

A FOSSIL BEAR FROM NORTHEASTERN BRAZIL, WITH A PHYLOGENETIC ANALYSIS OF THE SOUTH AMERICAN EXTINCT TREMARCTINAE (URSIDAE)

E. TRAJANO and H. FERRAREZZI
Dept. Zoologia, Inst. Biociências da USP, C.P. 20520
01452-990 S. Paulo SP, Brazil

ABSTRACT—The skull with mandible of a fossil tremarctine bear from Ubajara county, northeastern Brazil, is described and compared to other specimens belonging to the nominal species, *Arctodus* (*Pararctotherium*) *brasiliensis*. It differs from the other almost complete skull, from Minas Gerais State, in having a shorter, more slender rostrum, larger braincase, and smaller teeth. We also propose a phylogenetic hypothesis and correspondent classification for the genera of Tremarctinae, using cladistic methodology. *Arctodus* and *Arctotherium* are recognized as separate genera, with the latter including two subgenera, *Arctotherium* and *Pararctotherium*. The Ubajara bear is tentatively identified as *Arctotherium* (*P.*) *brasiliense* (comb. nov.).

INTRODUCTION

During a cave survey in December 1978, a speleological team discovered an almost complete skull of a short-faced bear in a small cave in Ubajara County, State of Ceará, NE Brazil. It was originally identified as *Arctodus* (*Pararctotherium*) *brasiliensis* Lund, and its discovery was briefly reported (Dias Neto et al., 1980). However, the skull was not studied in detail until now.

Kurtén (1966, 1967) recognized two genera and at least seven species of short-faced Pleistocene bears, subfamily Tremarctinae: the Neotropical *Tremarctos ornatus* (the only living species); *T. floridanus*, *Arctodus pristinus*, and *A. simus* from North America; and *A. bonariensis*, *A. pamparus*, and *A. brasiliensis* from South America. Other poorly known species from South America include *Arctodus enectum* (Paula Couto, 1960) and *A. angustidens* (Kraglievich, 1926). Several genera were created for the American fossil bears (see Kraglievich, 1926, and Kurtén, 1966, 1967, for taxonomic revision). For instance, Paula Couto recognized two genera (Paula Couto, 1960) or subgenera (Paula Couto, 1979) of South American extinct bears, *Arctotherium* and *Pararctotherium*, the latter including *Arctodus brasiliensis*. Kurtén (1967) considered all tremarctine genera, except *Tremarctos*, as junior synonyms of *Arctodus*.

Kurtén's classification was followed by Perea and Ubilla (1983, 1985), who distinguished two morphological patterns in the extinct genus *Arctodus*: pattern "G" (large forms) and pattern "P" (small forms). They assigned *A. brasiliensis*, with some restrictions, to pattern "P," characterized by inflated frontal region and auditory bullae, U-shaped postpalatine margin, lateral margin of mesopterygoid fossa independent from the styloid apophysis, and foramen rotundum emerging in the orbit independent of the alisphenoid canal.

We describe here a fossil bear from NE Brazil, specimen GP/2T-4 of the Departamento de Paleontologia e Estratigrafia, Instituto de Geociências da USP (Fig. 1). The well preserved, mineralized skull and right mandible were lying at the surface of a river gravel deposit in a 130 m cave, the Gruta do Urso Fossil (Fossil Bear cave), in the National Park of Ubajara. It is the second nearly complete skull of Brazilian bears, showing characters not visible in other specimens of *A. brasiliensis*, and represents a considerable extension to the northeast of the geographic range of South American tremarctines.

The bear from Ubajara is compared to the known species of Tremarctinae, and its systematic position is discussed. A phylogenetic hypothesis of the genera of Tremarctinae is presented. We recognize *Arctotherium* as a separate genus, including the extinct South American tremarctines, with two subgenera: *Arctotherium* and *Pararctotherium*. The bear from Ubajara is classified as *A. (P.) brasiliense* (comb. nov.).

MATERIAL AND METHODS

Morphological terms and measurement definitions (Table 1) follow DeBlase and Martin (1981) and Hidalgo (1988). Measurements were taken with dial calipers.

Table 1 lists cranial and dental measurements of the Ubajara specimen (GP/2T-4) and of those previously identified as *A. brasiliense*: MHN1 and MHN3 (respectively P3 and P41 in Paula Couto, 1960) from Pedro Leopoldo County, Minas Gerais State, deposited in the Museu de História Natural da Universidade Federal de Minas Gerais (MHN). This table also provides measurements, from the literature, of fragmentary specimens of *A. brasiliense* from Minas Gerais (MHN4 or P40, mandible of MHN1, and others) and from Tarija, Bolivia (MACN). Specimen MHN1, col-

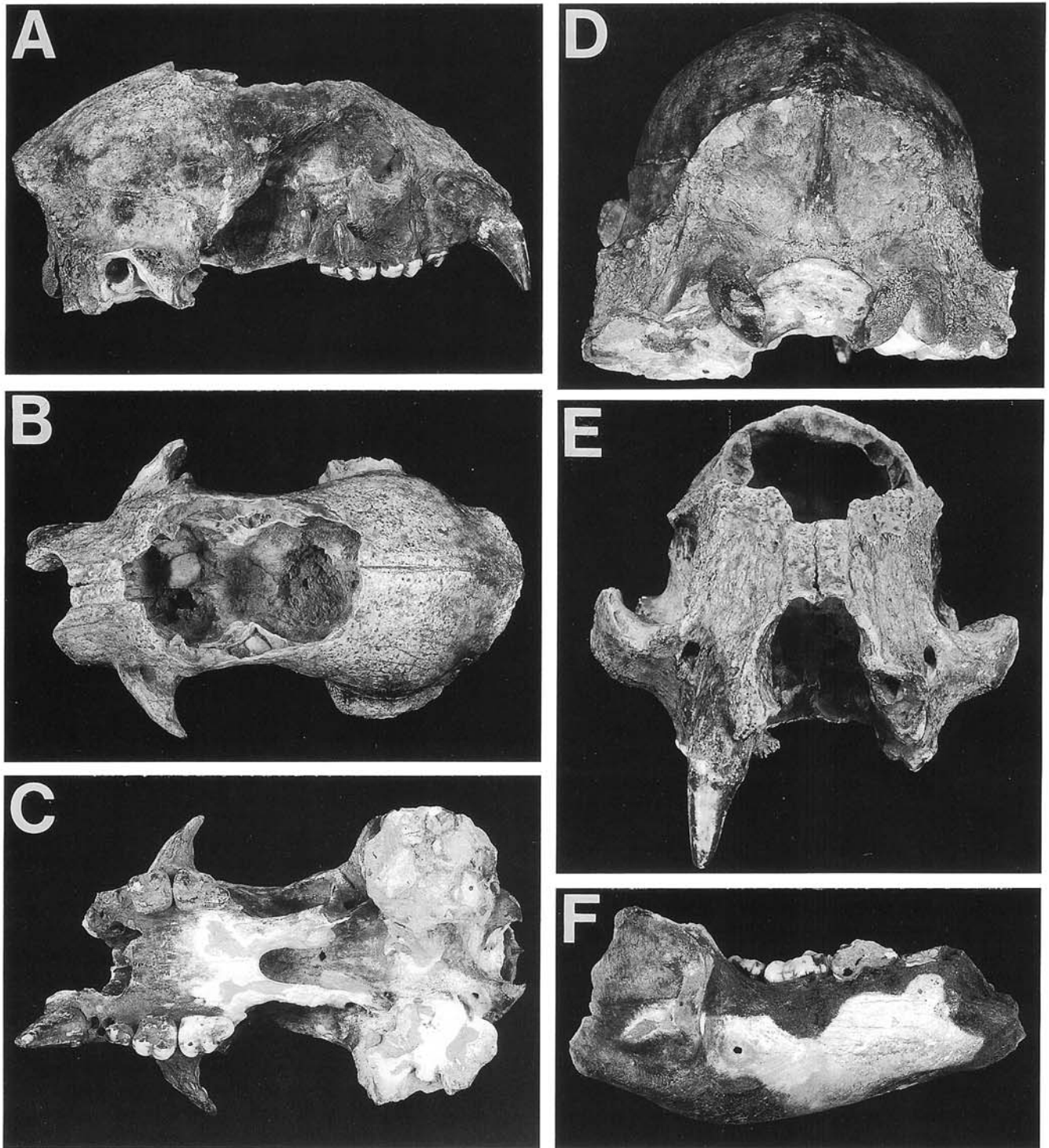


FIGURE 1. Skull (A–E) and mandible (F) of *Arctotherium brasiliense* (GP/2T-4) from Ubajara, Ceará state, Brazil. Skull shown in lateral (A), dorsal (B), ventral (C), occipital (D) and rostral (E) views; right mandible shown in lateral (F) view.

lected by H. V. Walter in Lapa da Lagoa Funda (Walter, 1940), is the only nearly complete skull beside that of Ubajara.

The proportions of the Ubajara specimen and *A.*

brasiliense from Minas Gerais and Tarija were graphically compared with *A. pamparum* and *A. bonariense* using ratio diagrams (Simpson, 1941). Here, we used the means of two specimens of *A. pamparum* and four

TABLE 1. Measurements (mm) of skull, mandible, and teeth of the Ubajara bear (Ceará state, Brazil) and additional specimens of *Arctotherium brasiliense* from localities in Minas Gerais state (Brazil) and Tarija, Bolivia. Except for GP/2T-4, MHN 1, and MHN 3, data are from Winge (1895), Paula Couto (1960), and Kurtén (1967). Asterisk indicates approximated or calculated measurement.

Skull and mandible	Ubajara GP/2T-4	Lagoa Funda		Tarija MACN
		MHN 1	MHN 3	
Total length (TL)	245*	233*	—	—
Basal length (BL)	215*	203	—	—
Condylobasal length (CL)	240*	—	—	—
Palatal length (PL)	120*	130	—	—
Nasal width (NW)	42*	—	—	—
Rostral width at C (RW)	76*	82*	—	—
Interorbital width (IW)	77	67*	—	—
Maximal frontal width (FW)	104	92*	—	—
Postorbital constriction (PC)	77	74*	61	—
Braincase width	110	100*	95	—
Bicondylar width (BW)	60.5	—	—	—
Mandibular height at P (MHP)	45	—	—	45
Mandibular height at M2 (MHM2)	46.5	—	—	41
Mandibular height at M3	52.2	—	—	—

Upper teeth	Ubajara GP/2T-4	Lagoa Funda		Escrivânia types	Sumidouro	
		MHN 1	Other		CN2201	CN2202
C length (CL)	25.5	20.7	—	—	—	—
C width (CW)	19.0	17.7	—	23.5	—	—
P4 length (P4L)	14.2	18.4	19.0	18.0	15.3	—
P4 width (P4W)	10.4	13.3	—	—	—	—
M1 length (M1L)	21.0	23.2	24.0, 20.0	22.7	22.4	—
M1 width (M1W)	19.7	22.2	22.8, 16.8	22.0	21.5	—
M2 length (M2L)	26.4	30.7	25.4, 34.0	30.7	28.8	29.3
M2 width (M2W)	19.6	22.4	17.3, 22.5	20.0	20.5	20.3
C-M2 length	97.0	102	—	105	—	—
P1-P4 length	24.5*	32.2	28.5	31.0	—	—
P1-M2 length	70.7	84.3	—	—	—	—

Lower teeth	Ubajara GP/2T-4	Lagoa Fundu	Escrivânia types		Tarija MACN
			CN5249	Other	
P4 length (P4L)	8.2*	—	—	—	—
M1 length (M1L)	24.6	—	24.3	27.5	27
M1 width (M1W)	—	—	14.2	—	17
M2 length (M2L)	22.0	26.0	22.0	25.0	24
M2 width (M2W)	16.1	18.0	16.7	17.0	17
M3 length (M3L)	14.8	18.0	16.5	—	—
M3 width (M3W)	13.3	15.5	13.9	—	—
P1-P4 length	—	—	—	22.5*	30
M1-M3 length	61.8	—	—	58.5*	—
M2-M3 length	37.0	44	—	35.5*	—

specimens of *A. bonariense* (in some cases, fewer measurements were available).

Cranial characters were polarized by out-group comparison method (Watrous and Wheeler, 1981; Madisson et al., 1984). We used the Ursinae as the first out-group. For those characters common to all Tremarctinae, the closely related Giant Panda, *Ailuropoda melanoleuca*, was used as a second out-group.

For the character analysis, we examined skulls of the following Ursinae: *Ursus americanus*, *U. arctos*, *U. thibetanus*, *Melursus ursinus*, *Helarctos malayanus*, from the Museu Nacional do Rio de Janeiro (MNRJ), *U.*

americanus, *U. arctos*, *U. maritimus*, from the Museum of Vertebrate Zoology at Berkeley, California (MVZ), *U. thibetanus* and *Arctodus simus*, from the Museum of Paleontology of the University of California, Berkeley (UCMP). Additional information on *Tremarctos* and *Arctodus* species was obtained from Kurtén (1966, 1967), Kraglievich (1926), Paula Couto (1960), and Perea and Ubilla (1985). Morphological data on *A. melanoleuca* were extracted from Davis (1964). We follow the classification of Honacki et al. (1982).

Considering the high individual variation in size and

cranial proportions observed in ursids, and the fact that series are not available for South American fossil bears, we limited the analysis to qualitative characters. Emphasis was given to those characters formerly used to define species or groups of species within the Tremarctinae.

SYSTEMATIC PALEONTOLOGY

Family URSIDAE

Subfamily TREMARCTINAE

Genus *ARCTOTHERIUM* Bravard, 1857

Diagnosis—Molars and P4 wider than in *Tremarctos* and *Arctodus*, M1 at least as wide as long; three anterior upper premolars compressed in a triangular arrangement between canine and P4.

Subgenus *PARARCTOTHERIUM* Ameghino, 1904

Diagnosis—Smaller than *A. (Arctotherium)*; U-shaped postpalatine margin; without a defined lingual cusp on P4; auditory bulla inflated; alisphenoid canal opens separate from the foramen rotundum.

A. (PARARCTOTHERIUM) BRASILIENSE (Lund, 1838) comb. nov.

Diagnosis—Postpalatine margin extends posteriorly to the last molar; size smaller than *A. enectum* and *A. pamparum*.

The above systematic arrangement and diagnoses were made in accordance with the phylogenetic hypothesis adopted below. The characters mentioned were inferred as synapomorphies, with the exception of the shape and position of the postpalatine margin.

Referred Material—GP/2T-4 (Fig. 1).

Description—Skull short, deep, and convex in general form, rostrum and respective bones short; nasal plane, not convex, with parallel longitudinal borders; ascending processes of premaxilla with parallel borders and a relatively wide fronto-premaxilla suture; premaxillary process of frontal short; a single infraorbital foramen (vertical diameter = 8.0 mm) with a 10.8 mm long canal opening on the face at the level of the anterior half of the first molar; maxilla relatively short; jugal process with a wide base, originating at the level of M1; zygomatic arches salient anteriorly; postorbital process pointed downward; braincase wide and inflated; sagittal crest practically absent, slightly developed only on the posteriormost portion of the parietals; distinct sagittal suture; occipital (lambdoid) crest distinct, but not well developed; a vertical nuchal crest restricted to the upper half of the supraoccipital; paroccipital process relatively strong; opening of external auditory meatus large; auditory bulla large, inflated, and elevated over the basioccipital surface; foramen magnum horizontally elliptical; postpalatine margin U-shaped and posterior to the last molars; choanae deep; alisphenoid canal opening into orbit independently of the fo-

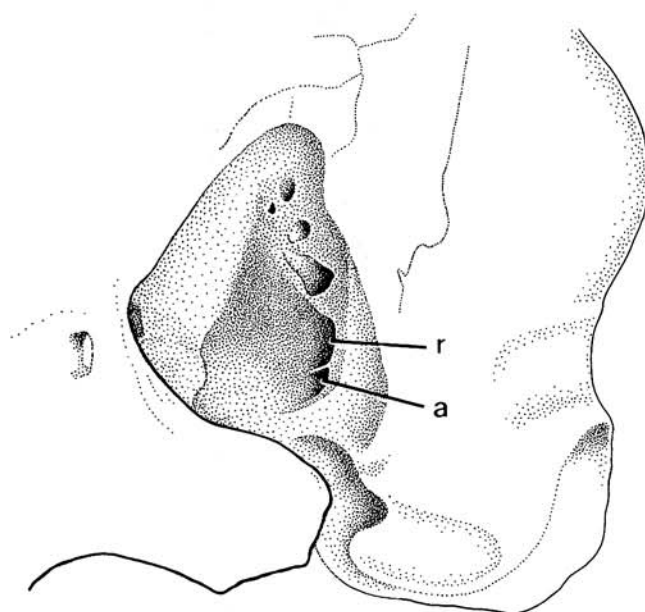


FIGURE 2. Orbital view of the alisphenoid region of *Arcotherium brasiliense* from Ubajara, showing alisphenoid canal (a) opening separate from the foramen rotundum (r).

ramen rotundum (Fig. 2); optic, ethmoid, lacrimal, and other cranial foramina in the usual condition for ursids.

Mandible as in other tremarctine bears: large and deep masseteric fossa separated from premasseteric fossa by a strong crest or bony septum almost vertically disposed just behind the M3; premasseteric fossa shallow, less deep than in *Tremarctos* and the North American *Arctodus*.

Upper tooth rows laterally bowed, dental formula I? C1/1 P4/4 M2/3. Tooth crowns moderately worn, indicating that it was a fully grown but not old individual. Upper arcade slightly asymmetrical, one of the first left premolars may have been lost during life. Resorption of bone tissue at the molar root level (roots partially exposed at the facial side) indicate that this animal had an occlusion problem probably related to this asymmetry (M. Novelli, pers. comm.). Dental morphology as described for *A. brasiliense* (Paula Couto, 1960). Upper canines large, transversally elliptical; P1-3 compressed in a triangular arrangement between canine and P4, with no diastema; P4 larger than the space occupied by P1-3, showing a somewhat triangular crown; P4 with a large anteroexternal cusp (paracone), a much smaller posteroexternal cusp (metacone), and an extremely reduced, virtually absent, lingual cusp; crown of M1 grossly quadrangular, with a somewhat rounded posterior margin; M1 and M2 with a small parastyle, no metastyle, a large paracone, and a low metacone; lingual cusps of molars (protocone and hypocone) less distinct and lower than external cusps; M2 longer than M1 due to the elongated talon. Lower dentition: premolars, if single rooted, four in number;

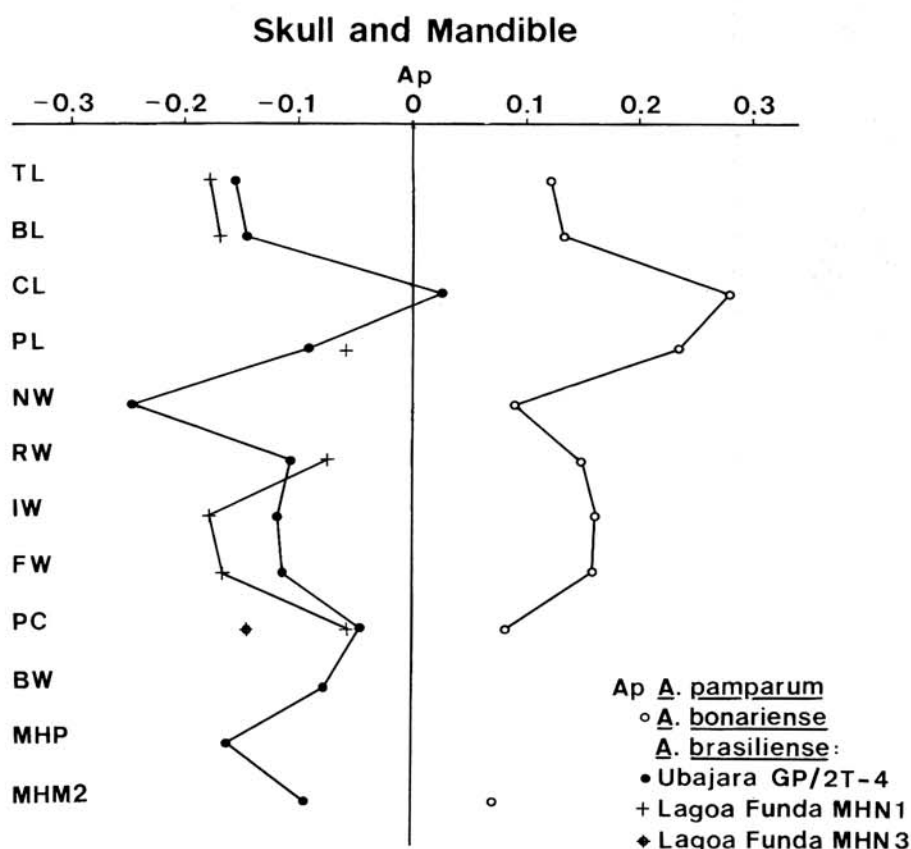


FIGURE 3. Ratio diagrams for skull and mandible measurements of individual specimens of *Arctotherium brasiliense* compared to means of *A. pamparum* and *A. bonariense*. See Table 1 for abbreviations.

p1 out of line, displaced medially; p2 close to canine; p4 larger than anterior premolars; diastema absent; m2 large, with a distinct metaconid and three small posterointernal tubercles; protoconid and hypoconid low; m3 smaller than m1 and m2, showing a wide and subelliptical crown, without distinct cusps except very low protoconid and hypoconid.

The measurements of the Ubajara skull, mandible, and teeth are presented in Table 1, as well as those of other specimens previously assigned to *A. brasiliense*. The differences in size and proportions between these specimens and the closely related *A. pamparum* and *A. bonariense* can be appreciated in the ratio diagrams of Figures 3–5.

We found no major qualitative differences between the specimen from Ubajara and those previously assigned to *A. brasiliense* from Minas Gerais State. Paula Couto (1960) mentions the well developed sagittal and lambdoid crests as being diagnostic features of this species, but this condition is observed only in the specimens MHN 3 and MHN 4 (braincases), and is absent in MHN 1 as well as the Ubajara skull. The differences observed in the development of the sagittal crest may be due to sexual dimorphism rather than to interspecific variation. Under this assumption, MHN 1 and

the Ubajara specimens are probably females, while MHN 3 and MHN 4 are likely males. Paula Couto (1960) also refers to an almost circular foramen magnum, directed posteriorly, which would differ from the elliptical foramen of the Ubajara skull. However, we were unable to examine the only specimen of *A. brasiliense* with an intact occipital region (MHN 4), and since the figures in the literature are unclear, we consider this a questionable feature. Finally, MHN 1 has distinctly more rugose molar crowns than the Ubajara specimen, but this difference is probably due to more pronounced wear in the latter. Except for the sagittal crest, the incomplete braincase which constitutes the MHN 3 specimen is more similar in general form and size to the Ubajara specimen than to MHN 1.

In general, the Ubajara skull is larger than the other known specimens of *A. brasiliense* in total length and interorbital, frontal, and braincase widths (Table 1). However, the new specimen has a narrower and shorter rostrum, as indicated by the rostral width and palatal length measurements (Fig. 3). The smaller rostrum is also reflected in the relatively smaller size of the upper last premolar and molars (Fig. 4), and the more laterally bowed tooth rows. The lower second and third molars are smaller (Fig. 5), but the first is within the

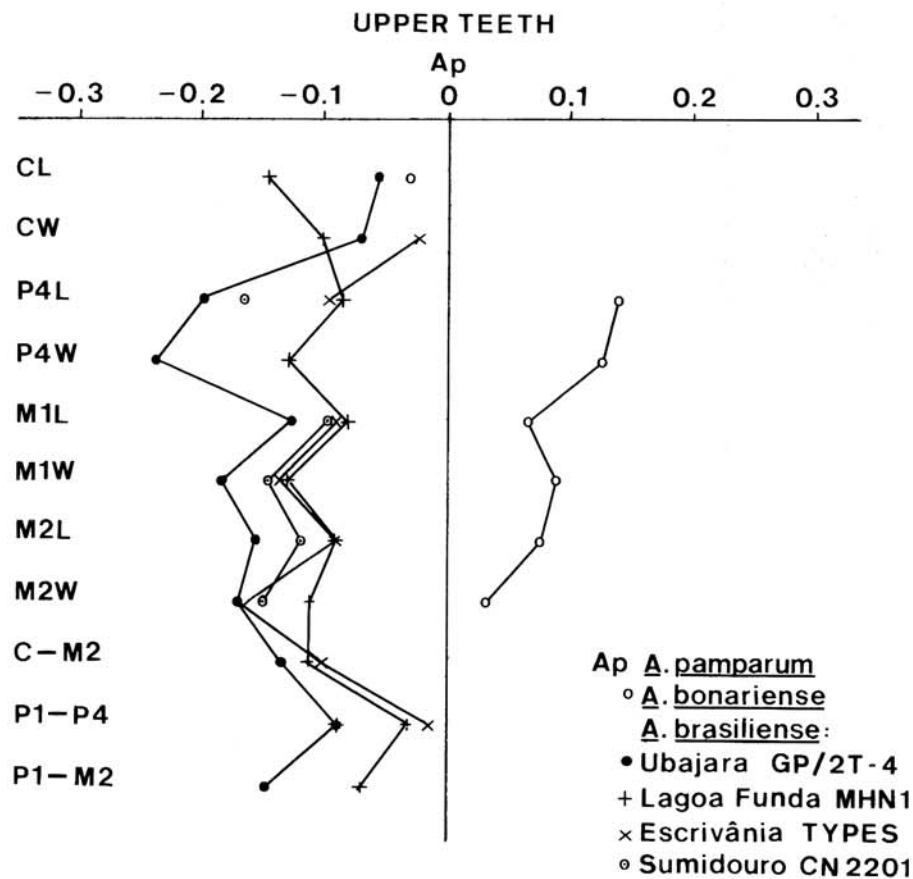


FIGURE 4. Ratio diagrams for upper tooth measurements of individual specimens of *Arctotherium brasiliense* compared to means of *A. pamparum* and *A. bonariense*. See Table 1 for abbreviations.

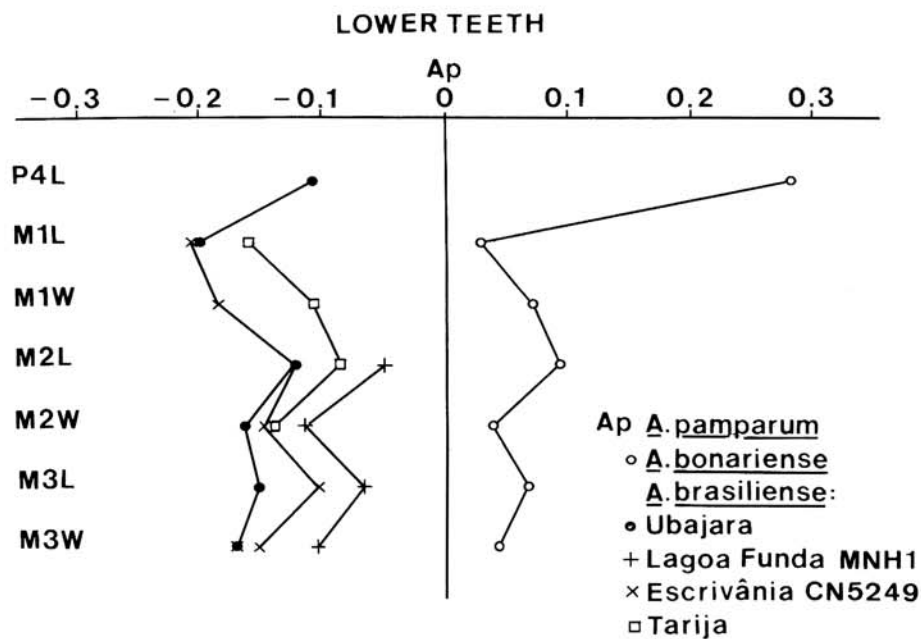


FIGURE 5. Ratio diagrams for lower tooth measurements of individual specimens of *Arctotherium brasiliense*. See Table 1 for abbreviations.

range of variation of that species. The upper canine is an exception in being larger in the Ubajara specimen than in that from Lagoa Funda.

The infraorbital foramen of the Ubajara skull is distinctly larger and has a shorter canal than that of MHN 1 (vertical diameter of foramen = 5.4 mm; canal length = 15.8 mm). The anterior portion of the zygomatic arch of the Ubajara specimen also differs in having a more open angle in relation to the longitudinal axis of the skull and an anteriormost position just behind the level of the infraorbital foramen. In the MHN 1 specimen the jugal process is less salient and originates posteriorly, at the level of M2.

CLADISTIC ANALYSIS OF TREMARCTINAE BEARS

The subfamily Tremarctinae includes the poorly known Pliocene genus *Plionarctos*, the genus *Tremarctos* (with an extant and an extinct species), and a number of extinct Pleistocene species currently placed in *Arctodus* (sensu lato). All the North American nominal species of the genus *Arctodus* were reduced by Kurtén (1967) to two valid species, *A. pristinus* and *A. simus*. *Arctotherium* (sensu stricto) includes the larger South American species, considered synonyms of *A. bonariense* by Kurtén (1967). *Pararctotherium* was created for the smaller South American forms, recognized as three distinct species, *A. enectum*, *A. pamparum*, and *A. brasiliense* (Paula Couto, 1960). The following comparisons are restricted to the better known species of Tremarctinae, with special reference to the *Pararctotherium* group. Unfortunately, most of the features analyzed are unknown for *A. enectum*. The cladistic analysis of characters 1–12, including cranial and dental features, resulted in the phylogenetic hypothesis shown in Figure 6, with the respective supporting synapomorphies.

Monophyly of the Tremarctinae

Among the selected features of the Tremarctinae, characters 1 and 2 are here considered equivocal, but characters 3 and 4 are considered unambiguous synapomorphies.

1. Entepicondylar foramen of humerus—Among known ursids, this foramen is a unique feature of the Tremarctinae, but its presence is variable in *Ailuropoda*. The polarity of this character depends on the phylogenetic position of Tremarctinae among other ursid groups, including the extinct Agriotheriinae.

2. Short rostrum—The longer rostrum, with a well developed diastema between the canine and premolars, is a common feature of the majority of the Ursinae and *Ailuropoda* (see Davis, 1964 for rostral comparison between *Ursus* and the Giant Panda), and is probably a plesiomorphic character. The reduced rostrum (Fig. 1A–C), with associated short nasal and maxillary bones, is a derived feature shared by the Tremarctinae, but is also present in *Helarctos*, and, to a lesser extent, *Selenarctos*. Whether this similarity between these taxa

is due to common ancestry or is the result of convergence depends on the monophyly of the subfamily Ursinae. If independently derived in the two ursid subfamilies, the short face may be another synapomorphy of the Tremarctinae.

3. General form of skull—The members of Ursinae, *Ailuropodidae*, and other generalized Carnivora (such as canids), have a more elongated, lower and less convex skull, which is here considered primitive in relation to the shorter, deeper and convex skull (Fig. 1A), diagnostic of the Tremarctinae. More extreme conditions of this feature are found in the large South American *Arctotherium*.

4. Premasseteric fossa—The presence of a distinct premasseteric fossa, separated from the masseteric fossa by a strong bony septum (Fig. 1F), is a unique feature interpreted as another synapomorphy corroborating the monophyly of Tremarctinae.

Relationships Within the Tremarctinae

5. Relatively wider molars—All species of *Arctodus*, *Arctotherium*, and *Pararctotherium* differ from *Tremarctos* and other ursids in having proportionally larger and wider upper and lower molars, with flatter occlusal surfaces. This is the main character supporting the genus *Arctodus* (sensu lato; Kurtén, 1967). Within this group, the South American fossil taxa share an additionally derived feature (5'), considered a synapomorphy of *Arctotherium* + *Pararctotherium*: all the molars and the P4 are even wider than in the North American *Arctodus*, especially the extremely broad (as wide as long or wider than long) and almost quadrate M1 (Fig. 1C).

6. Anterior upper premolars (P1–3) compressed in a triangular arrangement—*Tremarctos* and the North American fossil species of *Arctodus* share with other ursids an arrangement of premolars in which they are relatively well aligned between the canine and P4; this condition is interpreted as symplesiomorphic. All the South American fossil species show a derived condition in which the three anterior premolars lie in a triangular arrangement within a short diastema between the canine and P4 (Fig. 1C). This feature is therefore interpreted as another synapomorphy of *Arctotherium* + *Pararctotherium*.

7. V-shaped postpalatine margin—The plesiomorphic state common to all Ursinae and most of the Tremarctinae is a U-shaped postpalatine margin (Fig. 1C), while the V-shaped, anteriorly narrower postpalatine margin is a uniquely derived feature corroborating the monophyly of the large South American forms of the taxon *Arctotherium*.

8. Loss of the lingual cusp of P4—As far as we are aware, all Tremarctinae and other Ursidae, with the exception of *Pararctotherium* species, have a well developed lingual cusp on P4, which is here considered the primitive condition. A weakly developed, to nearly absent lingual cusp on P4 is therefore inferred as a synapomorphy of *A. pamparum* and *A. brasiliense*.

9. Inflated auditory bulla—Among the members of

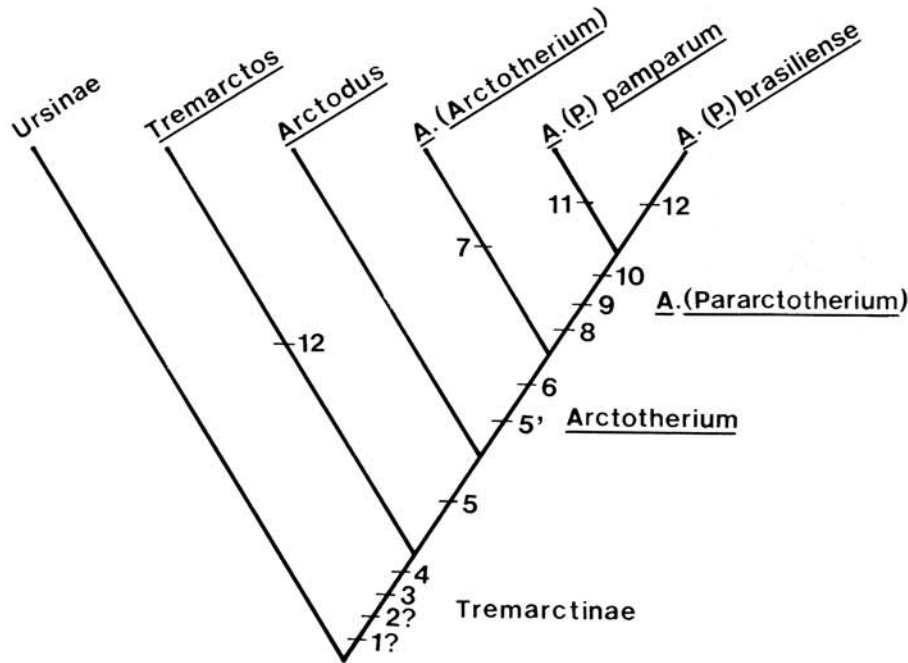


FIGURE 6. Proposed phylogenetic hypothesis for the subfamily Tremarctinae using other Ursidae and *Ailuropoda* as outgroups. See text for the description of inferred synapomorphies 1–12.

the family, the well developed, inflated bulla is clearly another synapomorphic feature shared by *A. pamparum* and *A. brasiliense*, contrasting with the flat bulla of all other Ursidae.

10. Alisphenoid canal opening separate from the foramen rotundum—Among ursines and some tremarctines (at least in *Tremarctos ornatus* and *Arctotherium*), the alisphenoid canal opens in a common vestibule with the foramen rotundum. The condition in which the alisphenoid canal opens into the orbit independently of the foramen rotundum (Fig. 2) is also diagnostic of *Pararctotherium*.

11. Postpalatine margin not extending posteriorly to the last molar—Although variable, the extension of the postpalatine margin posterior to the last molar (Fig. 1C) is common to all ursines and the majority of tremarctine taxa. The extreme condition where the postpalatine margin reaches the level of the last molars, observed in *A. pamparum*, is an autapomorphic feature diagnostic of this species.

12. Reduced size—The size variation observed in the Ursinae and Tremarctinae is remarkable. Members of the *Pararctotherium* group are relatively smaller than other extinct tremarctines, and *A. (P.) brasiliense* is the smallest species of this taxon. However, the species of *Tremarctos* are smaller yet, and the most parsimonious argument is that reduced size was independently acquired by these two taxa.

DISCUSSION

Most ursid species show a great range of individual variation unrelated to their geographic distribution.

There is notable sexual dimorphism in size and shape of skulls; males are larger (sometimes twice as large as females) and have well developed lambdoid crests (Mondolfi, 1989). This variability, observed among distantly related, not contemporaneous species such as *Tremarctos ornatus*, *Ursus americanus*, and *U. spelaeus*, is probably a general feature of the family. Thus, it is clear that an appropriate sample is needed to define ursid species and that the identification of single specimens is only possible if they share apomorphic qualitative characters and/or discontinuous size and proportions with well defined species.

Unfortunately, this is not the case with *Arctotherium brasiliense*. We were unable to find any secure apomorphy for this species. Cranial measurements are within the range of other bear species and apomorphies exhibited by this taxon are shared with *A. pamparum*. The only possible autapomorphy of *A. brasiliense* is small size, if one considers that the larger size of *A. pamparum* and *A. bonariense* is a primitive character for the *Arctotherium* clade (see below).

The Ubajara specimen differs from the Lagoa Funda specimen (MHN 1) in skull proportions and tooth sizes (see Figs. 3–5). These differences may be due to spatial and/or temporal differences in populations of *A. brasiliense* from central and northeastern Brazil (age data for these specimens is not available). However, it is also possible that they belong to different, but closely related species, because they are more similar to each other than to any other bears. On the other hand, specimen MHN 3, a braincase from Minas Gerais, is very similar to that from Ubajara. It is possible that there were two bear species, perhaps contemporaneous, in

central Brazil, at least one of them also occurring in the northeast. In view of the variation observed in ursids, the lack of series for the Brazilian fossil bears, and the fragmentary nature of the holotype of *A. brasiliense* (fragment of right upper and left lower jaws), the taxonomic position of the Ubajara bear is still doubtful. Because the bear from Minas Gerais is closest, both morphologically and geographically, the best decision is to refer to the Ubajara bear as *A. brasiliense*.

The taxonomic history of fossil tremarctines is very confusing, with a number of insufficiently characterized species and genera (see Kraglievich, 1926; Paula Couto, 1960; Kurtén, 1966, 1967). Our cladistic analysis of the better known taxa of Tremarctinae, with special reference to the South American fossils, resulted in an unambiguous pattern of synapomorphies, supporting the phylogenetic hypothesis depicted in Figure 6.

The monophyly of the subfamily Tremarctinae is corroborated, but the same cannot be stated for all its components. We were unable to discover any unequivocal synapomorphy uniting the two species of *Tremarctos*, and the monophyly of this genus is questionable. The monophyly of the genus *Arctodus* (sensu lato, including *Arctotherium* and *Pararctotherium*) is poorly corroborated by the present data. The North American species of this genus are grouped together only by general similarity, and new data are needed to evaluate their phylogenetic relationships with the South American taxa. However, all South American fossil species can be regarded as a monophyletic group defined by unique dental features. Within this assemblage are the species currently grouped under *Arctotherium* and *Pararctotherium*, two well defined monophyletic groups.

The genus *Arctodus* is restricted to the North American species (*A. pristinus* and *A. simus*, sensu Kurtén, 1967) and is left as a metataxon (a group whose monophyly is not yet determined). The taxon *Arctotherium* is here considered a distinct genus and is expanded to include all South American extinct bears, with *Pararctotherium* as a subgenus. *Arctotherium* (*Pararctotherium*) *brasiliense* and *A. (P.) pamparum* share a number of unique features indicative of a sister group relationship, but the position of *A. (P.) enectum* is not known, due to a paucity of data. The identities of the three species of this group are mainly supported by differences in size, although *A. (P.) pamparum* has a distinct autapomorphy.

Except for what is implicit in the different classifications formerly proposed, little has been discussed about phylogenetic relationships of the tremarctine bears. Much of the controversy on the generic classifications of previous authors is due to incongruences generated by indiscriminate use of both synapomorphies and symplesiomorphies in the definition of genera, as well as in inferences of phylogenetic relationships. Although we agree with Kraglievich (1926) that North and South American extinct tremarctines belong to different genera, the suggestion that *A. brasiliense*

may represent an intermediate form (Kraglievich, 1926; Kurtén, 1967) is refuted by our results.

Kraglievich (1926) proposed two independent dispersal events, from North to South America, to explain the origin of the larger (*Arctotherium*) and smaller (*Pararctotherium*) taxa. Based on the present phylogenetic hypothesis, we consider this an unnecessary assumption. Even if dispersal from North America is accepted, only one event is needed to explain the origin of *Arctotherium* (as here defined). Therefore, the subclades *A. (Arctotherium)* and *A. (Pararctotherium)* are more parsimoniously explained as having originated and differentiated in South America, after the establishment of a common ancestral species on the continent.

Another possible explanation for the origin of these taxa is the hypothesis that the ancestor was widely distributed on the two continents and a subsequent vicariant event was responsible for the isolation and differentiation of the genera *Arctodus* and *Arctotherium* (as here defined), respectively, in North and South America. The geographic distribution of the South and North American species of *Tremarctos* presents a similar problem. The present knowledge of the phylogeny and zoogeography of the Tremarctinae appears insufficient to support specific hypotheses about centers of origin for the subfamily and its genera, or to decide between the role of dispersion and of vicariance in the evolutionary history of these bears.

Bears seem to be primarily temperate mammals—they occur mostly in the temperate Northern Hemisphere and present physiological specializations related to seasonal climates, such as delayed implantation (Mead, 1989; Peyton, in press). Ursids do not occur in lowland tropical forest and tropical savannah below 500 m elevation, or in deserts with less than 125 mm of annual precipitation; in South America they are presently restricted to the Andes mountains from Venezuela to the border between Bolivia and Argentina (Peyton, in press).

The presence of bears in northeastern Brazil indicates a paleoclimate cooler than today, and a time period assignable to a Pleistocene glacial period. In Brazil, conspecifics (or members of a sister species) of the Ubajara bear also occurred in Minas Gerais State. Bears from Ubajara and Minas Gerais may represent two populations of a vicariant species widely distributed at least in northeastern and central Brazil, or may be the result of dispersal from the south, probably through central Brazil.

Bears in general are adapted to moving about in rough mountainous or hilly country or in forest, and they exhibit arboreal specializations (Ewer, 1973). However, tremarctine bears possess characters suggestive of adaptation to open areas. For example, the long limbs of *T. ornatus* and *Arctodus* would allow greater mobility and long distance sighting in open vegetation (Peyton, in press), and the development of the auditory apparatus (inflated bulla) in *Arctotherium brasiliense* and *A. pamparum* may be related to adaptation to dry

climates (Mares, 1976). Thus, since glacial periods in South America are associated with a general drying and expansion of open vegetation (Ab'Saber, 1977), *Pararctotherium* species probably expanded their ranges during glacial maxima, following the expansion of open vegetation.

The premaseteric fossa and the associated zygomaticomandibularis muscles are adaptations to a largely herbivorous diet in *T. ornatus* (Peyton, 1980; Mondolfi, 1983). The generalized occurrence of the premaseteric fossa in Tremarctinae suggests that a predominantly herbivorous diet is ancestral for this taxon. A well developed fossa is associated with ability to grind tough, fibrous food (Peyton, 1980). Considering that dry vegetation, where the Ubajara bear probably lived, is in general highly fibrous, its shallow premaseteric fossa indicates that this species was less herbivorous or fed on softer plant material than the spectacled bear.

ACKNOWLEDGMENTS

We thank the following persons and institutions for allowing us to examine ursid material: Instituto de Geociências da USP; Castor Cartelli, Museu de História Natural da UFMG; Museu Nacional do Rio de Janeiro; and James L. Patton and Anthony Barnosky, from the Museum of Vertebrate Zoology and Museum of Paleontology, respectively of the University of California at Berkeley. Special thanks are also due to James Patton, Bernard Peyton, and Meika A. Mustringi for valuable suggestions on the manuscript.

LITERATURE CITED

- Ab'Saber, A. N. 1977. Espaços ocupados pela expansão dos climas secos na América do Sul, por ocasião dos períodos glaciais quaternários. *Paleoclimas*, São Paulo 3:1–18.
- Davis, D. D. 1964. The giant panda: a morphological study of evolutionary mechanisms. *Fieldiana: Zoology Memoirs* 3:1–339.
- DeBlase, A. F., and R. E. Martin. 1981. *A Manual of Mammalogy, with Keys to Families of the World*. William C. Brown Co., Dubuque, 436 pp.
- Dias Neto, C. M., C. F. Lino, and I. Karmann. 1980. Nota sobre o urso fóssil de Ubajara-Ceará. Abstracts for the 31st Congresso Brasileiro de Geologia, Camburiú. Sociedade Brasileira de Geologia.
- Ewer, R. F. 1973. *The Carnivores*. Cornell University Press, Ithaca, New York, 494 pp.
- Hidalgo, T. T. P. 1988. Osos (Mammalia, Carnivora, Ursidae) del Pleistoceno Iberico: I. Filogenia; Distribución estratigráfica y geográfica. *Estudio anatómico y métrico del cráneo*. *Boletín Geológico Minero* 99:3–46.
- Honacki, J. H., K. E. Kinman, and J. W. Koepl. 1982. *Mammal Species of the World*. Allen Press Inc. and the Association of Systematic Collections, Lawrence, Kansas, 694 pp.
- Kraglievich, L. 1926. Los arctotérios norteamericanos (*Tremarctotherium*, n. gen.) en relación con los de Sud América. *Anales del Museo Nacional de Historia Natural Bernardino Rivadavia* 34:1–16.
- Kurtén, B. 1966. Pleistocene bears of North America. 1. Genus *Tremarctos*, spectacled bears. *Acta Zoologica Fennica* 115:1–120.
- . 1967. Pleistocene bears of North America. 2. Genus *Arctodus*, short-faced bears. *Acta Zoologica Fennica* 117:1–60.
- Maddison, W. P., M. J. Donoghue, and D. R. Maddison. 1984. Outgroup analysis and parsimony. *Systematic Zoology* 33:83–103.
- Mares, M. A. 1976. Convergent evolution of desert rodents: multivariate analysis and zoogeographic implications. *Paleobiology* 2:39–63.
- Mead, R. A. 1989. The physiology and evolution of delayed implantation in carnivores; pp. 437–464 in J. L. Gittleman (ed.), *Carnivore Behaviour, Ecology and Evolution*. Cornell University Press, Ithaca, New York.
- Mondolfi, E. 1983. The feet and baculum of the spectacled bear, with comments on the ursid phylogeny. *Journal of Mammalogy* 64:307–310.
- . 1989. Notes on the distribution, habitat, food habits, status and conservation of the spectacled bear (*Tremarctos ornatus* Cuvier) in Venezuela. *Mammalia* 53:525–544.
- Paula Couto, C. 1960. Um urso extinto do Brasil. *Boletim da Sociedade Brasileira de Geologia* 9:5–27.
- . 1979. *Tratado de Paleomastozoologia*. Academia Brasileira de Ciências, Rio de Janeiro, 590 pp.
- Perea, D., and M. Ubilla. 1983. *Arctodus pamparus* (Amegh.) (Mammalia, Ursidae) en sedimentos Lujanenses del Dep. Rio Negro, Uruguay. *Resúmenes y Comunicaciones de las Jornadas de Ciencias Naturales* 3:88–91.
- and ———. 1985. Caracterización de dos patrones morfológicos en Tremarctinae (Carnivora, Ursidae) extinguidos de Sudamerica. *Actas de las Jornadas de Zoología del Uruguay* 1985:25–27.
- Peyton, B. 1980. Ecology, distribution and food habits of spectacled bears, *Tremarctos ornatus*, in Peru. *Journal of Mammalogy* 61:639–652.
- . In press. Family Ursidae Gray, 1825; in A. L. Gardner, S. Anderson, and J. L. Patton (eds.), *Mammals of South America*, Vol. 2. University of Chicago Press.
- Simpson, G. G. 1941. Large Pleistocene felines of North America. *American Museum Novitates* 1136:1–27.
- Walter, H. V. 1940. Urso extinto "*Arctotherium brasiliensis*" da caverna de Lagoa Funda, Minas Gerais. *Gráfica Guarani*, Rio de Janeiro.
- Watrous, L. E., and D. Q. Wheeler. 1981. The out-group comparison method of character analysis. *Systematic Zoology* 30:1–11.
- Winge, H. 1895. Jordfundne og nulevende Rovdyr (Carnivora) fra Lagoa Santa, Minas Geraes, Brasilien. *Med Udsigt over Rovdyrenes indbyrdes Slaegtskab*. *E Museo Lundii* 2:1–103.

Received 19 October 1992; accepted 23 July 1993.