig. $3A_3$, A_4) to elongate and elliptical closer to the outer enamel surface (OES; Fig. $3A_5$), according to the angle of the section plane through the prisms. This indicates a slight curvature of the prisms toward the OES. Scarce enamel tubules are present near the dentine (Fig. $3A_3$). Crystals of interprismatic material lie at approximately 45° with respect to prisms.

The description of numerical density and distribution of enamel prisms has been very informative in multituberculate enamel studies (see Fosse 2003 for a review). In *Argentodites* enamel, mean prism central distance is 6.51 μm, yielding 27,247 prisms per mm^2. Prism size and numerical density correspond to the normal prismatic type seen in numerous recent mammalian enamels.

Enamel characteristics are similar to those of ptilodontoids; furthermore, *Argentodites* shares the co-occurrence of circular and arcade-shaped prisms with *Mesodma* (Ptilodontoidea) and the microcosmodontid *Microcosmodon* (Carlson and Krause 1985; Fosse et al. 1985). *Argentodites* has mostly circular prisms, like *Mesodma* (which we figure for comparison in Fig. 3B).

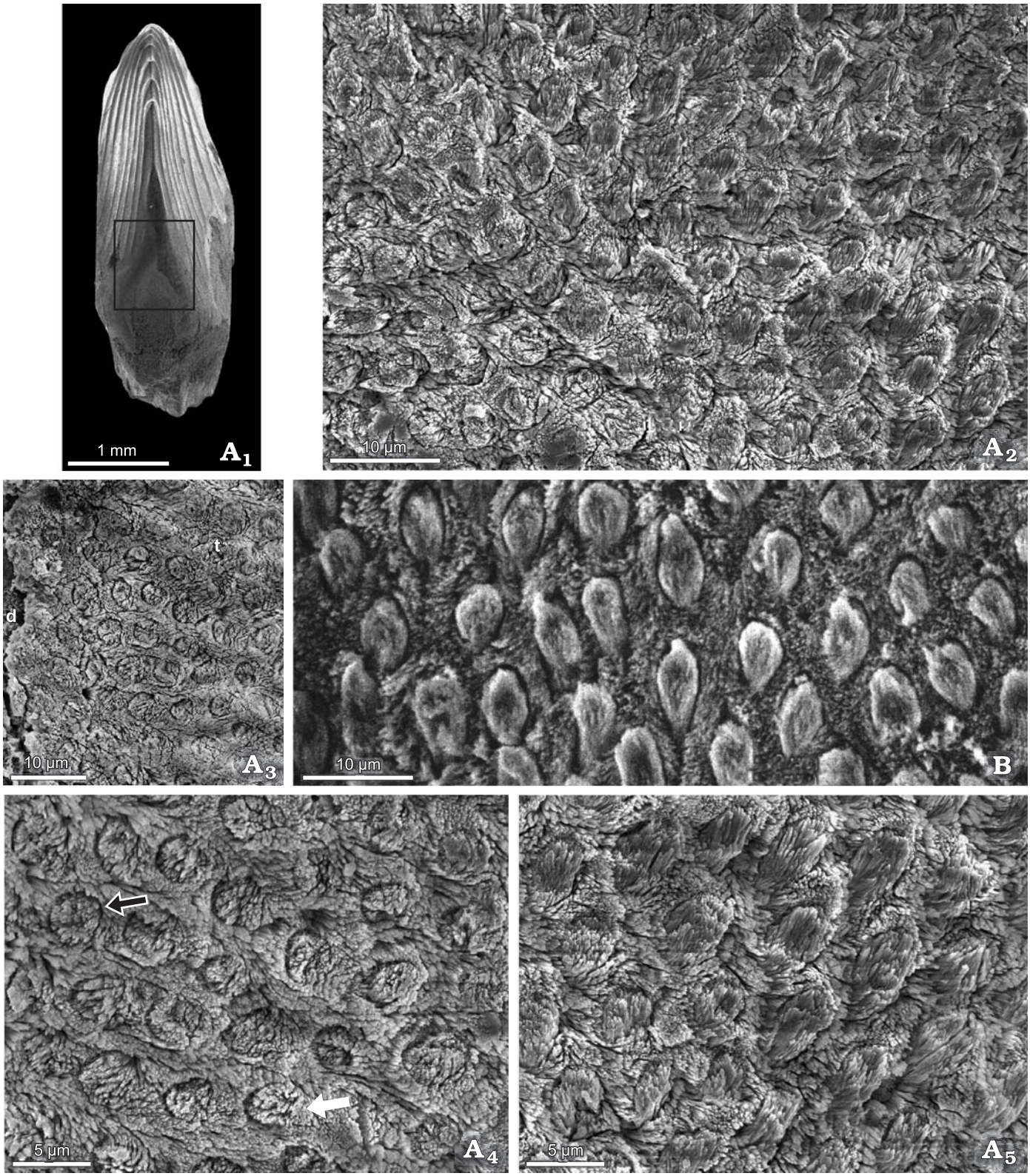

Fig. 3. SEM micrographs of etched enamel surfaces of **A**. *Argentodites coloniensis* gen. et sp. nov., MPEF 604 (Upper Cretaceous La Colonia Formation, Chubut Province, Argentina) and **B**. A ptilodontoid multituberculate *Mesodma* sp., PMO 169.283 (Early Paleocene Ravenscrag Formation, Saskatchewan, Canada). A_1**.** Anterior view of p4 of *A. coloniensis,* etched enamel zone shown within the square. A_2. Enamel section tangential to the row of cusps showing prism arrangement. Dentine in lower left corner. A_3. Area near the dentine; t, enamel tubules, d, dentine. A_4. Detail of A_2 showing prisms with circular cross section, closer to the dentine. Black arrow, closed prism sheath; white arrow, open prism sheath. A_5. Another detail of A_2, showing elongated prisms. **B**. *Mesodma* sp., enamel showing prism arrangement, in the same scale as A_2, in order to enable a comparison.

Discussion and conclusions

The discovery of multituberculate mammals in Upper Cretaceous deposits of Argentina has obvious paleogeographic implications. Pascual (2006) indicated that the history of land mammals on South America can be characterized by two major phases, which he termed the Gondwanan Episode and South American Episode. During the Gondwanan Episode the mammal fauna consisted almost exclusively of endemic Gondwanan lineages, the best record of which is from the Patagonian region of Argentina. The characteristic feature of this fauna is the lack of therian mammals with tribosphenic molars. The second South American Episode is dominated by therian mammals with tribosphenic molars, which arrived from North America by the very end of the Cretaceous.

The presence of two genera of multituberculate mammals in the Upper Cretaceous deposits of Patagonia—*Argentodites*, and an unnamed taxon represented by MACN-RN 975—shows that during the Early or Late Cretaceous, in spite of isolation, some Laurasian mammals reached South America. As *Argentodites* differs from Laurasian cimolodontans in several important characters (see Diagnosis), we assign it to Cimolodonta tentatively, assuming that the group to which it belongs might have developed several other characters, which differentiate it from the Laurasian cimolodontans.

MACN-RN 075 has a bladelike p4 of multituberculate pattern. Because it is rectangular rather than arcuate in labial view, it resembles members of the paraphyletic multituberculate suborder "Plagiaulacida". As the "Plagiaulacida" survived on the northern hemisphere apparently only through the Albian (Kielan-Jaworowska et al. 2004; Hahn and Hahn 2006a), the unnamed "plagiaulacidan" from the Los Alamitos Formation (or its ancestors) possibly arrived in South America before the Late Cretaceous. The time of arrival of *Argentodites* is uncertain. It might have originated from Laurasian Early Cretaceous unknown members of Cimolodonta (which had normal prismatic enamel and retained some "plagiaulacidan" characters), and consequently, arrived in South America at the same time as the taxon represented by MACN-RN 975, or during the Late Cretaceous, at the same time as other North American immigrants, like some dinosaurs (e.g., Gayet et al. 1992; Bonaparte 1994, 1996).

Other purported multituberculate mammals from the Cretaceous of Morocco (Sigogneau-Russell 1991; Hahn and Hahn 2003) have been removed by Butler and Hooker (2005) to the Haramiyida (see also Hahn and Hahn 2006b). Another mention of Gondwanan multituberculates is an abstract by Krause and Grine (1996), who reported the finding (not figured) of a fragment of a multituberculate molar in rocks of the Upper Cretaceous Maevarano Formation of Madagascar.

Although these findings are modest, they show that multituberculates may well have had a wider geographical distribution on the continents of Gondwana, than previously thought.

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References

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

Bonaparte, J.F. 1996. Cretaceous tetrapods of Argentina. *Münchner geowissenschaftliche Abhandlungen A* 30: 73–130.

Butler, P.M. and Hooker, J.J. 2005. New teeth of allotherian mammals from the English Bathonian, including the earliest multituberculates. *Acta Palaeontologica Polonica* 50: 185–207.

Carlson, S.J., and Krause, D.W. 1985. Enamel ultrastructure of multituberculate mammals: an investigation of variability. *Contributions from the Museum of Paleontology, University of Michigan* 27: 1–50.

Cope, E.D. 1884. The Tertiary Marsupialia. *American Naturalist* 18: 686–697.

Fosse, G. 2003. Calculation of numerical density of enamel prisms in multituberculate enamels: A review. *Acta Palaeontologica Polonica* 48: 657–660.

Fosse, G., Kielan-Jaworowska, Z., and Skaale, S.G. 1985. The microstructure of tooth enamel in multituberculate mammals. *Palaeontology* 28: 438–449.

Gayet, M., Rage, J.C, Sempere, T., and Gagnier, P.Y. 1992. Modalités des échanges de vertebras continentaux entre l'Amérique du Nord et l'Amérique du Sud au Crétacé supérieur et au Paléocène. *Bulletin de la Societé géologique de France* 163: 781–791.

Hahn, G. and Hahn, R. 2003. New multituberculate teeth from the Early Cretaceous of Morocco. *Acta Palaeontologica Polonica* 48: 349–556.

Hahn, G. and Hahn, R. 2006a. *Catalogus Plagiaulacidorum cum Figuris (Multituberculata Suprajurassica et Subcretacea)*. Fossilium Catalogus I: Animalia. Pars 140, 344 pp. Backhuys Publishers, Leiden.

Hahn, G. and Hahn, R. 2006b. Evolutionary tendencies and systematic arrangement in the Haramiyida (Mammalia). *Geologica et Palaeontologica* 40: 173–193.

Kielan-Jaworowska, Z. and Bonaparte, J.F. 1996. Partial dentary of a multituberculate mammal from the Late Cretaceous of Argentina and its taxonomic implications. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* 145: 1–9.

Kielan-Jaworowska, Z., Cifelli, R.L., and Luo, Z.-X. 2004. *Mammals from the Age of Dinosaurs: Origins, Evolution, and Structure*. 630 pp. Columbia University Press, New York.

Krause, D.W. and Grine, F.E. 1996. The first multituberculates from Madagascar: implications for Cretaceous biogeography. *Journal of Vertebrate Paleontology* 16 (Supplement to No. 3): 46A.

Marsh, O.C. 1880. Notice on Jurassic mammals representing two new orders. *American Journal of Science* 20: 235–239.

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

Pascual, R. 2006. Evolution and geography: The biogeographic history of South American land mammals. *Annals of the Missouri Botanical Garden* 93: 209–230.

Sigogneau-Russell, D. 1991. First evidence of Multituberculata (Mammalia) in the Mesozoic of Africa. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1991: 119–125.