N. Jb. Geol. Paläont. Abh.
2008, vol. 250/1, p. 1–8, Stuttgart, October 2008, published online 2008

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

Leopoldo H. Soibelzon, La Plata, **M. R. Romero, D. Huziel Aguilar,** San Salvador, and **V. B. Tartarini,** La Plata

With 3 figures and 1 table

Soibelzon, L. H., Romero, M. R., Huziel Aguilar, D. & Tartarini, V. B. (2008): A Blancan (Pliocene) short-faced bear from El Salvador and its implications for Tremarctines in South America. – N. Jb. Geol. Paläont. Abh., **250**: 1–8; Stuttgart.

Abstract: We present here a deciduous tooth recovered from the Blancan (Pliocene) Río Tomayate locality (Republic of El Salvador) and assign it to cf. *Arctotherium* (South American 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 Ensenadan (Early to Middle Pleistocene) of the Pampean Region of Argentina; 5200 km from the Panamian Isthmus. Among Ensenadan sediments the oldest ones are those of "las toscas del Río de La Plata" locality (Pampean Region). The age of these sediments is 1Ma and they correspond to Chron C1r2r. 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 to Central America and may represent the basal stock for short-faced bears in South America.

Key words: Ursidae, Tremarctinae, *Arctotherium*, Central America, Blancan, Pliocene.

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 (Tedford & Martin 2001). *Arctodus* contains two North American Late Pliocene and Pleistocene species: *A. pristinus* and *A. simus*. The oldest record for *Arctodus* is Blancan IV (Late Pliocene), and the youngest is Rancholabrean (Kurtén 1967; Richards et al. 1996). *Arctotherium* comprises five South American Pleistocene species: *A. angustidens*, *A. vetustum*, *A. bonariense*, *A. wingei* and *A. tarijense* (see Soibelzon 2004a; Soibelzon et al. 2005). *Tremarctos* includes two species, *T. floridanus* 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

DOI: 10.1127/0077-7749/2008/0250-0001 0077-7749/08/0250-0001 $ 2.00

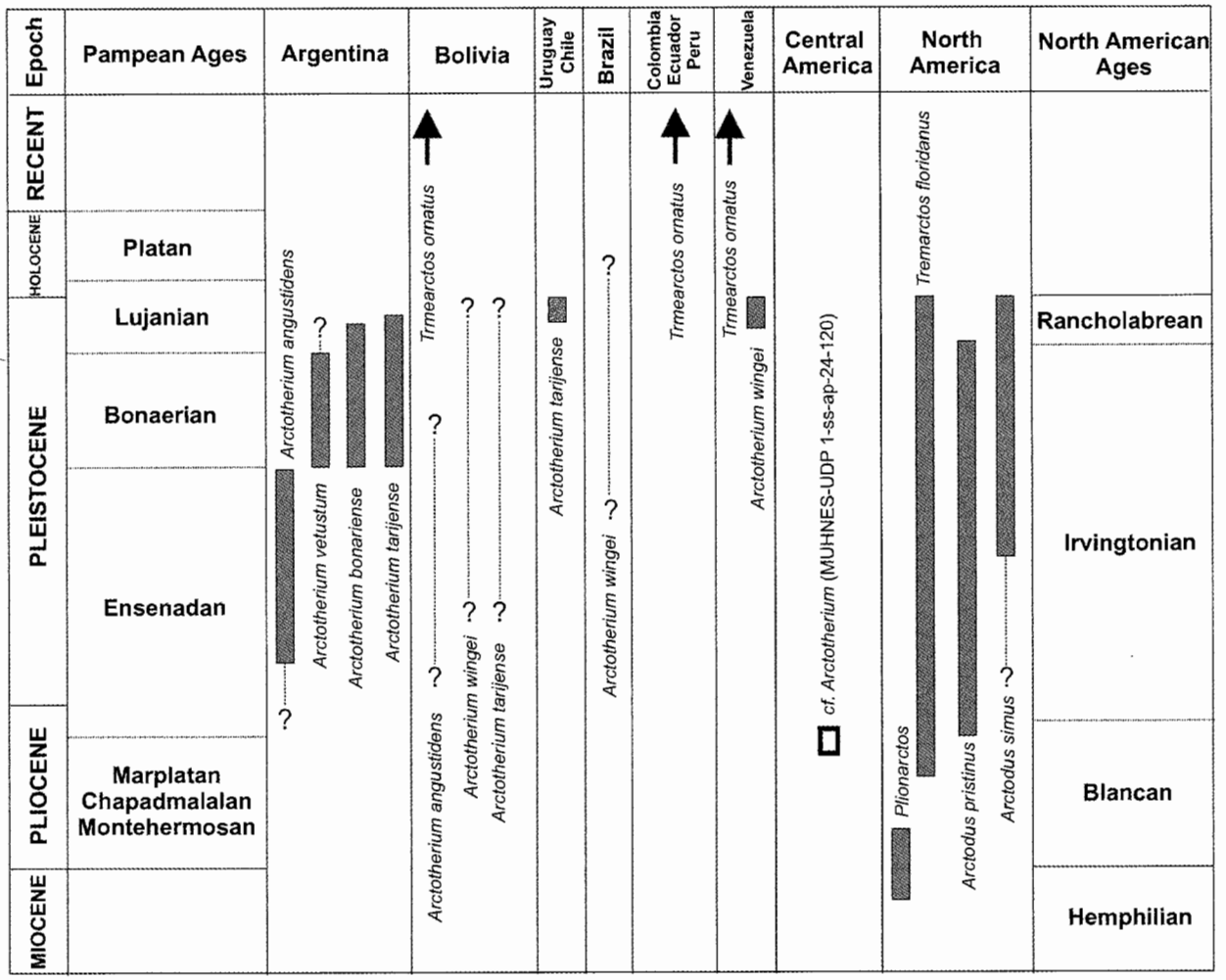

Fig. 1. Chronological chart of the late Cenozoic in North and South America showing the biochrons and geographic distribution of all Tremarctinae taxa and cf. *Arctotherium* MUHNES-UDP 1-ss-ap-24-120 (modified from SOIBELZON et al. 2005, chronostratigraphic units according to WOODBURNE et al. 2006).

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 Panamian Isthmus, as part of the "Great American Biotic Interchange" (GABI, MARSHALL et al. 1982). The oldest reported record of a tremarctine bear in South America corresponds to *Arctotherium angustidens* which is first recorded in the Ensenadan of the Pampean Region of Argentina (SOIBELZON 2004a, SOIBELZON et al. 2005). Among Ensenadan (Early to Middle Pleistocene) sediments the oldest ones are those of "las toscas del Río de La Plata" (Pampean Region). The age of these sediments is 1Ma and they correspond to Chron C1r2r. In the northern portion of South America *Arctotherium* (*A. wingei*) is recorded only in the Late Pleistocene (SOIBELZON & RINCÓN 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 Pliocene of Río Tomayate, El Salvador (Fig. 3) and analyze the biogeographic significance of the discovery. After this study we assigned this deciduous tooth to cf. *Arctotherium.* Deciduous premolars of short-faced bears are scarce in the fossil record, they are only known from one South American species: *Arctotherium tarijense* (see SOIBELZON & CARLINI 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 northern most 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 SOIBELZON & CARLINI (2004) (i. e. the last deciduous premolar is dp4) to facilitate comparisons. The meaning of the chronostratigraphic/geochronologic units used is that expressed in WOODBURNE et al. (2006). Measurements were taken with dial calipers to the nearest mm.

Abbreviations. – AMNH: Vertebrate Paleontology Collection, American Museum of Natural History, USA. CM: Carnegie Museum, USA. LACM: Los Angeles County Museum, USA. MACN-pv: Colección del Departemento Paleontología de Vertebrados, Museo Argentino de Ciencas Naturales "Bernardino Rivadavia", Argentina. MLP: Colección del Departemento Paleontología de Vertebrados, Museo de La Plata, Argentina. MNHN AC: Muséum National d'Histoire Naturelle, Anatomie Comparée, Paris, France. MUHNES-UDP: Depósito de paleontología de Vertebrados de La Unidad de Paleontología; Museo de Historia Natural de El Salvador, El Salvador. UF: Vertebrate Paleontology Collection, Florida University, USA. dp4: fourth lower deciduous premolar, m1: first lower molar, mm: millimeters. Specimens used for comparison. – Definitive teeth: *Arctodus pristinus* – UF 97258, UF 81692, UF 81693, UF 81694, UF 64300, UF19397, AMNH 95696, AMNH 95696, AMNH 22578. *Arctodus simus* – AMNH 25531, AMNH 25531, AMNH 127691, AMNH 98969, AMNH 98969, CM 38359, LACM 122434, UF 170690 (cast). *Tremarctos floridanus* – UF10333, UF3566, UF7454 and those published by KURTÉN (1966). The specimens of *Arctotherium* used for comparison are those listed in SOIBELZON (2004a).

Deciduous teeth: *A. tarijense* MACN-pv 8582 (described in SOIBELZON & CARLINI 2004). *Melursus ursinus* MNHN AC 10998 *Ursus arctos* MNHN AC 1896-346 and those described in KOBY (1952), TERZEA (1969) and TORRES (1988).

3. Systematic paleontology

Class Mammalia LINNAEUS, 1758
Order Carnivora BOWDICH, 1821
Family Ursidae GRAY, 1857
Subfamily Tremarctinae MERRIAM & STOCK, 1925
cf. *Arctotherium* BURMEISTER, 1879
Fig. 2A, B

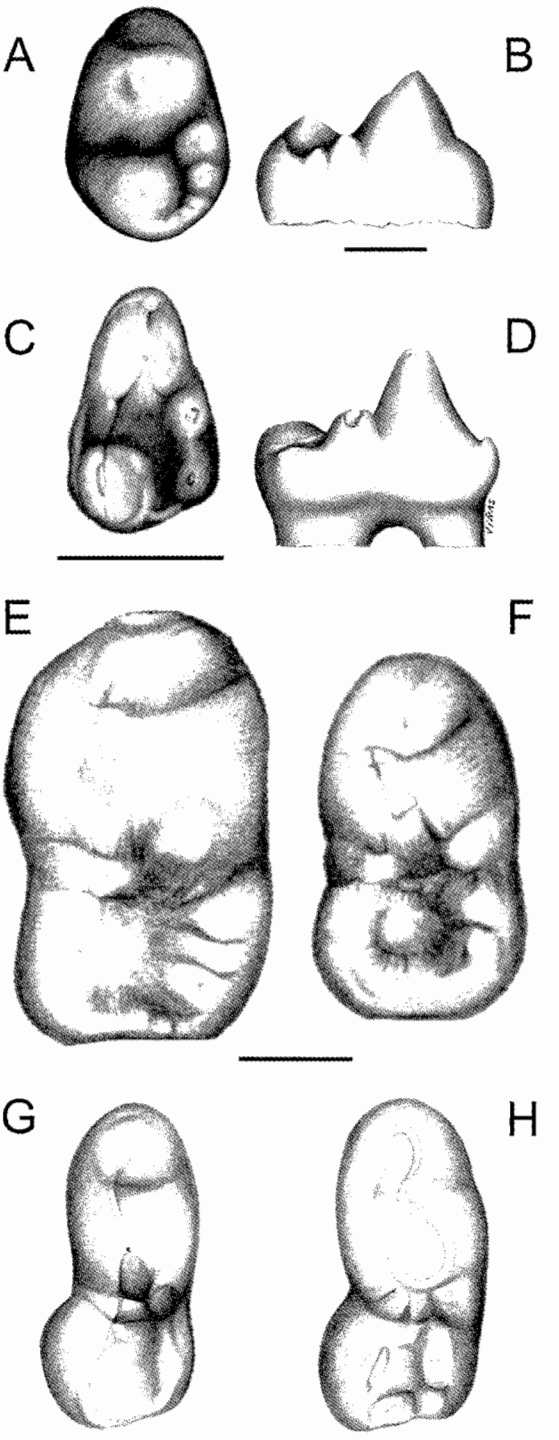

Fig. 2. A, B – dp4 of cf. *Arctotherium* sp. (MUHNES-UDP 1-ss-ap-24-120), A: occlusal view, B: labial view; **C, D** – dp4 of *A. tarijense* (MACN 8582) C: occlusal view, D: labial view; **E** – m1 of *A. angustidens* (MMPH 18); **F** – m1 of *A. tarijense* (MACN 2667); **G** – m1 of *Arctodus pristinus* (UF 81694); **H** – m1 of *A. simus* (UF 57550). Scale bars equal 1 cm.

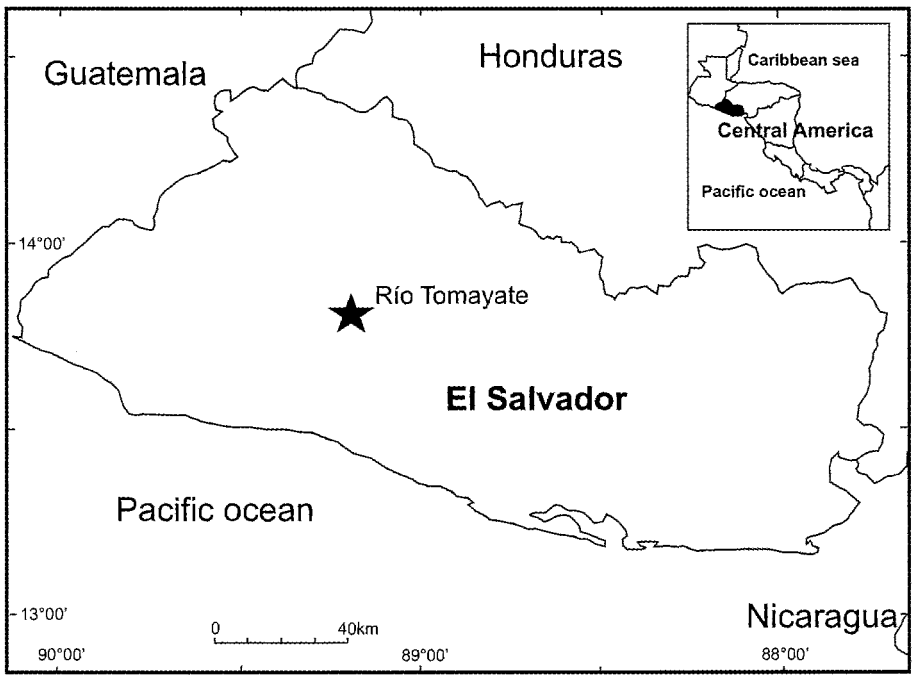

Fig. 3. Map of El Salvador showing the Río Tomayate locality (San Salvador department, El Salvador).

Referred specimen: MUHNES-UDP 1-ss-ap-24-120, left fourth lower deciduous premolar (Fig. 2A, B).

Locality and age: Río Tomayate (13° 49' 06" N, 89° 11' 26" W), República de El Salvador (Fig. 3). C1 Member of Cuscatlán Formation, Blancan (Late Pliocene, Fig. 1). The C1 member corresponds to the uppermost Pliocene and is composed of fluvial and lacustrine detritus. A partial skull of *Borophagus hilli* was found in this member, this species is recorded only in Blancan sediments.

Description: The crown of the dp4 (MUHNES-UDP 1-ss-ap-24-120) is slightly compressed labiolingually, 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 Tremarctinae) on the postero-labial side of the protoconid near its base (Soibelzon 2002a, 2004b, Soibelzon & Carlini 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 tremarctine bears; Sapority (1949) described the order of eruption of milk teeth of *Tremarctos ornatus* and Soibelzon & Carlini (2004) described a deciduous incisor and some premolars (among them a dp4) of *Arctotherium tarijense*. First we compare the dp4 of cf. *Arctotherium* with that of Ursinae (the other subfamily of Ursidae recorded in America), then we contrast it with the dp4 of *Arctotherium tarijense* (MACN-pv 8582) 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) on the dp4 of cf. *Arctotherium* (MUHNES-UDP 1-ss-ap-24-120), *Ursus* and *Arctotherium tarijense* (MACN-pv 8582); and m1 of *Arctotherium tarijense*, *A. angustidens*, *Arctodus pristinus*, *A. simus* and *Tremarctos floridanus*. MDL: greatest mesiodistal length; BLW: greatest buccolingual width; MDL and BLL measured between landmarks at the limit of the crown. M: mean; N: sample size; R: range; SD: standard deviation. [1]Except *U. spelaeus* because this species is not recorded in America; additional data taken from KOBY (1952). [2]Additional data taken from KURTÉN (1966).

	cf. *Arctotherium*		Ursinae[1]		*Arctotherium tarijense*		*Arctodus pristinus*		*A. angustidens*		*A. simus*		*Tremarctos floridanus*[2]	
	MDL	BLW	MDL	BLW	MDL	BLW	MDL	BLW	MDL	BLW	MDL	BLW	MDL	BLW
dp4	28.2	19.5	9.9	4.8	15.5	8.2								
M					35	21	26	14	39.9	25.2	30	16	21	10
R			6.3-12.7	2.8-6.5	33-38	21-22	23-29	12-16	38-42	14-18	28-33	14-18	20-23	9.6-11.8
m1														
SD			2.7	1.6	0.19	0.07	0.23	0.13	0.19	0.18	0.19	0.16	0.9	0.53
N	1		5		4	5	9		26		8		17	20

primary and the next set secondary (JERNVALL 1995). 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/m1 respectively and, the dP4 occludes on dp4 in the juvenile in much the same way as the M1 occludes on the m1 in the adult. On the other hand, their corresponding permanent premolars (except for P4) are simpler (SOIBELZON & CARLINI 2004).

In order to compare the dp4 of cf. *Arctotherium* with other taxa we used morphology and size. Size is a good character to compare deciduous and definitive teeth since in all Ursidae definitive teeth are larger than deciduous ones (L. SOIBELZON, pers. obs.). Among South American short-faced bears this situation was verified for *A. tarijense* by SOIBELZON & CARLINI (2004) (see Table 1). The opposite situation (i.e. deciduous teeth bigger than definitive molars) was never observed in bears (L. SOIBELZON, pers. obs.).

Comparisons between dp4 of cf. *Arctotherium* and dp4 of Ursinae. – The morphology of cf. *Arctotherium* (MUHNES-UDP 1-ss-ap-24-120) corresponds to Tremarctinae instead to Ursinae based on its size (see Table 1), heavy build, the number of apices that form the metaconid (one apex in MUHNES-UDP 1-ss-ap-24-120 and Tremarctinae; two apices in Ursinae), and the comparative size of the protoconid in relation with the paraconid and metaconid (protoconid larger than paraconid and metaconid in Tremarctinae and MUHNES-UDP 1-ss-ap-24-120; protoconid slightly larger than paraconid and metaconid in Ursinae). In addition the trigonid is very laterally compressed in Ursinae and the talonid is projected labially in the area of the hypoconid.

Comparisons between dp4 of cf. *Arctotherium* and dp4 of *A. tarijense*. – The dp4 of cf. *Arctotherium* (MUHNES-UDP 1-ss-ap-24-120) and that of *A. tarijense* (MACN-pv 8582; Fig. 2C, D, Table 1, see SOIBELZON & CARLINI 2004 for more details) exhibit the same fundamental morphology. The dp4 of cf. *Arctotherium* is less laterally compressed, the talonid is shorter and the distal margin is very rounded. The main trigonid cusps (parconid, protoconid and metaconid) of cf. *Arctotherium* and *A. tarijense* show the same arrangement. In the talonid area the entoconid is placed forwards in cf. *Arctotherium* much closer to the metaconid and the hypoconid

is displaced towards the midline. These differences are similar to the differences observed between the m1 of *Arctotherium angustidens* (Fig. 2E), the oldest species of *Arctotherium* (see above), and *A. tarijense* (Fig. 2H) the youngest species of this taxon (see Fig. 1). SOIBELZON (2002a, 2004b) suggested that *A. tarijense* 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 tremarctine bears apart from those already noted (SAPORITI 1949; SOIBELZON & CARLINI 2004) and, as far as we know, there are not specimens in paleontological collections in any other museum apart from those housed at MACN-pv and MLP (Argentina) and described in SOIBELZON & CARLINI (2004). This implies that we could not compare the dp4 presented here with those of other taxa apart from *A. tarijense*.

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

Comparisons between dp4 of cf. *Arctotherium* and m1 of *Tremarctos*. – The same morphological characters that distinguish cf. *Arctotherium* and *Arctodus* differentiates the dp4 of cf. *Arctotherium* and m1 of *Tremarctos*. In addition the m1 of *Tremarctos* is substantially smaller than MUHNES-UDP 1-ss-ap-24-120 (see Table 1) therefore it cannot have belonged to *Tremarctos*.

Finally, the morphology and size of dp4 from Río Tomayate resembles that of m1 of the oldest species of *Arctotherium* (A. *angustidens*). 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 holartic 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 & OBANDO 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). FLORENTINO 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. vetustum*), which he believed to be "Mesopotamian" in age (Late Miocene). This hypothesis was accepted by CARLOS AMEGHINO (1916), but MERRIAM et al. (1916), MERRIAM & STOCK (1925), and KRAGLIEVICH (1926) 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 (*Arctodus pristinus,* Blancan IV, Late Pliocene, Fig. 1) and a South American short-faced bear (*Arctotherium angustidens*, Ensenadan, Early Pleistocene, Fig. 1). However, there is no fossil record for short-faced bears prior to the Ensenadan south of the Panamian Isthmus.

According to WEBB (1991), the most successful holartic families involved in the GABI diversified north of the Panamian Isthmus before the interchange, which suggests that the origin of *Arctotherium* must be related to geodispersal (*sensu* LIEBERMAN 2000). The fossil record of *Arctotherium* in South America also indicates that cladogenetic events occurred

in intertropical areas. For example, *A. wingei* (exclusively), *A. vetustum*, *A. angustidens,* and *A. tarijense* have been recorded in those areas (SOIBELZON et al. 2005).

The specimen here described indicates that *Arctotherium* was near the Panamian Isthmus by the Late Pliocene and possibly migrating southwards. In addition, this new finding may indicate that *Arctotherium* did not first appear in South America, as previously assumed (Ensenadan of the Pampean Region of Argentina (SOIBELZON 2004; SOIBELZON et al. 2005)).

This new find may support the hypotheses of WEBB (1991) and SOIBELZON (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.

Acknowledgements

The reviewers, BLAINE SCHUBERT and MARTÍN UBILLA, provided useful comments on an earlier version of this manuscript. The authors thank Dr. ALEJANDRO KRAMARZ (MACN-pv), Dr. WEBB (FMNH); Dr. TEDFORD (AMNH), Dr. ANDY CURRANT (NHM, London), Drs. CHRISTIAN DE MUIZZON and FRANCIS RENAULT (MNHNP AC) for allowing us to study the material. The authors also thank PAULA POSADAS and LUCAS POMI for their useful comments and CONICET; ANPCyT PICT 38171/05; for financial support.

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Manuscript received: October 23rd, 2007.
Revised version accepted by the Stuttgart editor: November 23rd, 2007.

Addresses of the authors:

L. H. SOIBELZON, Departamento Científico Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque, 1900 La Plata, Buenos Aires, Argentina;
e-mail: lsoibelzon@fcnym.unlp.edu.ar

M. R. ROMERO, D. HUZIEL AGUILAR, Unidad de Paleontología, Consejo Nacional Para La Cultura y El Arte (CONCULTURA), Final Calle Los Viveros, Colonia Nicaragua, San Salvador, El Salvador.

V. B. TARTARINI, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, 122 y 60 (1900) La Plata, Buenos Aires, Argentina.