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THE LARGEST KNOWN BEAR, *ARCTOTHERIUM ANGUSTIDENS*, FROM THE EARLY PLEISTOCENE PAMPEAN REGION OF ARGENTINA: WITH A DISCUSSION OF SIZE AND DIET TRENDS IN BEARS

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ABSTRACT—The South American giant short-faced bear (*Arctotherium angustidens* Gervais and Ameghino, 1880) is one of five described *Arctotherium* species endemic to South America and it is known for being the earliest, largest, and most carnivorous member of the genus. Here we report an extraordinarily large *A. angustidens* individual exhumed from Ensenadan sediments (early to middle Pleistocene) at Buenos Aires Province, Argentina. Based on overall size, degree of epiphyseal fusion, and pathologies, this bear was an old-aged male that sustained serious injuries during life. Body mass of the bear is estimated and compared to other ursid species based on a series of allometric equations. To our knowledge, this specimen now represents the largest bear ever recorded. In light of this discovery, we discuss the evolution of body size in *Arctotherium* (from large-to-small) and compare this to bears that exhibited different evolutionary trajectories. We suggest that the larger size and more carnivorous nature of *A. angustidens*, compared to later members of the genus, may reflect the relative lack of other large carnivores and abundance of herbivores in South America just after the Great American Biotic Interchange.

INTRODUCTION

ARCTOTHERIUM ANGUSTIDENS Gervais and Ameghino, 1880 belongs to the Tremarctinae subfamily (Carnivora: Ursidae), a diverse and endemic group of American bears that includes small to gigantic species recorded from late Miocene to recent times (Fig. 1; see Kurtén, 1966, 1967; Tedford and Martin, 2001; Soibelzon, 2004a; Soibelzon et al., 2005; Schubert et al., 2010, Schubert, 2010). Of these, 1) *Plionarctos* Frick, 1926 is recorded from the late Miocene to the early Pliocene of North America with two described species, *P. edensis* Frick, 1926 and *P. harroldorum* Tedford and Martin, 2001; 2) *Arctodus* Leidy, 1854 of North America is known from late Pliocene until the end of the Pleistocene and contains two species, *Arctodus pristinus* Leidy, 1854 and *Arctodus simus* (Cope, 1879); 3) *Arctotherium* Burmeister, 1879 comprises five South American species, all recorded during the Pleistocene; and 4) *Tremarctos* Gervais, 1855 includes two species, *T. floridanus* Gildey, 1928 from the late Pliocene and Pleistocene of North America and the only living tremarctine, *T. ornatus* (Cuvier, 1825) of South America (Soibelzon, 2004a; Soibelzon et al., 2005). *Arctodus* and *Arctotherium*, sister taxa commonly known as giant short-faced bears, contain the largest tremarctine species *Arctodus simus* and *Arctotherium angustidens*, and the evolution of these species was independent.

The tremarctine bears arrived in South America, like all other eutherian carnivorans, through the Panamanian Isthmus as part of the Great American Biotic Interchange (GABI) (Soibelzon, 2004b; Soibelzon and Prevosti, 2007). This interchange occurred after the marine barrier that separated South and North America disappeared during the late Pliocene, ~2.6 Ma (Marshall et al., 1982; Iturralde-Vinent and MacPhee, 1999; Woodburne et al., 2006). After the GABI *Arctotherium* spreads across South America, eventually resulting in five species: *Arctotherium angustidens*, which is restricted to the Ensenadan (early–middle Pleistocene), *Arctotherium vetustum* Ameghino, 1885, known only in the Bonaerian (middle Pleistocene), and three Bonaerian and Lujanian (middle Pleistocene–early Holocene) species, *Arctotherium wingei* Ameghino, 1902, *Arctotherium bonariense* (Gervais, 1852), and *Arctotherium tarijense* Ameghino, 1902 (Fig. 1; see Soibelzon, 2004a; Soibelzon et al., 2005; Soibelzon and Rincon, 2007 for a detailed discussion on *Arctotherium* taxonomy).

Tremarctines display a wide range in body size, from gigantic (e.g., *Arctotherium angustidens* and *Arctodus simus*, up to ~1,200 kg) to medium-sized (e.g., *Arctotherium tarijense* and *Arctodus pristinus*, up to ~400 kg) and relatively small (e.g., *Arctotherium wingei* and *Tremarctos ornatus*, up to ~150 kg) (Soibelzon and Tartarini, 2009). Two evolutionary tendencies have been detected for the South American *Arctotherium* radiation: 1) body size reduction from the giant *Arctotherium angustidens* to the smallest *Arctotherium wingei* (≤250 kg) (Soibelzon and Tartarini, 2009) and 2) diet modification from the more carnivorous *A. angustidens* to the primarily herbivorous *A. wingei* (Figueirido and Soibelzon, 2009).

We present here an extraordinarily large specimen of *Arctotherium angustidens*, the South American giant short-faced bear, recovered from an excavation in Ensenadan sediments in La Plata City, Buenos Aires Province, Pampean Region, Argentina. These remains appear to represent the largest bear ever recorded; based on proportions of the long bones and their overall robust structure (Fig. 2). Besides describing the remains and quantifying their size, this report: 1) further illustrates the dramatic size differences between earlier and later forms of *Arctotherium*; and 2) discusses disparate evolutionary trends in Pleistocene bears of South America, North America, and Europe.

LOCALITY AND AGE

Workers discovered the fossil remains during construction of San Juan de Dios hospital and Dr. Agustín Sempé donated them to La Plata Museum in 1935. San Juan de Dios hospital is located in La Plata City, Buenos Aires Province, Argentina (S 34°56′49.14″ and W 57°56′55.56″). The sediments where the specimen (MLP 35-IX-26-3 to 7) was recovered correspond to Ensenadan age. This is inferred because the depth (9.6 m) where the fossils were found is similar or lower than the depth

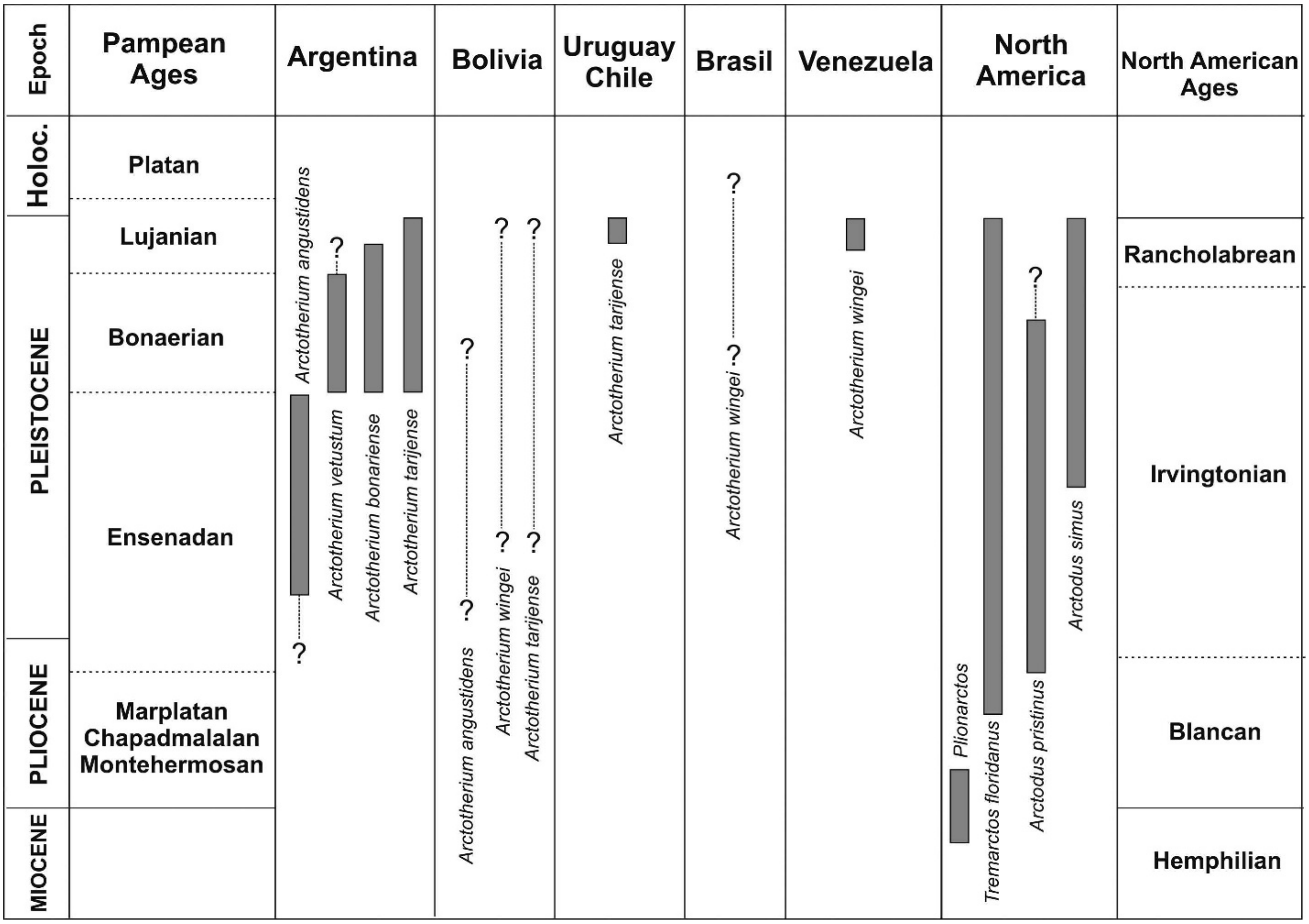

FIGURE 1—Geographic and temporal distribution of fossil Tremarctinae taxa (modified from Soibelzon et al., 2008).

at which the Ensenadan/Bonaerian (E/B) boundary (middle Pleistocene) was established at three other localities; Teatro Argentino (S 34°55′5.21″ and W 57°57′3.93″; E/B boundary detected at 10 m; Riggi et al., 1986), J. Hernandez quarry (S 34°54′35″ and W 58°00′15″, E/B boundary detected at 9.4 m, Tonni et al., 1999) and El Cristo quarry (S 57°57′30″ and W 34°55′, E/B boundary detected at 5.5 m, Bidegain et al., 2005; Imbellone and Cumba, 2003). All three of these localities are ~20 m above sea level. The age for the specimen is also supported by the known records of *Arctotherium angustidens*, all of which are from Ensenadan sediments (Soibelzon, 2004a; Soibelzon et al., 2005).

MATERIAL AND METHODS

We followed Marks and Erickson (1966) and Schubert and Kaufmann (2003) to infer the relative age of the individual based on the degree of epiphyseal fusion of some postcranial elements. Morphological terms follow Sisson (1965). Body mass of South American short-faced bears were recently estimated by Soibelzon and Tartarini (2009) using allometric equations published by other authors (e.g., Van Valkenburgh, 1990; Anyonge, 1993; Viranta, 1994; Christiansen, 1999; Egi, 2001). The study by Soibelzon and Tartarini (2009) compared more than sixty equations based on teeth, skull and postcranial measurements, and found the most reliable predictor of body size for large specimens was six measurements of the humerus (proposed by Anyonge, 1993; Egi, 2001; Christiansen, 1999) and one on the radius (formulated by Viranta, 1994) (for more details see Soibelzon and Tartarini, 2009). Thus, the size of the individual described here is estimated based on the preserved humerus and radius using these seven equations (see Table 1).

The chronostratigraphic/geochronologic units used herein follow the usage by Woodburne et al. (2006): Ensenadan (late Pliocene to middle Pleistocene), Bonaerian (middle Pleistocene to late Pleistocene) and Lujanian (late Pleistocene to early Holocene). Measurements were taken with a Venier caliper. Additional specimens of *A. angustidens* mentioned here are described in Soibelzon (2004a).

The following abbreviations are used in the text: E/B, Ensenadan/Bonaerian boundary; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; MLP, Museo de La Plata, Argentina. ETVP, East Tennessee State University Vertebrate Paleontology Laboratory.

SYSTEMATIC PALAEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order CARNIVORA Bowdich, 1821
Family URSIDAE Gray, 1825
Subfamily TREMARCTINAE Merriam and Stock, 1925
Arctotherium Burmeister, 1879
ARCTOTHERIUM ANGUSTIDENS Gervais and Ameghino, 1880
Figure 3.1–3, Table 2

Referred specimens.—MLP 35-IX-26-3 left ulna; MLP 35-IX-26-4 left radius; MLP 35-IX-26-5 left humerus; MLP

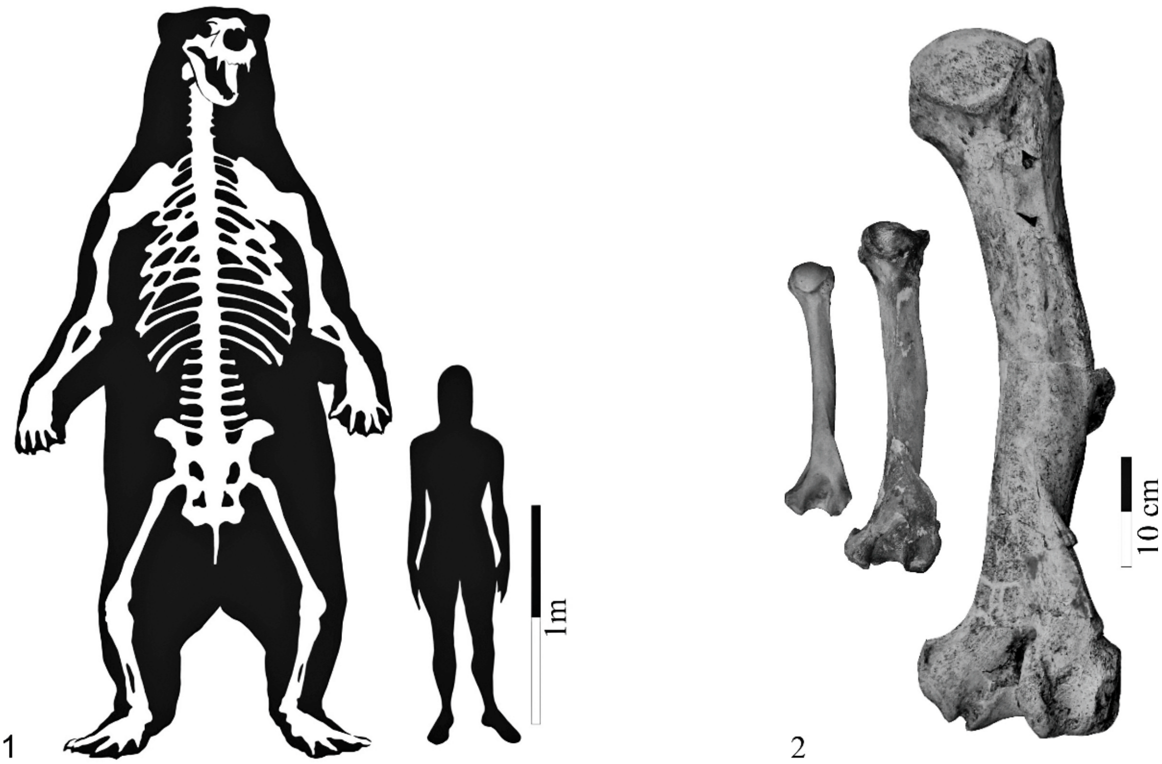

FIGURE 2—Size comparisons. *1*, comparison between the specimen reported here and an average sized woman; *2*, right humeri of an average sized (72 kg) *Tremarctos ornatus* MLP-M 1.I.03.62, (left); an above-average sized (208 kg) *Ursus americanus* ETVP 7074, (center); and the *Arctotherium angustidens* reported here MLP 35-IX-26-6, (right).

35-IX-26-6 right humerus; MLP 35-IX-26-7 right ulna and radius. All these numbers correspond to a single individual (Fig. 3, Table 2). All bones are well preserved except the distal end of the right ulna (MLP 35-IX-26-7) that was restored. Several elements (a fragment of scapula, some metacarpals and phalanges) of this individual that are listed in the collections catalogue are currently missing from the MLP collections.

Comments.—The specimen described here is undoubtedly an old adult specimen due to the high degree of epiphyseal fusion (see Marks and Erickson, 1966; Schubert and Kaufmann, 2003). Interestingly, during the Ensenadan a high proportion of old *Arctotherium* specimens are recorded (Soibelzon, 2004a) compared with the Bonaerian and Lujanian records.

Sexual dimorphism, with males being larger than females, occurs in all living bears and is more extreme in the larger species (Stirling, 1993; Stirling and Derocher, 1993). A number of authors have discussed sexual dimorphism in North American short-faced bears because two distinct sizes have been noted (e.g., Kurtén, 1967; Kurtén and Anderson, 1980; Churcher et al., 1993; Scott and Cox, 1993; Schubert and Kaufmann, 2003; Schubert et al., 2010; Schubert, 2010). While similar studies have not yet been done on *Arctotherium angustidens*, we infer that the individual described here was a male based on its exceedingly large size.

Both humeri (MLP 35-IX-26-6 and MLP 35-IX-26-5, Figs. 2.2 and 3.1, respectively) show extreme osteogenic changes over the deltoid crest. These pathologies indicate periostic reaction that may be due to an infection process derived from a deep injury. The left humerus was more affected and also shows osteogenic changes over the caudal border of the *m. brachialis* sulcus, as well as sulcus remodeling and new vascular growth (Fig. 3.1). This evidence indicates the animal survived a long time after the wounds occurred (W. Acosta pers. comm., 2009).

The distal third of the left radius shaft (MLP 35-IX-26-7) exhibits periostic reaction but the distal articular surface is not affected. On the caudal side and lateral border (at the boundary of the second and third portions of the bone shaft) there is a remodeled osseous callus implying the occurrence of a fissure. These pathologies indicate the presence of an infection derived from injuries.

TABLE *1*—Equations used for body mass prediction. HGDDE = Humerus greatest diameter of distal epiphysis. HMSC = Humerus mid shaft circumference. HGL = Humerus greatest length. RPEGD = Radius proximal epiphysis greatest diameter. ID = equation identification. SEE percent standard error of the estimation. Modified from Soibelzon and Tartarini (2009).

Element	Measurement	Equation	ID	%SEE	References
Humerus	HGL	$\log y = 2.93 * \log x - 5.11$	H1	51	Anyonge, 1993
	HGL	$\log y = 0.0000001 + 3.682 * \log x$	H2	11	Christiansen, 1999
	HGL	$\ln y = -11.16 + \ln x * 2.892$	H3	10.1	Egi, 2001
	HMSC	$\log y = 2.47 * \log x - 2.72$	H4	29	Anyonge, 1993
	HMSC	$\log y = 0.001 + 2.604 * \log x$	H5	34	Christiansen, 1999
	HGDDE	$\ln y = 0.002 + 2.511 * \ln x$	H6	53	Christiansen, 1999
Radius	RPEGD	$\log y = 2.51 * \log x - 1.71$	R1	34	Viranta, 1994

FIGURE 3—*Arctotherium angustidens* specimens reported here. *1*, MLP 35-IX-26-5 left humerus in caudal view; *2*, MLP 35-IX-26-3 left ulna in lateral view; *3*, MLP 35-IX-26-4 left radius in lateral view. Black arrow points to a pathology. Scale bar is 10 cm.

TABLE 2—Measurements (mm) of the specimen MLP 35-IX-26 of *Arctotherium angustidens*. Measurements follow Merriam and Stock (1925).

	Right	Left
Humerus measurements		
Greatest length	620	615
Greatest anteroposterior diameter of proximal epiphyses	156	153
Greatest width of proximal epiphyses	130	134
Transverse diameter of shaft at middle	84	90
Anteroposterior diameter of shaft at middle	91	93
Greatest width of distal epiphyses	185	184
Ulna measurements		
Greatest length		570
Greatest width of olecranon process	87	85
Width from posterior border to tip of coronoid process	107	109
Least distance from sigmoid notch to posterior border	66	70
Greatest diameter of distal epiphyses	63	62.5
Radius measurements		
Greatest length	500	49
Greatest diameter of proximal epiphyses	79	81
Width of shaft at middle	57	56
Greatest diameter of distal epiphyses	109	111

RESULTS AND DISCUSSION

The specimen described here has an estimated body mass ranging from 983 to 2,042 kg depending on the equations considered (Tables 3 and 4). The highest predicted value is probably unrealistic, although the size of this individual is much higher than other known specimens (see Table 5). All predicted body masses based on humeral measurements are shown in Table 3. The mean and median (considering all equations) are 1,588 and 1,749 kg respectively. Thus, we suggest that the body mass of this gigantic bear was between these two values. To our knowledge, this makes the *A. angustidens* described here the largest known bear, and probably the most powerful terrestrial carnivoran of the late Cenozoic.

Extant bears range between ~45 and ~750 kg (Garshelis, 2009). Average weights for North American bears are: black bear *Ursus americanus* Pallas, 1780, 76.5 kg for males and 54 kg for females (Larivière, 2001); polar bear *U. maritimus* Phipps, 1774, 150 to 800 kg (DeMaster and Stirling, 1981); brown bear *U. arctos* Linnaeus, 1758, 80 to 600 kg (Pasitschniak-Arts, 1993). Wood (1981) reported a record of ~1,002 kg for the largest recent bear, a male *U. maritimus* hunted in the 1800s in northwest Alaska. *Tremarctos ornatus* range from 60 to 175 kg (Novack, 1999).

During the Pleistocene there were three gigantic bears: *Arctotherium angustidens* in South America, *Arctodus simus* in North America and the cave bear *Ursus spelaeus* Rosenmüller, 1794 (the largest *Ursus* species) in Europe. These bears are among the largest terrestrial mammalian carnivorans that ever lived (see Table 5 for a size comparison) and they presented several anatomical innovations (e.g., broad skulls with laterally expanded zygomatic arches, cheek teeth that are more bunodont with more prominent cusps; see Kurtén, 1967; Torres, 1988; Soibelzon, 2002a; Soibelzon, 2004a; Soibelzon and Figuerido, 2009) that distinguish them from the general pattern of most Pleistocene-Recent *Ursus*. It should be noted that there are other relatively large bears in the Mio-Pliocene fossil record, such as *Indarctos* Pilgrim, 1913 and *Agriotherium* Wagner, 1837 (Hunt, 1996, 1998). However, these taxa were extinct by the early Pleistocene (Tedford et al., 2004; Hunt, 1998), their systematic and taxonomic positions are problematic (e.g., Hunt, 1998; Krause et al., 2008), and most importantly, they are not known to have attained the size of the largest *Arctodus simus* or *Arctotherium angustidens* specimens (Hunt, 1998; Sorkin, 2006). Therefore, we do not consider them further here.

Arctodus, *Ursus spelaeus*, and *Ursus maritimus* all reached their largest known sizes during the late Pleistocene. In Europe the late Pleistocene polar bears (*U. maritimus*) were markedly larger than recent ones (see Kurtén, 1964) and the European giant cave bears (body mass of 700 kg or more; Christiansen, 1999) that appeared in the middle Pleistocene became extinct near the Pleistocene-Holocene boundary (see Kurtén, 1958). Kurtén (1967) established the body mass of the largest *Arctodus simus* specimens as ~590–630 kg and Christiansen (1999) estimated 700–800 kg for males with exceptional specimens slightly over 1,000 kg. The *Arctodus* lineage begins with the medium-sized *Arctodus pristinus*, which disappears from the fossil record near the Irvingtonian-Rancholabrean boundary, and ends with the gigantic *Arctodus simus* which goes extinct at the end of the Pleistocene (Fig. 1; Emslie, 1995; Schubert et al., 2010; Schubert, 2010). The records of *A. simus* from northern and central Utah (Nelson and Madsen, 1983; Gillette and Madsen, 1992; Schubert, 2010), Alaska and Yukon (Kurtén and Anderson, 1980; Matheus, 2001; Barnes et al., 2002), Kansas (Gobetz and Martin, 2001; Schubert, 2010), and Florida (Schubert et al., 2010) suggest that the late Rancholabrean (latest Pleistocene) population of *Arctodus simus* contained the largest known individuals (Schubert, 2010).

Kurtén (1955) suggested that Northern Hemisphere bear evolution in the Quaternary was extremely rapid and he interpreted this as resulting from changes in population structure and more extreme climatic oscillations. Along these lines, Bergmann's Rule has been invoked as an explanation for the existence of excessively large *Arctodus simus* individuals in the late Pleistocene (e.g., Kurtén and Anderson, 1980; Gillette and Madsen, 1992). While it is possible that Bergmann's Rule played a role in developing larger *A. simus*, there are other potential explanations that cannot be ruled out at this time (e.g., relative abundance of prey, carnivoran competition, and varying degrees of carnivory vs. herbivory over time).

TABLE 3—Body mass estimations (kg) of *Arctotherium angustidens* from humeral measurements (mm) applying the equations H1 to H6 (see Table 1). HGL = Humerus greatest length. HMSC = Humerus mid shaft circumference. HGDDE = Humerus greatest diameter of distal epiphysis. Modified from Soibelzon and Tartarini (2009).

Specimen	HGL	H1	H2	H3	HMSC	H4	H5	HGDDE	H6	Mean	Median
MLP 35-IX-26-5	61.5	1,151.9	1,856.2	1,654.6	26.5	1,842.5	2,042.3	18.4	983.4	1,588.5	1,748.6
MLP 35-IX-26-6	62.0	1,179.5	1,912.4	1,693.8	26.2	1,791.4	1,982.7	18.5	986.0	1,591.0	1,742.6
MACN 5132	54.0	786.9	1,149.9	1,135.9	22.0	1,163.5	1,258.0	20.5	1,276.0	1,128.4	1,156.7
MLP 82-X-22-2	49.5	609.8	834.7	883.2	16.0	529.9	548.9	13.6	452.8	643.2	579.4
MLP 10-15					17.5	661.2	693.2	13.4	438.7	597.7	661.2
MLP 00-VII-10-1					22.0	1,163.5	1,258.0	18.0	920.5	1,114.0	1,163.5

Figueirido and Soibelzon (2009) provided dietary inferences for *Arctotherium* by applying geometric morphometric and ecomorphology methodologies. They found that even though *Arctotherium* species were mostly omnivorous, diet composition changed through time from the most carnivorous and largest species *A. angustidens* to the smallest and most herbivorous *A. wingei*. Figueirido and Soibelzon (2009) proposed that *A. angustidens* had an omnivorous diet composed of a variety of components, but with a predominance of animal remains. This does not imply that active hunting was the unique strategy for feeding, since its large size and great power may have permitted the bear to fight for prey killed by the other large Pleistocene carnivores (e.g., the saber-tooth cat *Smilodon populator* Lund, 1842). Scavenging megaherbivore carcasses was probably another frequent way of feeding for *A. angustidens* (Soibelzon, 2002a); a similar strategy has been invoked for *Arctodus simus* (see Schubert and Wallace, 2009 for discussion). In support of this dietary behavior for *Arctotherium angustidens*, some fractures on the fourth upper premolars and lower molars were identified and attributed to chewing on hard objects like bones (Soibelzon, 2002a, 2002b; Figueirido and Soibelzon, 2009). Among these pathologies, broken crowns or loss of some teeth *in vivo* are the most common (Acosta and Soibelzon, 2009). High percentages of broken teeth in carnivorans have been attributed to predatory or scavenging behavior (e.g., Van Valkenburgh, 2007).

The Pleistocene evolution of *Arctotherium* in South America is distinctly different from the evolutionary trajectory of bears in North America and Europe. The massive species *A. angustidens* became extinct at the end of the Ensenadan (Fig. 1) (middle Pleistocene) and the two smaller species *A. wingei* and *A. tarijense* survived until the late Lujanian (latest Pleistocene-early Holocene, Soibelzon et al., 2005; Soibelzon and Tartarini, 2009). This implies that different selective pressures operated in South America in comparison to North America and Europe. Because size diminution occurred in *Arctotherium* as climate cooled, Bergmann's Rule can be dismissed as a causal agent. We suggest that selective pressures on *Arctotherium angustidens* may have related directly to the GABI, particularly the abundance of herbivores and relative paucity of large carnivores in the early Pleistocene (see Soibelzon et al., 2009; Figueirido and Soibelzon, 2009). Van Valkenburgh (2007) suggested the appearance of large size and carnivory is often a response to an ecological opportunity afforded by the decline or extinction of previously dominant hypercarnivorous taxa. In the case of *Arctotheium*, we suggest it could be a response to the abundance of large prey in an ecosystemn with only two large carnivores: the short-faced bear (*A. angustidens*) and the saber-tooth cat *Smilodon*. Over time, the post-GABI large carnivore guild increased in diversity and *Arctotherium* species shifted their diets towards more herbivory and decreased in size. We hypothesize that *Arctotherium* shifted its diet towards higher degrees of omnivory and herbivory to avoid growing competition with other large carnivorans.

TABLE 4—Body mass estimations (kg) from radius measurement (mm) applying the equation R1 (see Table 1). RPEGD = Radius proximal epiphysis greatest diameter. Modified from Soibelzon and Tartarini (2009).

Specimen	RPEGD	R1
MLP 35-IX-26-4	7.84	1,108
MLP 35-IX-26-7	7.8	1,094
MLP 00-VII-10-1	6.95	819.2
MLP 10-21	5.3	414.9
MLP 09-I-5-1	6.9	804.5
MACN 9609	6.9	804.5

Although the gigantic Pleistocene bears of South America, North America, and Europe experienced differing evolutionary histories in terms of size, the fossil record indicates that *Arctotherium*, *Arctodus*, and *Ursus spalaeus* become extinct near the Pleistocene-Holocene boundary. Today South America is inhabited by one ursid species, *Tremarctos ornatus* (smaller than its sister species, *T. floridanus*, and one of the most plesiomorphic taxa of Tremarctinae, Soibelzon, 2002a). North America maintains three species (*U. arctos*, *U. maritimus* and *U. americanus*) and Europe has two living species (*U. arctos* and *U. maritimus*). All of these survivors of the Pleistocene-Holocene transition are 'morphologically conservative' compared to the specialized *Arctotherium*, *Arctodus* and *U. spelaeus*.

Thus, the pressures that ruled the late Pleistocene/early Holocene ecosystems, in parts of the world where these bears lived, seem to have favored less specialized taxa (i.e., those with more 'conservative morphologies' and medium to small size) than those with more 'specialized morphologies' and gigantic to large sizes (*Arctotherium*, *Arctodus* and *U. spelaeus*). These larger taxa were probably more constrained

TABLE 5—Humeral measurements (mm) of the largest bear species. *Arctodus simus* from Merriam and Stock (1925); Kurtén (1967); Richards and Turnbull (1995); Churcher et al. (1993); *Ursus spelaeus* taken from Torres (1988); *Arctotherium angustidens* (a) from Soibelzon and Tartarini (2009), (b) and (c) specimens described here MLP 35-IX-26-6 and MLP 35-IX-26-5, respectively; *U. maritimus* provided by Christiansen (pers. comm., 2009). GL = Mean value of greatest length and range in parentheses. N = number of individuals measured. SGW = Mean value of greatest width of shaft at middle and range in parentheses.

Species	N	GL	N	SWG
A. angustidens				
(a)	3	548 (476–620)	3	58.6 (47.9–69.4)
(b)	1	620	1	84
(c)	1	615	1	90
A. simus	13	465 (438–594)	17	47.7 (46.2–64)
U. spelaeus	20	382 (343–448)	63	44.4 (33–56)
U. maritimus	5	338.7 (311–385)	5	39.3 (32–46.5)

and consequently less flexible in the face of major ecosystem reorganizations.

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