A Blancan (Pliocene) short-faced bear from El Salvador and its implications for Tremarctines in South America

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With 3 figures and 1 table


Abstract: We present here a deciduous tooth recovered from the Blancan (Pliocene) Río Tercayate locality (Republic of El Salvador) and assign it to cf. Arctotherium (South America short-faced bears) based on its morphology and size. Carnivores, like many other taxa, entered South America from North America during the “Great American Biotic Interchange” (GABi). We think that this individual was part of the stock that entered South America and may have been ancestral to later Arctotherium species. It has been postulated that Arctodus and Arctotherium are sister groups that make up the “short-faced bears clade”. Until now, Arctotherium had only been recorded in South America; the oldest record corresponds to Arctotherium angustidens from the Eosenan (Early to Middle Pleistocene) of the Pampean Region of Argentina; 5200 km from the Panamanian isthmus. Among Eosenan sediments the oldest ones are those of “las tocas del Río de La Plata” locality (Pampean Region). The age of these sediments is 1Ma and they correspond to Chron C12r. In the northern portion of South America (Venezuela) Arctotherium specimens are only recorded from the Late Pleistocene. Thus, the new specimen provides the earliest record of Arctotherium, extends the distribution of this taxon in Central America and may represent the basal stock for short-faced bears in South America.

Key words: Ursidae, Tremarctinae, Arctotherium, Central America, Blancan, Pleistocene.

1. Introduction

The bear genera that constitute the subfamily Tremarctinae (Carnivora: Ursidae) are distributed exclusively in America. Of these, Plionarctos is recorded from the Late Miocene to the Early Pliocene of North America with two species (Trethew & Martin 2001). Arctodus contains two North American species, Arctodus cf. Pliocene and Pleistocene species: A. pristinus and A. simus. The oldest record for Arctodus is from Blancan IV (Late Pliocene), and the youngest is from Rancholabrean (Küster 1967; Richards et al. 1996).

Arctotherium comprises five South American Pleistocene species: A. angustidens, A. vechiatus, A. tomari- ence, A. wingei and A. tarigense (see Soibelzon 2004a; Soibelzon et al. 2005). Tremarctos includes two species, T. borissoni from the Late Pliocene and Pleistocene of North America and the only living Tremarctinae, T. ornatus of South America, which has not been recorded as a fossil (see Fig. 1).

The short-faced bear clade (Soibelzon 2002a, 2002b, 2004b), composed of Arctotherium (in South America, and after the present contribution in Central America) and Arctodus (in North America), was a
group of gigantic to medium sized bears that were endemic to the Americas.

Short-faced bears (*Arctotherium*) arrived in South America from North America, through the Panamanian Isthmus, as part of the “Great American Biotic Interchange” (GABI, MARSHACK et al. 1982). The oldest reported record of a *hominid* hominin in South America corresponds to *Arctotherium angustidens* which is first recorded in the Ensenadan of the Pampean Region of Argentina (SOBELSON 2004a, SOBELSON et al. 2005). Among Ensenadan (Early to Middle Pleistocene) sediments the oldest ones are those of “las tocas del Río de La Plata” (Pampean Region). The age of these sediments is 1.8 Ma and they correspond to Chron C1r2t. In the northern portion of South America *Arctotherium (A. vincenti)* is recorded only in the Late Pleistocene (SOBELSON & RENCON 2007; see Fig. 1).

The aim of this work is to describe a fourth lower deciduous premolar (dp4, Fig. 2A, B) that was recovered from the Late Pleistocene of Rio Tognate, El Salvador (Fig. 7) and analyze the biogeographic significance of the discovery. After this study we assigned this deciduous tooth to *Arctotherium*. Deciduous premolars of short-faced bears are scarce in the fossil record, they are only known from one South American species: *Arctotherium variens* (see SOBELSON & COULIN 2004). The present con-
tribution establishes a more precise date for the potential immigration of short-faced bears into South America and extends the distribution of Arctotherium to Central America. Here we present the oldest and northernmost record of Arctotherium.

2. Material and methods

Morphological terms and measurement definitions follow Koby (1952) and Torres (1988) but we numbered the deciduous premolars mesiodistally as Terzea (1969) and Sobelzon & Carlini (2004) (i.e. the last deciduous premolar is dp4) to facilitate comparisons. The meaning of the chronostatigraphic/geochronologic units used is that expressed in Wendel- Burns et al. (2006). Measurements were taken with dial calipers to the nearest mm.


3. Systematic paleontology

Class Mammalia LINNAEUS, 1758
Order Carnivora BOWDICH, 1821
Family Ursidae LINNAEUS, 1758
Subfamily Tremarctinae MERGANS & STOCK, 1925
 cf. Arctotherium BURMEISTER, 1879

Fig. 2 A, B

Fig. 2. A, B - dp4 of cf. Arctotherium sp. (MUHNES-UDP 1-ne-sp-24-120); A: occlusal view, B: labial view; C, D - dp4 of A. tarijense (MACN 8582); C: occlusal view, D: labial view; E - m1 of A. angustidens (MPME 18); F - m1 of A. tarijense (MACN 2667); G - m1 of Arctodus primus (UF 81694); H - m1 of A. simus (UF 57550). Scale bars equal 1 cm.
Referred specimen: MUNIES-UDP 1-iv-ap-24-120, left fourth lower deciduous premolar (Fig. 2A, B).

Locality and age: Rio Tomayate (13° 40' 00" N, 89° 1' 26" W), República de El Salvador (Fig. 3). C1 Member of Coscatlán Formation, Blancon (Late Pliocene, Fig. 1). The C1 member corresponds to the uppermost Pliocene and is composed of fluvial and lacustrine detritus. A partial skull of *Doryphagus hillii* was found in this member, this species is recorded only in Blancon sediments.

Description: The crown of the dp4 (MUNIES-UDP 1-iv-ap-24-120) is slightly compressed labio-lingually, the labial margin is almost straight, the lingual margin is slightly convex and the mesial and distal margins are rounded (Fig. 2A, B). The trigonid shows three main cusps, paraconid, protoconid and metaconid, and an accessory small cusp (always present in *Tremarctos*) on the postero-labial side of the protoconid near its base (Sofferzon & Carlins 2004). The dp4 paraconid lies on the mesial margin of the crown and is rounded and 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 amount of 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. A thin cingulum runs along the labial side of the talonid at the level of the hypoconid.

4. Comparisons

There are two previous studies on deciduous teeth of *Tremarctos ornatus* and *Sofferzon & Carlins* (2004) described a deciduous incisor and some premolars (among them a dp4 of *Arctotherium sarmiento*). First we compare the dp4 of cf. *Arctotherium sarmiento* (MACN-pw 8352) and finally with the m1 of *Arctodus* (North American short-faced bears).

Here we compare the morphology of dp4 with that of m1 based on the following information: In most mammals the milk dentition is replaced once, a condition called diphyodonty, the first set is called
### Table 1. Measurements (mm) of dp4 of cf. Arctotherium (MUYNES-UDP 1-10-ap-24-120) and cf. A. tarjiense (MUSIC-UDP 1-11-ap-24-120) compared to Ursidae (cf. A. stuarti, cf. A. brevirostris, A. miersi, A. isabellae, cf. A. barroi) from the late Miocene and Pliocene of Europe (see Table 1, Trench 2). Additional data taken from Vrba (1981b). All data in millimeters.

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### Notes

- The morphology of dp4 of cf. Arctotherium with MUYNES-UDP 1-10-ap-24-120 resembles that of Ursidae more than cf. A. tarjiense. However, the dp4 of cf. Arctotherium is smaller in size than that of Ursidae.
- The comparison between dp4 of cf. Arctotherium and cf. A. tarjiense shows that the former is more similar to Ursidae in terms of size and morphology.
- The dp4 of cf. Arctotherium is characterized by a shorter and more constricted talonid, while the talonid of cf. A. tarjiense is more expanded.
- The presence of a distinct entoconid and hypoconid in cf. Arctotherium suggests a closer relationship to Ursidae than to cf. A. tarjiense.
is displaced towards the midline. These differences are similar to the differences observed between the m1 of *Arctothenium anquidens* (Fig. 2E), the oldest species of *Arctotherium* (see above), and *A. tarjense* (Fig. 2H) the youngest species of this taxon (see Fig. 1). *Soibelzon* (2002a, 2004b) suggested that *A. tarjense* is the most specialized species of *Arctotherium*, well differentiated from the ancestral stock that arrived in South America. Unfortunately, up to the present, there are no other published descriptions of milk teeth in trematocine bears apart from those already noted (Saporta 1949; Soibelzon & Cardili 2004) and, as far as we know, there are no specimens in paleontological collections in any other museum apart from those housed at MACN-pv and MLP (Argentina) and described in Soibelzon & Cardili (2004). This implies that we could not compare the dp4 presented here with those of other taxa apart from *A. tarjense*.

**Comparisons between dp4 of cf. *Arctotherium* and m1 of *Arctodus***. The m1 of *Arctodus* (Fig. 2G, H) is differentiated from *Arctotherium* (and MUHNS-UDP 1-ss-ap-24-120) based on the occlusal shape of the crown, with *Arctotherium* (Fig. 2E, F) having a more quadrato shape and the preceding being more rectangular. This difference is based on the fact that *Arctodus* has a compressed trigonid, a well defined ectolophid, and a labially projected talonid. In *Arctotherium* (and MUHNS-UDP 1-ss-ap-24-120) the trigonid is laterally expanded, the ectolophid is poorly defined and the talonid is less projected labially. In addition the size of MUHNS-UDP 1-ss-ap-24-120 (Table 1) is more consistent with that of the m1 of *Arctotherium anquidens* (the oldest species recorded in South America, Fig. 1) than with the m1 size of *Arctodus*.

**Comparisons between dp4 of cf. *Arctocyon* and m1 of *Tremarctos***. The same morphological characters that distinguish cf. *Arctot-"therium* and *Arctodus* differentiate the dp4 of cf. *Arctotherium* and m1 of *Tremarctos*. In addition the m1 of *Tremarctos* is substantially smaller than MUHNS-UDP 1-ss-ap-24-120 (see Table 1) therefore it cannot have belonged to *Tremarctos*. Finally, the morphology and size of dp4 from Rio Tomayate resembles that of m1 of the oldest species of *Arctotherium* (Saporta, 1945). Unfortunately, this species is known only from definitive teeth. Because of this and the rarity of deciduous premolars of short-faced bears, we could not make a definitive determination.

**5. Discussion and conclusions**

Eutherian carnivores arrived in South America, like many other taxa of holarctic origin during the GABI. This interchange occurred after the marine barrier that separated South America and North America disappeared in the Late Pliocene ca. 2.8 Ma (Coates & Orand 1996).

Short-faced bears (*Arctotherium*) arrived in South America within this context. The absence of *T. ornatus* in the fossil record of either North or South America may indicate that this species differentiated during the Holocene from *T. floridanus*, its sister group (Soibelzon et al. 2005; see Fig. 1). Consequently, a subsequent second immigration event is needed to explain the occurrence of the only recent South American bear (*T. ornatus*, spectacled bear, see Fig. 1). FIorentino Ameghino (1885, 1906) suggested a South American origin for the Tremarctinae subfamily on the basis of the erroneous stratigraphic provenance of the specimen MACN-pv 1277 (*A. verutum*), which he believed to be “Mesopotamian” in age (late Miocene). This hypothesis was accepted by Carlos Ameghino (1916), but Meiriam et al. (1916), Meiriham & Stock (1925), and Keagleovich (1929) placed the stratigraphic provenance of MACN-pv 1277 in doubt and, in turn, questioned Ameghino’s (1885, 1906) hypothesis.

Soibelzon (2002a, 2004b) proposed that *Arctodus* and *Arctotherium* are sister groups that together make up the “short-faced bears” clade. In addition, Soibelzon (2002a) and Soibelzon et al. (2005) hypothesized that the time of divergence of these two taxa was late Blancan on the basis of the oldest record of a North American short-faced bear (*Arctotherium praestanum*, Blancan IV, Late Pliocene, Fig. 1) and a South American short-faced bear (*Arctotherium angustidens*, Eocene, Early Pleistocene, Fig. 1). However, there is no fossil record for short-faced bears prior to the Ensenadan south of the Panamanian isthmus.

According to Wehli (1991), the most successful holarctian families involved in the GABI diversified north of the Panamanian Isthmus before the interchange, which suggests that the origin of *Arctotherium* must be related to the geographic area (umor Lieberman 2000). The fossil record of *Arctotherium* in South America also indicates that cladogenetic events occurred.
in intertropical areas. For example, A. virgata (exclusively), A. versata, A. angustidentata, and A. terri- jense have been recorded in those areas (Sobreilzon et al. 2005).

The specimen here described indicates that Arctochoerus was near the Panamanian Inlandus from the Late Pliocene and possibly migrating southwards. In addition, this new finding may indicate that Arctochoerus did not first appear in South America, as previously assumed (Eisenmann of the Pampean Region of Argentina (Sobreilzon et al. 2004; Sobreilzon et al. 2005)). This new find may support the hypotheses of Wrans (1992) and Sobreilzon (2002a) that in the Blancan short-faced bears were moving from North to South America. Almost one million year later they were first recorded in the Pampean Region of Argentina.

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