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Deciduous teeth morphology of some tremarctines (Ursidae, Tremarctinae). Descriptions, comparissons and possible evolutive implications

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Abstract. The morphology of some deciduous teeth of *Arctotherium tarijense* and *A. latidens* (Ursidae: Tremarctinae) is here described and compared for the first time. The crown morphology of dP4 and dp4 is similar to that of M1 and m1. The general morphology of dP / dp4 in *A. tarijense* and Ursinae is similar, but their permanent morphology dentition is different. The dP / dp4 of *A. tarijense* seems to bear a generalized set of characters (i.e. crown outline, the protocone and parastyle of dP4, the metaconid and hypoconid of dp4); unfortunately these teeth cannot be compared with their homologues in other tremarctines. Consequently, we are unable to include these characters in the phylogenetic analysis of the Tremarctinae subfamily in order to know whether the phylogenetic relationships are affected or not. It is noteworthy, that if these characters were present in M / m1 of *A. tarijense*, at least, some of them could be undoubtedly regarded as plesiomorphic features. In this respect, is the deciduous teeth morphology more conservative than that of permanent teeth?

Resumen. Morfología de los dientes deciduos de algunos tremactinos (Ursidae, Tremarctinae). Descripciones, comparaciones y posibles implicancias filogenéticas. Se describe y compara la morfología de algunos dientes deciduos de *Arctotherium tarijense* and *A. latidens* (Ursidae, Tremarctinae) por primera vez. La morfología del dP4 y dp4 es muy similar a la del M1 y m1. La morfología general de los dP / dp4 en *A. tarijense* y Ursinae es similar, aunque, la morfología de sus dientes definitivos es muy diferente. Los dP / dp4 de A. tarijense parecen poseer un conjunto de caracteres generalizados (en relación con el contorno de la corona, el protocono y el parastilo del dP4, el metacónido y el hipocónido del dp4). Desgraciadamente no es posible comparar esas piezas con sus homólogas en otros tremarctinos, por lo que no es posible incluir estos caracteres en el análisis filogenético de la subfamilia Tremarctinae con el fin de saber si sus relaciones filogenéticas se ven afectadas o no. Es importante remarcar que si esos carcateres estuviesen presentes en los M / m1 de *A. tarijense*, al menos algunos de ellos podrían ser interpretados como plesiomorfías. En este sentido, ¿la morfología de los dientes deciduos es más conservadora que la de los definitivos?

Key words. Ursidae, Tremarctinae, *Arctotherium*, deciduous tooth.

Palabras clave. Ursidae, Tremarctinae, *Arctotherium*, dientes deciduos.

Introduction

The Ursidae family comprises three lineages: Ursinae, Tremarctinae and Hemicyoninae (a basal subfamily of Ursidae that is recorded in the Miocene and Pliocene of North America and has some morphological affinities with tremarctines); Amphicyonidae is the sister group of Ursidae (Wyss and Flynn, 1993).

The four genera of the bear subfamily Tremarctinae (Carnivora: Ursidae) are distributed exclusively in America. 1) *Plionarctos* Frick is recorded from the Late Miocene to the Early Pliocene of North America with two species: *P. edensis* Frick and *P. harroldorum* Tedford and Martin. 2) *Arctodus* Leidy contains two North American Late Pliocene and Pleistocene species: *A. pristinus* Leidy and *A. simus* (Cope). 3) *Arctotherium* Bravard includes five South American species: *A. latidens* Bravard, restricted to the Ensenadan (Early to Middle Pleistocene), *A. vetustum* Ameghino registered only in the Bonaerian (Middle Pleistocene), and three Bonaerian - Lujanian (Middle Pleistocene to Early Holocene) species *A. brasiliense* (Lund), *A. bonariense* (Gervais) and *A. tarijense* Ameghino (Soibelzon, 2002). Finally, 4) *Tremarctos* Gervais has two species T. floridanus (Gildey) from the Late Pliocene and Pleistocene of North America, and the only living Tremarctinae *T. ornatus* (Cuvier) of South America, which has not yet been recorded as a fossil. Regarding the origin of the South American fossil bears, it is noteworthy that these bears arrived in South America from North America during the Great American Biotic Interchange (Marshall *et al*, 1984).

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The Tremarctinae are a monophyletic and sister taxon to the Ursinae (Trajano and Ferrarezzi, 1994; Talbot and Shields, 1996). *Plionarctos* and *Tremarctos* constitute the basal clade of the Tremarctinae (spectacled bears), and *Arctodus* and *Arctotherium* (short-faced bears) later diverging taxa. Within the clade formed by the five *Arctotherium* species, A. vetustum and *A. brasiliense* are more basal than *A. latidens*, and *A. bonariense* and *A. tarijense* are later diverging species (Soibelzon, 2002).

During the taxonomic and phylogenetic revision of the South American fossil bears (Soibelzon, 2002), one us (LS) found an incomplete juvenile specimen of *A. tarijense* with deciduous teeth, two isolated milk teeth of A. tarijense? and another one of *A. latidens* in old collections of Museo de La Plata and Museo Argentino de Ciencias Naturales "Bernardino Rivadavia".

Many studies have been made of the morphology of deciduous teeth of ursines such as *Ursus arctos* and *U. spelaeus* (see Koby, 1952; Radulescu and Samson, 1959; Terzea, 1969; Torres, 1988 and references therein) but there is no available information for tremarctines.

Kraglievich (1934) reported the discovery of deciduous teeth of South American short-faced bears, found in 1923 at Km 150 of "Canal 9" (at 4 m depth), Buenos Aires Province, Argentina. These teeth were associated with a femur and tibiae of an adult specimen of *A. tarijense.* The present study includes the re-examination of this material, the first morphological comparison of deciduous teeth of tremarctines and high quality anatomical illustrations. In addition, a radiograph of a juvenile mandible of *A. tarijense* is shown. Unfortunately, no deciduous teeth of the single extant *Tremarctos ornatus,* are known. Since commonly only low quality photographs of bears deciduous teeth published in old papers that are really difficult to access, are available, we expect that this study will provide an identification key for tremarctine deciduous teeth in other collections and, useful characters for phylogeny. Our results suggest that some characters of the milk dentition of *A. tarijense* are significant to understanding the evolution of cheek teeth patterns and as source of characters for future phylogenetic analyses.

Abbreviations. MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; MHJ: Museo Histórico de Junín, Junín, Argentina; MLP: Museo de La Plata, La Plata, Argentina. MNHN AC Museum National d'Histoire Naturelle, Anatomie Comparée, Paris, France. MDL: maximum mesiodistal length; BLL: maximum buccolingual length. d: deciduous tooth.

Material and methods

A. tarijense Ameghino. MACN 8582 left premaxilla fragment with dI2 and I1-2 in their alveoli; left maxilla fragment with dP3 and dP4; upper dC; left mandible fragment with dp4, and i1-3, lower C, p1, p4, m1 and m2 in their alveoli; right mandible fragment; one metapode and two phalanges, from Km 150 of "Canal 9", Buenos Aires Province, Argentina; Lujanian (Late Pleistocene).

A. tarijense ? MLP 92-XI-28-1, right dP4, from Camet Norte, Mar Chiquita, Buenos Aires Province, Argentina; Lujanian (Late Pleistocene) (24.450 (150 14C yr BP, at 37º 49´S / 57º 29´ W; see Pardiñas *et al*., 1998). MLP 92-XI-27-1, left dP4, from Centinela del Mar 38° 26´ S / 58° 14´ W, General Alvarado, Buenos Aires Province, Argentina; Belgranian (Last Interglacial ca. 130 Ka, Isla *et al*., 2000).

A. latidens MACN 6132, right upper dC, from Miramar, Buenos Aires Province, Ensenadan (Early-Middle Pleistocene).

The specimen MACN 8582 is identified as *A. tarijense* because it has also the m1-2, but the other two (MLP 92-XI-28-1 and MLP 92-XI-27-1) are only isolated dP4 and it is impossible to make a secure specific determination, for this reason we identified them as *A. tarijense*?

Specimens of Ursinae used for comparisons: *Melursus ursinus* MNHN AC 10998

Ursus arctos MNHN AC 1896-346 and those described in Koby (1952), Terzea (1969) and Torres (1988).

Morphological terms and measurements definitions follow Koby (1952) and Torres (1988), but we numbered the deciduous premolars mesiodistally as Terzea (1969) and all recent authors (ie. the last deciduous premolar is dP/dp 4) to facilitate comparisons. Measurements were taken with dial calipers to the nearest mm.

Description

The morphology of the second upper deciduous incisor (dI2) (MACN 8582) is quite different from that of the corresponding permanent tooth (figures 1A-C, table I). In labial view, the upper margin of the crown is rounded, and the mesial and distal margins join toward the base of the crown. In occlusal view, the tooth is sub-triangular in section. An enamel crest crosses the lingual margin mesio-distally, and in the middle of this crest a low cusp is developed. The crown is implanted obliquely and slightly rotated mesially. The root is mesio-distally compressed and sub-triangular in section, as well as the crown.

The upper deciduous canine crown (dC) (MACN 8582) is distally curved and the apex is distally and labially directed (figures 1D-E, table I). Both the crown and the root are labiolingually compressed. The lingual side has a thin enamel edge running from the neck to the crown apex. The distal side is convex,

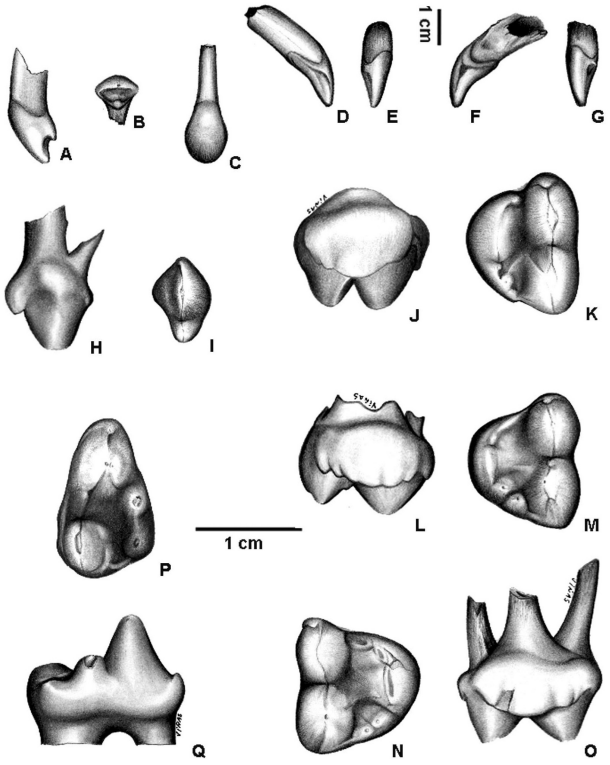

Figure 1. *Arctothenium tarijense*, MACN 8582: left dI2. **A,** lateral view; **B,** occlusal view; **C,** labial view; left dC; **D,** mesial view; **E,** labial view. *A. latidens*, MACN 6132: rigth dC; **F,** mesial view; **G,** labial view. *A. tarijense*, MACN 8582: left dP3; **H,** lingual view; **I,** occlusal view; left dP4 (J) lingual view, (K) occlusal view. A. tarijense?, MLP 92-XI-27-1: left dP4; **L,** lingual view; **M,** occlusal view; MLP 92-XI-28-1: rigth dP4; **N,** occlusal view; **O,** lingual view. *A. tarijense*, MACN 8582: left dp4; **P,** occlusal view; **Q,** lingual view.
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and the mesial side is slightly flattened. The crown basal margin on the mesial side descends sharply and then ascends forming a V-shaped notch. At the lowest point of this notch there is a protuberance with two enamel crests obliquely diverging, one descending toward the apex of the crown, and the other rising through the tooth neck. The upper deciduous canine MACN 6132 (figures 1F-G) of *A. latidens* is morphologically similar to that of *A. tarijense* but more robust (table I). The edge that crosses the lingual side is much less conspicuous in A. latidens than in *A. tarijense*. This specimen also shows more wear on the apex of the crown and on the mesial protuberance, the latter produced by abrasion against the lower canine.

The third upper deciduous premolar crown (dP3) (MACN 8582) is laterally compressed, elongated mesio-distally (figures 1H-I, table I), and mesio-distally rotated. Two conspicuous cusps are aligned, the mesial one (paracone?) is much higher and has a wider base than the distal one (metacone?); a mesiodistally oriented enamel ridge connects both cusps. This ridge is thickest on the mesial margin of the crown base of the anterior cusp, where a small cuspule is developed. The dP3 has two roots, the mesial one being thinner.

The fourth upper deciduous premolar crown (dP4) is slightly wider than long in MACN 8582, but longer than wide in MLP 92-XI-28-1 and MLP 92-XI-27-1 (Table I). The labial margin is almost straight and longer than the lingual margin, which is very convex (figures 1J-O). The mesial and distal margins are almost straight and converge toward the lingual side. In oclusal view the crown is triangle-shaped. The two labial cusps are elongated mesiodistally, and both are much larger than the lingual cusps. The mesial cusp (paracone) is larger and slightly compressed than the distal cusp (metacone). The paracone is lingually inclined, while the metacone is vertical. A small but well differentiated cusp, the parastyle, arises in front of the paracone. Between the paracone and the metacone a very small cusp is developed in MLP 92-XI-27-1. A deep furrow runs mesiodistally between the labial and lingual cusps. On the lingual margin of the crown there are four or five relatively low cusps arranged in a mesiodistal series. The first cusp of the series is small and lies at the mesio-lingual angle. This cusp forms a continuous crest with the central cusp (protocone), which is larger. In two of the three specimens studied (MLP 92-XI-28-1 and MLP 92-XI-27-1) the protocone has two apices nearly indistinguishable one from each other (figures 1M-N). Two small cusps are behind the protocone, in front of the metacone, the distal cusp somewhat lower than the proximal. Two of the three specimens show on the lingual side of the metacone, an enamel crest descending toward the center of the crown. In one specimen (MACN 8582) it merges with another crest that comes from the two distal cusps of the lingual margin (Figure 1K), and in the other (MLP 92-XI-27-1) it is in direct contact with both distal cusps (Figure 1M). No cingulum is observed, other than a slight widening of the enamel running along the labial side of the metacone in one of the three specimens (MLP 92-XI-27-1). Deciduous P4 is the only deciduous tooth with three roots, two labial roots that belong to the paracone and the metacone, and one lingual root that corresponds to the series of cusps of the lingual margin.

The crown of the fourth deciduous premolar (dp4) (MACN 8582) is transversely compressed, the labial and distal margins are almost straight, the lingual margin is slightly convex and the mesial margin rounded (figures 1P-Q, table I). The trigonid shows

Table 1. Comparison of sizes of all known Tremarctinae deciduous teeth / *Comparación de tamaños de todos los dientes deciduos conocidos para los Tremarctinae.*

Taxon	*A. tarijense*		*A. tarijense?*		*A. tarijense?*		*A. latidens*	
	MACN 8582		MLP 92-XI-28-1		MLP 92-XI-27-1		MACN 6132	
	MDL	BLL	MDL	BLL	MDL	BLL	MDL	BLL
dI2	4,45	3,8						
dP3	8,4	5,7						
dP4	13,6	12,3	12,9	11,6	13,5	11,3		
dC	6	7					7.3	8,3
dp4	15,5	8,2						

MDL: maximum mesiodistal length (mm)
BLL: maximum buccolingual length (mm)
MDL and BLL measured between landmarks at the limit of the crown.

three main cusps, paraconid, protoconid and metaconid, and an accessory cusp (always present in Tremarctinae) on the posterolabial side of the protoconid near its base. The dp4 paraconid lies on the mesial margin of the crown and is relatively smaller than in m1. The protoconid is the most conspicuous cusp; it occupies all the width of the crown and completely separates the paraconid from the metaconid, as in m1. Three ridges descend from the apex of the protoconid, one on the antero-labial side toward the paraconid, another on the postero-labial side toward a small accessory cusp, and the third on the postero-lingual side extending toward the metaconid. The metaconid is placed on the lingual side of the crown just behind the protoconid and its size is similar to that of the metaconid of the m1.

Two cusps are present on the talonid area, hypoconid and entoconid, which are separated from the protoconid and metaconid by a deep notch. The hypoconid, larger than the entoconid, is placed on the labial margin. On the base of the cusp, on the lingual-mesial angle of the crown, there is a small enamel thickening. Also on the postero-lingual corner at the base of the hypoconid there is an enamel shelf, which together with a thin enamel crest running along the distal margin of the talonid toward the entoconid, closes the distal margin of the talonid. The entoconid is relatively small, formed by a single cusp, and is placed on the postero-lingual angle of the crown. An enamel crest connects the entoconid with the metaconid. A thin cingulum runs along the labial side of the talonid at the level of the hypoconid. The dp4, as well as the m1 has two roots, with the distal root larger than the mesial one.

A fragment of the left premaxilla (MACN 8582) preserves, in addition to the dI2, the I1 and I2 encrypted at the bottom of their alveoli. The enamel of the main cusp of both incisors is mineralized, while the enamel of the lingual margin and the area close to the neck of the crown is in a relatively early stage of development. The alveolus of the dI1 lies mesio-lingually to the dI2 and is approximately of the same size of the latter. The alveolus of the dI3 lies distal to the dI2.

The left hemimandible (MACN 8582, Figures 2.A-C) preserves most of the horizontal ramus, but it lacks the articular condyle and the ascending ramus. Three alveoli for the deciduous incisors are preserved labially. The alveolus of the di2 is very close to that of the di1 and both are similar in size. The alveolus of the di3 is larger than the other two, and it is located behind the di2. Below this area, the three permanent incisors remain inside the mandibular body. Externally only the apical end of the i1 and i3 are exposed to view. The i2 crown, which can only be seen by X-Ray, is located both distally and below the i1. The radiograph shows that the i1 has the most developed crown, and the most mineralized enamel.

On the alveolar margin, there is the alveolus for dp1, followed by one alveolus for dp2, two alveoli for the two roots of dp3, and the implanted dp4. The p1 is seen below the alveolus for the dp2, with a large portion of its apex mineralized (figures 2B-C). The p4 is observed in the radiograph between the two roots of dp4 (figures 2B-C). It is in a relatively earlier stage of development than p1. Labially to the alveoli of the dp1 and dp2, is the alveolus of the large deciduous canine. The permanent canine is seen below this alveolus in the radiograph (figures 2,B-C). Along the alveolar margin behind the dp4, the first stage in the development of the m1 alveolus may be observed. This area is damaged; consequently the alveoli of the m2 and m3 cannot be confidently reconstructed. During early preparation, the m1 and m2 (figures 2.D-G) were found below this area of the mandible and they were unfortunately removed from its natural place and kept separately in the collection. The m1 (figures 2.D-E) has all cusps fully developed, but the enamel is only mineralized on the paraconid, protoconid, metaconid and hypoconid. The enamel of the entoconid, the floor and the distal margin of the talonid, and all the lower margins of the crown

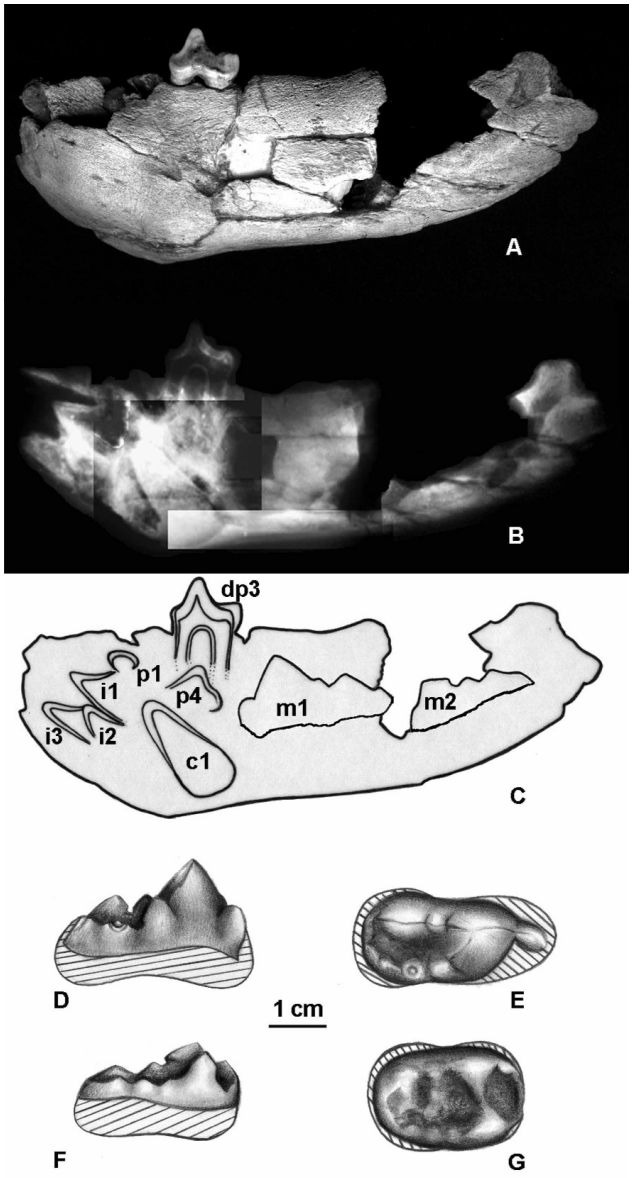

Figure 2. *Arctothenium tarijense*, MACN 8582: left hemimandible. **A,** external view; **B,** composed radiograph and **C,** hemimandible and teeth outlined from the radiograph with the addition of those of m1 and m2 in their assumed position. *A. tarijense*, MACN 8582: left m1; **D,** lingual view and **E,** occlusal view; MACN 8582: left m2; **F,** lingual view and **G,** occlusal view /
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are at a primary stage of maturation. The m2 (figures 2.F-G) shows a still earlier stage of development than the m1. The protoconid and metaconid are the most developed cusps and the hypoconid the least developed in accordance with the description of Tonge (1976). The remaining occlusal surface and the margin of the crown are at an early stage of development. On the talonid lingual margin, both cusps of the entoconid may be seen.

Comparisons and discussion

The general dental formula of adult Ursidae is I 3/3 C1/1 P 4/4 M 2/3. This is the dental formula of tremarctines, but ursines usually lack the P 2-3/2-3. The deciduous dental formula of *U. arctos* and *U. spelaeus* is dI 3/3 dC 1/1 dP 2-4/2-4, and some specimens of *U. spelaeus* have dP/dp 2 completely reduced (Koby, 1952; Radulescu and Samson, 1959; Terzea, 1969; Torres, 1988). Regarding the deciduous dental formula of *A. tarijense*, although there is not enough material to allow a definitive determination, it may be tentatively established as dI 3/3 dC 1/1 dP 1-4/1-4. This is coincident with the deciduous dental formula of T. ornatus deduced from the notes of Saporiti (1949).

In most mammals the milk dentition is replaced once, a condition called diphyodonty (hemiphyodontism by Mones, 1982), the first set is called primary and the next set secondary (Jernvall, 1995); then deciduous teeth and molars are both primary teeth. As Jernvall (1995) pointed out, the last deciduous premolars always resemble the first permanent molars. In this sense, the crown morphology of dP/dp4 in ursids is quite similar to that of M/m 1 respectively and, the dP4 occlude on dp4 in the juvenile in much the same way as the M1 occlude on the m1 in the adult. On the other hand, their corresponding permanent premolars (except for P4) are simpler.

Although the general morphology of dP/dp4 in *A. tarijense* resembles that of Ursinae (see Koby, 1952 for details) considered -as previously mentioned- the sister group of Tremarctinae, the adult dentition of this taxon is quite different (see Torres, 1988 and Kurtén, 1967 for more details).

When dP4 and dp4 of *A. tarijense* are compared with M1 and m1 respectively, significant morphological differences are seen. Moreover, these morphological features can be seen in the M1 and m1 of related tremarctine taxa, and in Ursinae, Hemicyoninae and Amphicyonidae.

Comparisons between dP4 and M1

The lingual side of the crown of dP4 of *A. tarijense* is very convex, but that of the M1 is slightly convex as in all other *Arctotherium* species (*A. bonariense, A. vetustum, A. latidens* and *A. brasiliense*). In the three other tremarctine genera (*Arctodus*, *Plionarctos* and *Tremarctos*) the lingual side of M1 is straight, as in most Ursinae. In dP4 of *U. spelaeus* the lingual side of the crown is slightly convex as in M1 of *Arctotherium.* The fourth upper deciduous premolar of *A. tarijense* is triangle-shaped in occlusal view, but M1 of all *Arctotherium* species is sub-quadrate and in the other three genera of Tremarctinae (*Tremarctos*, *Arctodus*

and *Plionarctos*) and in all ursines the M1 is sub-rectangular. First upper molars with very convex lingual sides and triangle-shaped in occlusal view were found only in Amphicyonidae (Carnivora) and in hemicyonines. The protocone of dP4 of *A. tarijense* is the largest cusp of the lingual row, this condition is only observed in the M1 of *A. latidens* (among Tremarctinae), in Hemicyoninae and in the dP4 of Ursinae. In the M1 of all other Tremarctinae and Ursinae, the protocone has the same size as the other lingual cusps. The dP4 of *A. tarijense* has a well differentiated parastyle. This cusp is reduced or absent in the M1 as well as in *A. latidens* and *A. bonariense*, but conspicuous in the most basal South American taxa (*A. vetustum* and *A. brasiliense*), in all other Tremarctinae, Ursinae and in most Hemicyoninae.

Comparisons between dp4 and m1

The entoconid of dp4 of *A. tarijense* is placed on the postero-lingual angle of the crown and formed by a single cusp. In all tremarctines (except for *Tremarctos*) the entoconid of m1 is placed forward on the lingual side of the talonid and has two or three apices. In some ursines such as *U. americanus* and all Hemicyoninae the morphology of the entoconid of m1 is the same as that of dp4 of *A. tarijense* and m1 of *Tremarctos*. In others such as *U. arctos* and *U. spelaeus*, the condition observed in m1 is that of most tremarctines. The hypoconid of dp4 of *A. tarijense* is large and consists of a single conical cusp. In all tremarctines (except for *A. latidens*), the hypoconid of m1 is mesiodistally elongated and has two apices separated by a shallow line in the enamel. In dp4 of *U. spelaeus* the hypoconid is represented by one or more cusps (Koby, 1952). In m1 of all Ursinae (except for *Ursus spelaeus*) and Hemicyoninae the hypoconid has the same morphology as that of dp4 of *A. tarijense* and m1 of *A. latidens*. It is noteworthy that the multiplication of main cusps on the molars is a common feature of *U. spelaeus* (Torres, 1988).

In addition, it is noteworthy that *A. tarijense* dI2 (MACN 8582) has a similar morphology than that of the ursine I2 but very different from that of tremarctine I2.

Summarizing, the dP4/dp4 of *A. tarijense* seem to bear a generalized set of characters (concerning the crown shape, the protocone and parastyle of dP4 and, the metaconid and hypoconid of dp4). Unfortunately these teeth cannot be compared with their homologues in other tremarctines. For this reason we cannot include these characters in the phylogenetic analysis of the Tremarctinae.

In this respect, is the deciduous teeth morphology more conservative than that of permanent teeth? Mottl (1934, cited in Koby, 1952) compared the dp4 of *U. spelaeus* with its m1 and observed that some features of dp4 may be considered primitive. Koby (1952) did not agree with this idea and expressed that the inferences of the author were not well supported. Flower (1871, cited in Woodward, 1892) considered that "the milk teeth of the Eutheria invariably show a more primitive pattern and shape than those of the permanent or second series which replace them". Von Koenigswald (1967: 779) considered that "this observation is not absolutely correct" and proposed two possibilities: mammalian posterior milk teeth could either preserve dental features characteristic of their ancestors (be "conservative") or precede the molars and replacement premolars in adapting to changing conditions (be "progressive"). This author considered that carnivores provided the best illustration about how conservative the last deciduous molars could be; and after a discussion of the evidence found in *Canis*, *Meles*, *Ursus*, *Hyaena* and *Felis* concluded that "That means in some carnivores we find preserved in last deciduous molars elements typical for the Miocene-Pliocene species some 10 million to 12 million years ago." (Von Koenigswald, 1967: 780).

As it can be seen, there is some evidence found by other authors in related taxa that support our hypothesis. Unfortunately, due to the scarcity of deciduous premolars of short-faced bears in the fossil record we cannot arrive at a definitive conclusion. But the observations on the morphology of the fourth upper and lower deciduous teeth of *A. tarijense* seems to be a good starting point. Detailed comparison with ursine deciduous and permanent teeth is planed as future work.

In addition, we can estimate the age of MACN 8582. In *T. ornatus* i1 is the first permanent tooth that erupts during the fifth month of life (see Saporiti, 1949). If we assume that the sequence of appearance of the permanent teeth in *A. tarijense* is similar to that of *T. ornatus*, MACN 8582 may have been approximately four to five months of age, as the i1 had not yet emerged. The large size of the permanent teeth involves a rebuilding of the jaw in this process; that may have been an important mortality factor (Ehrenberg, in Kurtén, 1958). On this sense, it is noteworthy the great difference in size between the deciduous and permanent teeth, for example M1 of *A. tarijense* is approximately twice the size of dP4.

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