

First report of a South American short-faced bears' den (*Arctotherium angustidens*): palaeobiological and palaeoecological implications

LEOPOLDO H. SOIBELZON, LUCAS H. POMI, EDUARDO P. TONNI,
SERGIO RODRIGUEZ AND ALEJANDRO DONDAS

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Here we report the first example of associated short-faced bear fossils from South America. The specimens represent three individuals referable to the Ensenadan (early to middle Pleistocene) species *Arctotherium angustidens* (Ursidae, Tremarctinae), the giant South American short-faced bear. Although the fossil record of short-faced bears in South America is very rich, they have not previously been recorded in association. These three individuals were found in a cave during quarry exploitation. We suggest that these bears represent the first record of a family group and open the discussion about cave utilization and hibernation or torpor by South American short-faced bears.

Leopoldo H. Soibelzon [lsoibelzon@fcnym.unlp.edu.ar], Lucas H. Pomi [lucaspomi@hotmail.com], Eduardo P. Tonni [eptonni@fcnym.unlp.edu.ar], Departamento Científico Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque, La Plata B1900FWA, Argentina; Sergio Rodriguez [rodriguezs@ymail.com] Facultad de Ciencias Naturales y Museo, 122 y 60, La Plata B1900FWA, Argentina; Alejandro Dondas [adondas@gmail.com] Museo Municipal de Mar del Plata, Plaza España, 7600 Mar del Plata, Argentina. Received 2.9.2008; revised 5.11.2008; accepted 14.11.2008.

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THE NAME short-faced bear (SFB) encompasses seven species from two genera: *Arctodus* Leidy, 1854 (North American SFB) and *Arctotherium* Burmeister, 1879 (South American SFB) of the subfamily Tremarctinae Merriam & Stock, 1925 (Kurtén 1967, Soibelzon 2004). These bears are recorded from the Blancan IV to Rancholabrean faunal stages (late Pliocene to early Holocene) in North America (Kurtén 1967), in the Blancan IV (late Pliocene) in Central America (cf. *Arctotherium*; Soibelzon *et al.* 2008) and from the Ensenadan to Lujanian (early Pleistocene to early Holocene) in South America (Soibelzon *et al.* 2005). SFB are assumed to have arrived in South America during the

event called the 'Great American Biotic Interchange' (GABI: Marshall *et al.* 1982).

Here we report three associated SFB from Buenos Aires province, Argentina. These individuals are assigned to the Ensenadan (early to middle Pleistocene) species *Arctotherium angustidens* Gervais & Ameghino, 1880, the giant South American SFB. Of the five *Arctotherium* species this is the only one recorded in the Ensenadan and it is the largest; among ursids only some individuals of *Arctodus simus* (Cope, 1879) approach its size (see Gobetz & Martin 2001 and Soibelzon 2002). Although the fossil record of SFB in South and North America is very rich, associated individuals are rare and this is the first reported occurrence of a potential female and her offspring. These individuals were found in a cave during quarry exploitation. We suggest that these bears could represent a family group of SFB

that were utilizing the cave for denning, and possibly even hibernation.

Geological setting

Locality and age

The fossils occur at 'Estancia El Casal' (37°50'30"S, 57°36'37"W), near Mar del Plata city, Buenos Aires Province (Fig. 1A). The remains were found at the lower level of a quarry and are assigned to the Ensenadan (Soibelzon *et al.* 2001) based on the record of *Glyptodon munizi* Ameghino, 1881, another exclusive Ensenadan species (Soibelzon *et al.* 2006) in equivalent strata. At the same quarry and level were recorded the xenarthrans *Scelidotherium* Owen, 1840 (MMMP 3984, 3986 to 3988, 3990 and 3992), *Scelidodon* Ameghino, 1881 (MMMP 3989), *Glyptodon munizi* (MMMP 3985, Soibelzon *et al.* 2006), *Glyptodon* sp. (Owen 1838; MMMP 3991) and the sabre-tooth cat *Smilodon populator* Lund, 1842 (MMMP 4048).

Geology

In the lower level of the quarry, two facies are recognizable, separated by a compact calcium carbonate (calcrete) horizon. The

uppermost is dominated by brown silt, reworked silt intraclasts and laminated structures. The lower facies (where the den was excavated) consists of massive reddish grey (5YR5/2) silt. Due to the destructive extraction method (see below) we were unable to study the detailed distribution of the sediments that filled the cave, and that is why we are unable to determine whether these bears died due to a natural disaster (eg. cave roof collapse) or some other reason. Other caves discovered near the bear's site are partially filled by sediment (i.e. not to the roof, Fig. 1B). The sediment inside these caves is laminated and loess-like. The sediment in which the SFB are embedded is also pinkish grey (5YR6/2) and loess-like. Overlying the lower level there is a uniform profile of massive and reddish grey (5YR5/2) silts with calcium carbonate layers.

Materials and methods

Fossil salvage

While exploiting a quarry to enlarge National Route 2, the operator of an excavator discovered the fossil remains and contacted the Museo Municipal de Mar del Plata

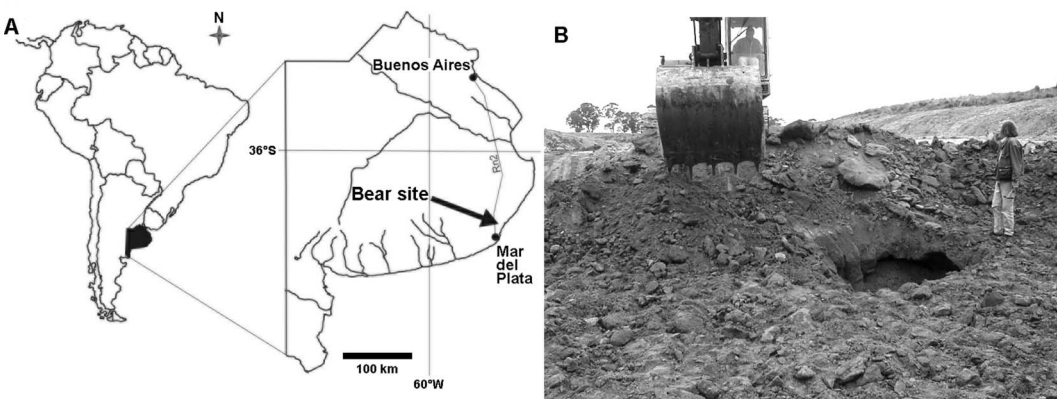


Fig. 1. A, Map of Buenos Aires province showing the bear fossil site. B, Photograph of a newly opened cave excavated in the same level as that from which the fossil bears were recovered.

(MMMP). By the time A. Dondas and L.H. Soibelzon arrived, a large portion of the specimens' postcranial skeletons had been transported (mixed with the rubble) to the route embankment and the entire level hosting the bears had been completely removed. We were able to salvage additional remains before exploitation resumed. Also, several workers had extracted some teeth from the largest specimen believing that they had monetary value. For these reasons a considerable amount of information was lost. Despite these setbacks, the discovery was a rare and fortuitous event because these bears were buried under more than ten metres of sediment.

Age determination of individuals

A relative age determination method for SFB was proposed by Soibelzon (2002). This author constructed five age categories (juvenile, young adult, adult, old adult and senile adult) based on the degree of enamel and dentine wear over definitive molars. Additionally, we follow Schubert & Kaufmann (2003) in order to infer the age and sexual maturity of SFB on the basis of the degree of fusion of epiphyses of some elements of the postcranial skeleton. Furthermore, for the first time we are able to evaluate the variation in the degree of fusion between skull bones of juveniles and adults of *Arctotherium*.

Sex determination

Kurtén (1967) and Torres (1988) used the canine labio-lingual width at the base of the crown in order to separate males from females in fossil bears. Soibelzon (2002) adapted this methodology to the abundant remains of *A. angustidens* using 15 size classes (of 5 mm increment) that spanned the complete range of canine sizes. This resulted in two well-separated groups: the individuals in the range 23.6 to 26 mm (mode in class 24.6–25) were interpreted as

females and those in the range 27.1 to 29.5 mm (mode in class 27.6–28) as males.

Referred specimens

MMMP 3982 represents a nearly complete skull with teeth and fragmentary mandible (Fig. 2A). MMMP 3980 is an incomplete skull and mandible with several teeth and some postcranial elements (Fig. 2B, C, D). MMMP 3981 is a fragmentary skull and incomplete mandible with several teeth (Fig. 2E, F). MMMP 3983 consists of juvenile postcranial elements (Fig. 2G). See Systematic palaeontology section below for further details.

Abbreviations and terminology

MMMP: Museo Municipal de Mar del Plata 'Lorenzo Scaglia,' Argentina. NHM: Natural History Museum, London, UK. I/i: upper and lower incisors. C: canines. M/m: upper and lower molars. P/p: upper and lower premolars.

The chronostratigraphic/geochronologic units used herein (Marplatan, Ensenadan, Bonaerian and Lujanian) follow the usage by Woodbourne *et al.* (2006). The sediment colours were determined using Munsell Soil Colour Charts. Fossil teeth measurements were taken with a dial calliper.

Systematic palaeontology

Class MAMMALIA Linnaeus, 1758

Order CARNIVORA Bowdich, 1821

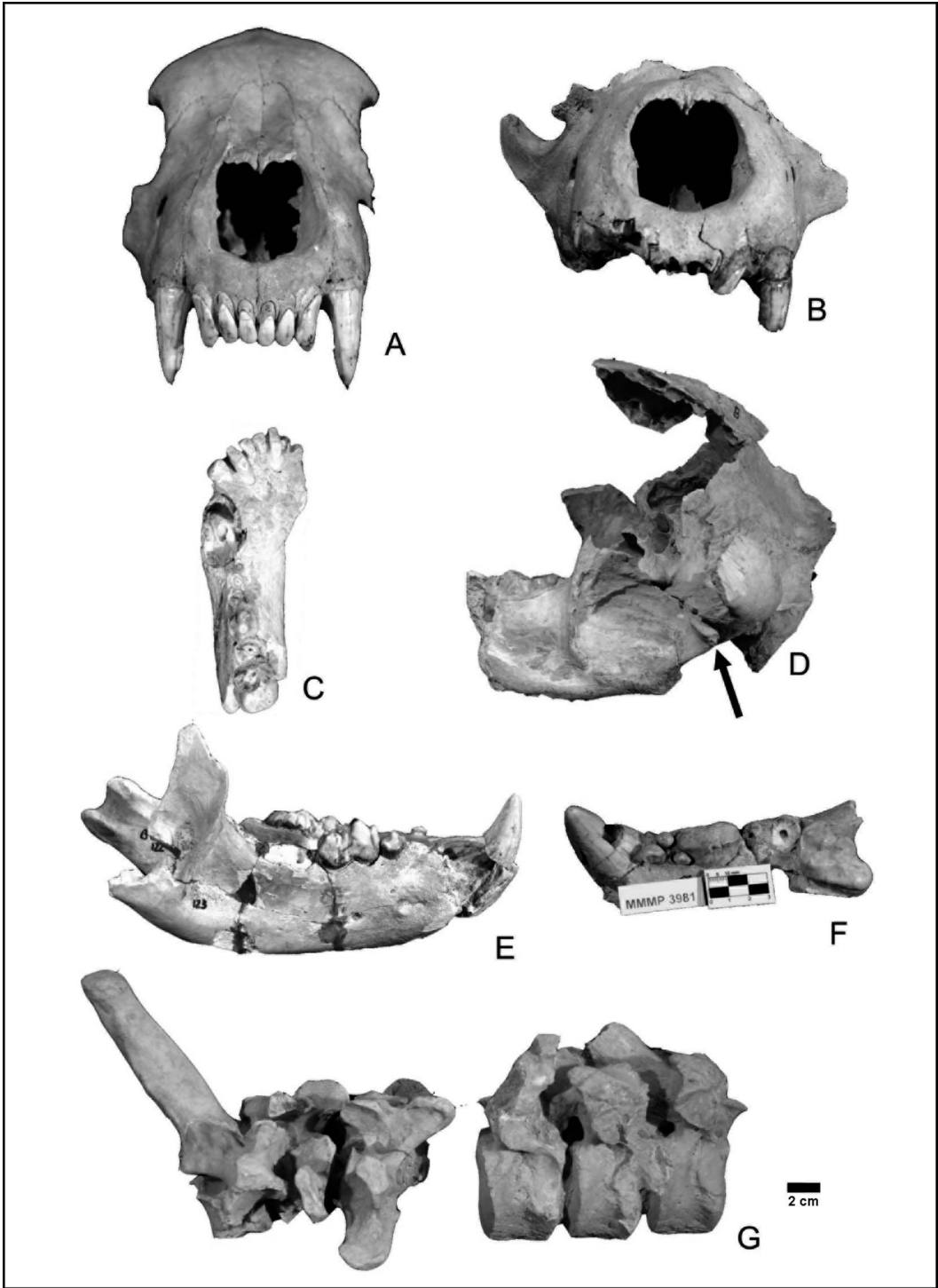
Family URSIDAE Gray, 1825

Subfamily TREMARCTINAE Merriam & Stock, 1925

Arctotherium Burmeister, 1879

Type species. *Arctotherium bonariense* (Gervais, 1852).

Age. early Pleistocene to early Holocene (Ensenadan to Lujanian).



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Distribution. Argentina, Venezuela, Bolivia, Brasil, Uruguay and Chile.

Arctotherium angustidens Gervais & Ameghino, 1880

Holotype. NHM 32915 to 32974, from the Ensenadan of 'toscas del Río de La Plata,' Buenos Aires, Argentina.

Geographic and stratigraphic distribution. Early to middle Pleistocene (Ensenadan) of the Pampean region of Argentina, Pleistocene of Bolivia (Soibelzon *et al.* 2005).

Diagnosis [following Soibelzon (2004)]. The dorsal border of the foramen magnum is complete (without indentation); there are two ante-orbital foramina; the neurocranium is large and laterally compressed; the sagittal crest is well developed; the zygomatic arches are laterally expanded; the tympanic bulla is flat; the postpalatine margin is V-shaped and does not overpass the distal end of M2. The distal lobes of both I1 and I2 are small; the mesial lobe of I3 is well developed. On P4, the distolingual cingulum is absent, and the protocone is well developed; the paracone is taller than the metacone. On M1, the crown is wider than long; the parastyle is poorly developed; the lingual border cusps are medium-sized; the hypocone has only one cusp; the protocone is the largest of the lingual cusps. On M2, the parastyle is small in relation to the paracone size, and the talon area is well developed and differentiated.

Description. MMMP 3982: Nearly complete skull broken in two halves and a fragment

of mandible. The first skull portion is broken ahead of the glenoid fossa ventrally and on the right side lacks the zygomatic process of the temporal and the entire skull roof but retains a lateral portion of the right parietal. The other skull portion is almost complete but is broken ventrally (conserving a portion of the palate) and at both sides under the frontals, both zygomatic arches were lost. This skull piece preserves all teeth except the left P4 and M1–2 (Fig. 2A). Finally, a distal portion of the left mandible (incomplete in front of m3) preserving the ascending ramous, the condyle and the angular process.

MMMP 3981: This is the most fragmentary individual of the three. Only a nearly complete mandible, some portions of the skull and several postcranial elements were recovered. The mandible is the best-preserved element of this specimen. It is incomplete on the right side behind the premasseteric fossa and on the left side all the ascending ramus is absent but the angular process is present. On the left side, the left p2, m1 talonid and m2 were preserved. On the right side, the c1, p1, p4 and m1 are implanted (Fig. 2E). Both m3 were found isolated. The recovered skull pieces include: the left and right zygomatic process of the temporal, the right one preserves the glenoid fossa; the left temporal region with the mastoid process, the tympanic bulla and the glenoid fossa (the mandibular condyle is attached); the isolated right occipital condyle; a fragment of the premaxilla with left I2–3 and right I2; the left maxilla with C (partially broken), P1–4 and M2 (Fig. 2F); and a small fragment of the right maxilla with M1–2. A small triangular portion of the left

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 Fig. 2. Examples of *Arctotherium angustidens* specimens. A, Anterior view of the juvenile male skull MMMP 3982. B, Anterior view of the female adult skull MMMP 3980. C, Left portion of mandible (MMMP 3980). D, Lateral view of the posterior half of the skull and left mandible (MMMP 3980), arrow indicates the mandible attached to the skull. E, Lateral view of a juvenile male mandible (MMMP 3981). F, Occlusal view of left maxilla (MMMP 3981). G, Lateral view of two articulated portions of juvenile vertebral column (MMMP 3983). Scale bar = 2 cm.

parietal with a segment of lambdoid and sagittal crests is retained. A ventral portion of the axis with the odontoid and both anterior articular processes is preserved. Several isolated portions of pelvis are present: a fragment of the right ischion with a portion of the right acetabulum and a fragment of the iliac fossa together with a large portion of the left ilium with the iliac fossa, the iliac crest and the sacro-iliac joint and a cranial portion of the sacrum.

MMMP 3980: There are two portions of skull and mandible belonging to this individual and several postcranial elements. The first skull portion is an anterior piece broken at the posterior end of the nasal bones and the anterior border of the orbits. This skull portion conserves the right P2–3, a lingual fragment of the P4 crown and M1–2, and left I3, C, P1–2 and M2 (Fig. 2B). The other fragment is the posterior half of the skull broken ventrally in front of the glenoid fossa level and dorsally conserves a fraction of the skull roof with a segment of sagittal crest and a portion of the right parietal. It also retains a distal portion of the left mandible (broken at the m2 talonid) attached by its condyle to the left glenoid fossa (Fig. 2D). On the mandible portion are two teeth: the m3 and the talonid of m2 (Fig. 2D). The other mandible portion includes the following teeth: right i1–2 and left i1–3, p4 and talonid of m1 (Fig. 2C). Apart from the cranial elements, there are some postcranial remains assigned to this specimen: a head and neck of the left femora, a patella, six lumbar vertebrae, and a portion of pelvis where the *sacrum*, the left ilium, acetabulum and ischium were preserved.

MMMP 3983: Under this number were catalogued those postcranial elements corresponding to juveniles that could not be assigned with certainty to any individual. Among the remains there is a fragmentary left femora lacking its head and distal epiphyses; a complete left tibia without its

distal epiphyses; a proximal portion of the left radius and ulna; and a left calcaneum. The vertebral elements recovered consist of one partial atlas lacking the right pleuroapophyses and spinous process, three cervical and 12 articulated thoracic vertebrae (Fig. 2G).

Comments. Since all roots of the absent teeth are *in situ* and show fresh fractured surfaces we assume that the teeth were present before the discovery but were removed alternatively because of the unusual extraction method or due to the actions of the quarry workers (see Materials and methods). The fragmentation of the cranial and postcranial material probably occurred from the same process, since all fractures are also fresh.

As indicated above, *A. angustidens* is the best known species of *Arctotherium* because it is relatively abundant in the fossil record. The new juvenile specimens, described here, provide information on the morphological changes of skull that occur during the transition from juvenile to adult. In this respect, it is evident that the skull is more vaulted in juveniles but wide and flat in adults. The nostril opening, the mastoid process, and the sagittal and lambdoid crests are all much larger and the palate wider in relation to the skull size in adults. The front is oblique and the nasals form a concave platform in juveniles; in adults the front is vertical and the nasals are very convex. The zygomatic arches are heavier and well separated from the skull in adults. In addition, the muscular insertion marks on the occipital region are stronger in adults.

The Minimum Number of Individuals (MNI) is three based on the number of premaxilla and molars. However, we could not discard the possibility that there were more than three individuals because of the incomplete recovery of postcranial elements and the very fragmentary nature of the recovered remains.

Palaeobiology

Were they a family group?

Using the relative age determination method of Soibelzon (2002; see Materials and methods) we established that the group was composed of an old adult individual (MMMP 3980), because the main cusps on its molars were removed by attrition resulting in flat crown surfaces, and two juveniles (MMMP 3981 and 3982) based on the absence of wear signals on their molars. Two of the three specimens were not osteologically mature when they died because all preserved epiphyses (MMMP 3983) were not fused. Schubert & Kaufmann (2003) described an SFB (*Arctodus simus*) and suggested that it died younger than 4–6 years old because it had several unfused epiphyses (except for those of the ulna and radius). They also proposed that this specimen was sexually mature based on a comparison with the Spectacled bear, at which age sexual maturity is attained. MMMP 3981 and 3982 were much younger than the SFB described by Schubert & Kaufmann (2003), since their radius and ulna epiphyses remain unfused. Hence, we contend that they were sexually immature.

Another criterion for age determination in mammals is the degree of fusion between skull bones. Again, MMMP 3981 and 3982 show characteristics of juveniles because some sutures that are fused in adults and senile bears are not fused on these two individuals (e.g. the inter-nasal, premaxillamaxillary, sagittal, squamosal, coronal and basioccipital-temporal sutures). Finally, MMMP 3980 is undoubtedly an old adult, since its skull bone sutures are barely visible, and all the epiphyses preserved are fused.

Based on canine width, the adult bear (MMMP 3980) falls into the female range (26 mm), and the two younger individuals fall into the male range (MMMP 3981, 28 mm and MMMP3982, 27.8 mm). The

sex was determined following the methodology described in the Material and Methods (see also Soibelzon 2002). Based on these comparisons, we propose that these bears were a family group consisting of an adult female and two young males.

Were they in a cave?

Unfortunately, we arrived after the level containing the SFB was excavated. However, the operator of the mechanical excavator asserted that the giant SFB were extracted from a cave (pers. com. to LHS and AD). Supporting evidence includes:

- (1) Articulated remains, such as the articular processes of the mandible attached to glenoid fossa of the cranium in skulls MMP 3980 and 3982 (Fig. 2D). There are also some articulated portions of a vertebral column (Fig. 2G). Hill (1979) and Hill & Behrensmeyer (1984) argued that skull-mandible articulation is lost early in the disarticulation process. The retention of these articulations indicates either rapid burial of the carcasses or preservation in a protected environment (such as a cave).
- (2) MNI is three individuals.
- (3) Many caves were observed in the Ensenadan level in adjacent sectors at the same quarry (Fig. 1B).
- (4) Cave utilization by members of the Ursidae is well known. There are other records of South American SFB preserved in late Pleistocene caves, but no complete specimens and no examples of *A. angustidens*. In southern Chile, a femora (Martin *et al.* 2004) and one incisor (Prevosti *et al.* 2003) of *Arctotherium tarijense* Ameghino, 1902 have been reported from a cave. *Arctotherium wingei* Ameghino, 1902 was recorded in Brazilian (e.g. skull and hemi mandible; Trajano &

Ferrarezzi 1994, Cartelle 1998) and Venezuelan caves (isolated teeth; Soibelzon & Rincón 2007).

Pampean caves are different from those of Brazil and Venezuela because they are palaeoburrows excavated in Pleistocene sediments (Vizcaíno *et al.* 2001). The occurrence of caves attributed to palaeoburrows built by extinct animals in the southeast of the Pampean region is well known (see Zárate *et al.* 1998, Vizcaíno *et al.* 2001, Dondas *et al.* 2006); the large ones were postulated to have been excavated by mylodontid sloths like *Scelidotherium* Owen, 1840 and *Glossotherium* Owen, 1840 (Frenguelli 1928, 1955, Zárate *et al.* 1998, Vizcaíno *et al.* 2001) and large armadillos: *Pampatherium* Ameghino, 1891, *Eutatus* Gervais, 1867 and *Proptraopus* Ameghino, 1891 (Imbellone & Teruggi 1988, Imbellone *et al.* 1990, Quintana 1992). A possible burrow excavator (*Scelidotherium*, MMMP 3984, 3986 to 3988, 3990 and 3992) was recorded at the same quarry and level hosting the SFB.

Why were these SFB in a cave?

There are several possible explanations for the co-occurrence of the SFB in a cave:

- (1) These bears were under hibernation, torpor or dormancy when they died.
- (2) They periodically frequented the cave, perhaps seeking prey or carrion.
- (3) They were using the cave as a den.

Hibernation, torpor or dormancy (usage varies depending on the interpretation by different authors) is a common behaviour in bears, e.g. in Brown, Polar, American Black bears and the extinct Cave bear (Nelson *et al.* 1980, Stiner 1998, Nowak 1999) living in seasonal environments, but there is no evidence of hibernation for the Spectacled bear (the only living Tremarctinae) and for

the Great Panda. The climate of the Pampean region was strongly seasonal in the Pleistocene (and today) because of its medium- to high-latitude location, hence favouring hibernation. Moreover, several glacial advances, including the Great Patagonian Glaciation (1.168–1.016 Ma), have been recognized in Patagonia during the Ensenadan (Rabassa *et al.* 2005) suggesting that seasonal dormancy would have favoured survival under the harsh climate. On the other hand, optimizing hibernation as a character on an Ursidae tree (such as that of Krause *et al.* 2008) resulted in the absence of hibernation at the Tremarctinae node because of the non-hibernation behaviour of the Spectacled bear. Nevertheless, this bear lives mainly in temperate to tropical environments where hibernation is not expected.

It is not likely that these three bears were together inside the cave looking for prey or carrion when they died because the probability of preservation during such incursions would appear to be low. Furthermore, there were no remains of potential prey mixed with those of bears as might be expected due to the excellent preservation of the bear specimens.

The most parsimonious hypothesis is that SFB undertook the generalized denning behaviour of most Ursinae (e.g. Cave bear and Brown bear in Europe and American Black bear, Polar bear and Brown bear in North America). However, we cannot completely exclude the other two hypotheses. Significantly, Schubert & Kaufmann (2003) postulated a denning behaviour in the North American SFB.

Unfortunately, due to the circumstances of the fossils recovery we can never be certain of the circumstances surrounding the animals' deaths. However, two hypotheses appear more probable among other scenarios: an episodic burial event (e.g. cave roof collapse) or death via starvation during hibernation or denning. There is no

evidence of *in vivo* fractures or lesions left by diseases.

Palaeoecology

Eutherian carnivores arrived in South America, like many other taxa of holarctic origin, through the Panamanian Isthmus as part of the GABI (Soibelzon & Prevosti 2007). This interchange occurred after the marine barrier that separated South America and North America disappeared around the Pliocene–Pleistocene boundary *ca* 2.6 Ma (see Woodbourne *et al.* 2006). SFB arrived in South America within this time frame.

Large carnivores were absent from the middle Pliocene to early Pleistocene of South America. Only the medium-sized carnivore *Thylacosmilus* Riggs, 1933 (Marsupial sabre-toothed ‘cat’), together with small and omnivorous procyonids (*Cyonasua* Ameghino, 1885 and *Chapadmalania* Ameghino, 1908) and phororhacoid birds were present. After the Plio–Pleistocene boundary (subsequent to GABI), the top predator guild in the South America Ensenadan ecosystems was composed of seven species: *Theriodictis platensis* Mercerat, 1891, *Procyon scagliorum* Kraglievich, 1952, *P. troglodytes* (Lund, 1838) and *Canis* (?) *gezi* Kraglievich, 1928 in the Canidae (Prevosti 2006), *Smilodon populator*, *Panthera onca* (Linnaeus, 1758) and *Puma* Jardine, 1834 in the Felidae (Soibelzon & Prevosti 2007) and *A. angustidens*, the giant SFB (the largest and most powerful mammalian predator of South American terrestrial ecosystems that ever existed).

The Ensenadan ecosystems were characterized by the high abundance of herbivorous megamammals [e.g. *Glyptodon munizi*, *Macrauchenioipsis ensenadensis* (Ameghino, 1888), *Megatherium gallardoi* C. Ameghino & Kraglievich, 1921 and *Panochthus intermedius* Lydekker, 1894 (Soibelzon 2008)]. This pattern involved indigenous herbivores, whose tendency to

gigantism reached its maximal expression at that time (see Alberdi *et al.* 1993), and only one megacarnivoran: the giant SFB.

It is interesting to explore the biological consequences and behavioural reactions that could have been triggered by the introduction of a megacarnivoran such as the giant SFB among the endemic pampean megafauna, not only as a recently arrived predator but also as a powerful competitor for dens. It has been reported that herbivores are able to quickly learn to adjust their behaviour in order to decrease predation risk after a recolonization of large carnivores in recent ecosystems. Predation risk may cause changes in behaviour of prey, i.e. changes in diet, temporal changes in feeding patterns, spatial changes in habitat use or changes in patch selection (Lima & Dill 1990).

It is noteworthy that before Ensenadan times (i.e. Marplatán) there are scarce records of large burrows in the Pampean region although putative burrow excavators (see above) were present. We suggest that this behaviour would have been acquired or generalized after the arrival of large carnivores. In this respect, Vizcaíno *et al.* (2001) suggested that giant sloths depended on burrows to escape predation but also that these animals used burrows to avoid, alternatively, excessively cold or warm climatic conditions in order to conserve energy and water, and to breed and even survive during the colder seasons because of the particular physiology of xenarthrans (see McNab 1985 and Vizcaíno & Loughry 2008). Therefore, the arrival of large carnivores appears to have affected the indigenous megafauna not only by the addition of the top predator node in the ecological net, but also by direct competition for dens.

Even if much more fieldwork is needed to understand the causes of the faunal turnover observed at the Ensenadan–Bonaerian boundary (middle Pleistocene), Cione & Tonni (1999) suggested that after

that time, the mammal communities changed drastically and were associated with body-size reduction of megamammals, including the SFB.

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References

- ALBERDI, M.T., BONADONNA, F.P., CERDEÑO, E., LEONE, G., LONGINELLI, A., PRADO, J.L., SÁNCHEZ, B. & TONNI, E.P., 1993. Paleoclimatic and paleobiological correlations by mammal faunas from Southern America and SW Europe. *Ciencias da Terra* 12, 143–149.
- AMEGHINO, F., 1881. *La antigüedad del hombre en el Plata*, Tomo Segundo. G. Masson, Paris & Buenos Aires, XIV + 640 pp.
- AMEGHINO, F., 1885. Nuevos restos de mamíferos fósiles oligocenos, recogidos por el profesor Pedro Scalabrini y pertenecientes al Museo provincial de la ciudad de Paraná. *Boletín de la Academia de Ciencias de Córdoba* 8, 3–207.
- AMEGHINO, F., 1888. Rápidas diagnosis de mamíferos fósiles nuevos de la República Argentina. *Obras Completas* 5, 471–480. Buenos Aires.
- AMEGHINO, F., 1891. Mamíferos y aves fósiles argentinas. Especies nuevas, adiciones y correcciones. *Revista Argentina de Historia Natural* 1, 240–259.
- AMEGHINO, F., 1902. Notas sobre algunos mamíferos fósiles nuevos o poco conocidos del valle de Tarija. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 3, 225–261.
- AMEGHINO, F., 1908. Notas preliminares sobre el *Tetraprothomo argentinus* un precursor del hombre del Mioceno Superior de Monte Hermoso. *Anales del Museo Nacional de Buenos Aires* 9, 1–82.
- AMEGHINO, C. & KRAGLIEVICH, L., 1921. Descripción del *Megatherium gallardoi* C. Ameg. descubierto en el Pampeano Inferior de la Ciudad de Buenos Aires. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 31, 135–156.
- BOWDICH, T.E., 1821. *An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travellers*. J. Smith, Paris, 115 pp.
- BURMEISTER, H., 1879. *Description physique de la République Argentine d'après des observations personnelles et étrangères. Tome troisième: Animaux vertébrés. Première partie: Mammifères vivants et éteints*, Paul-Emile Coni, Buenos Aires, 1–556 and Atlas.
- CARTELLE, C., 1998. Um pequeno urso do Pleistoceno final da Bahia. *Acta Geologica Leopoldensia* 46/47, 171–189.
- CIONE, A.L. & TONNI, E.P., 1999. Biostratigraphy and chronological scale of uppermost Cenozoic in the Pampean area, Argentina. In *Quaternary vertebrate paleontology in South America*, J. RABASSA & M. SALEMME, eds, *Quaternary of South America and Antarctic Peninsula Special Volume 12*, Balkema Press, Rotterdam, 23–51.
- COPE, E.D., 1879. The cave bear of California. *American Naturalist* 13, 791.
- DONDAS, A., ISLA, F.I. & CARBALLIDO, J.L., 2006. Megaestructuras orgánicas en sedimentos miramarenses del Partido de General Pueyrredón, Argentina. *Proceedings of III Congreso Argentino de Cuaternario y Geomorfología, Córdoba, Argentina, 11 to 13th October 2006*, 14 (abstract).
- FRENGUELLI, J., 1928. Observaciones geológicas en la región costanera sur de la Provincia de Buenos Aires. *Anales de la Universidad Nacional del Litoral* 2, 28–135.
- FRENGUELLI, J., 1955. Loess y limos pampeanos. La Plata, Argentina: *Universidad Nacional de La Plata. Serie técnica y didáctica* 7, 88.
- GERVAIS, P., 1848–1852. *Zoologie et Paléontologie françaises (animaux vertébrés) ou nouvelles recherches sur les animaux vivantes et fossiles de la France*, A. Bertrand, Paris, viii + 1–271.
- GERVAIS, P., 1867. Sur une nouvelle collection d'ossements fossiles de Mammifères recueillé par M. Fr. Seguín dans la Confédération Argentine. *Comptes rendus des séances de l'Académie des Sciences* 65, 279–282.
- GERVAIS, H. & AMEGHINO, F., 1880. *Les Mammifères fossiles de l'Amérique du Sur*, Igon Hnos, Buenos Aires & F. Salvy, Paris, xi + 225 pp.
- GOBETZ, K.G. & MARTIN, L.D., 2001. An exceptionally large Short-faced bear (*Arctodus simus*) from the Late Pleistocene (?)/Early Holocene of Kansas. *Current Research in the Pleistocene* 18, 97–99.
- GRAY, J.E., 1825. Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of genera apparently appertaining to each tribe. *Annals of Philosophy* 10, 337–344.
- HILL, A., 1979. Disarticulation and scattering of mammal skeletons. *Paleobiology* 5, 261–274.
- HILL, A. & BEHRENSMEYER, A.K., 1984. Disarticulation patterns of some modern East African mammals. *Paleobiology* 10, 366–376.

- IMBELLONE, P. & TERUGGI, M., 1988. Sedimentación crotovinica en secuencias cuaternarias bonaerenses. *Proceedings of II Reunión Argentina de Sedimentología, Buenos Aires, 1–5th August 1988*, 125–129.
- IMBELLONE, P., TERUGGI, M. & MORMENEO, L., 1990. Crotovinas en sedimentos cuaternarios del partido de La Plata. *Proceedings of Simposio Internacional sobre Loess. Características, cronología y significado paleoclimático del loess, Mar del Plata 1990*, 166–172.
- JARDINE, W., 1834. *The Naturalist's Library, Mammalia, Vol. II, the Felinae*. W.H. Lizars, Edinburgh, 266 pp.
- KRAGLIEVICH, J.L., 1928. Contribución al conocimiento de los grandes cánidos extinguidos de Sud América. *Anales de la Sociedad Científica Argentina* 106, 25–66.
- KRAGLIEVICH, J.L., 1952. Un cánido del Eocuaternario de Mar del Plata y sus relaciones con otras formas brasileras y norteamericanas. *Revista del Museo de Ciencias Naturales y Tradicional de Mar del Plata* 1, 53–70.
- KRAUSE, J., UNGER, T., NOÇON, A., MALASPINAS, A., STILLER, M., KOLOKOTRONIS, S., SOIBELZON, L.H., SPRIGGS, H., DEAR, P.H., BRIGGS, A.W., BRAY, S.C.E., O'BRIEN, S., RABEDER, G., MATHEUS, P., COOPER, A., SLATKIN, M., PÄÄBO, P. & HOFREITER, M., 2008. Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene–Pliocene boundary. *BMC Evolutionary Biology* 8(220). doi:10.1186/1471-2148-8-220.
- KURTÉN, B., 1967. Pleistocene bears of North America: 2. Genus *Arctodus*, short faced bears. *Acta Zoologica Fennica* 117, 1–60.
- LEIDY, J., 1854. Remarks on *Sus americanus*, or *Harlanus americanus* and on other extinct mammals. *Proceedings of the Academy of Natural Sciences of Philadelphia* 7, 89–90.
- LIMA, S.L. & DILL, L.M., 1990. Behavioral decisions made under the risk of predation—a review and prospectus. *Canadian Journal of Zoology* 68, 619–640.
- LINNAEUS, C., 1758. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*, Tomus I. Laurentii Salvii, Holmiae, Stockholm, 823 pp.
- LUND, P.W., 1838. Blik paa Brasiliens Dyreverden för Sidste Jordomvaeltning. Förste Afhandling: Indledning. Det kongelige Danske Vindenskabernes Selskabs naturvidenskabelige og mathematiskse, Afhandlinger 8, 27–60.
- LUND, P.W., 1842. Blik paa Brasiliens Dyreverden för sidste jordomvaeltning. Fjerde Afhandling: Forsaettelse af Pattedyrene. Lagoa Santa d. 30 Januar 1841. Copenhagen. K. *Danske videnskabernes Selskabs naturvidenskabelige og mathematiskse Afhandlinger* 9, 137–208.
- LYDEKKER, R., 1894. Contribution to a knowledge of the fossil vertebrates of Argentina. *Anales del Museo de La Plata (Paleontología)* 3, 1–118.
- MARSHALL, L.G., WEBB, S.D., SEPKOSKI, J.J. & RAUP, D.M., 1982. Mammalian evolution and the Great American Interchange. *Science* 215, 1351–1357.
- MARTIN, F.M., PRIETO, A., ROMÁN, M.S., MORELLO, F., PREVOSTI, F., CÁRDENAS, P. & BORRERO L., 2004. Late Pleistocene megafauna at Cueva del Puma, Pali-Aike lava field, Chile. *Current Research in the Pleistocene* 21, 101–103.
- McNAB, B.K., 1985. Energetics, population biology, and distribution of xenarthrans living and extinct. In *Evolution and Ecology of Armadillos, Sloths and Vermilinguas*, G.G. MONTGOMERY, ed., Smithsonian Institution Press, Washington, DC, 219–232.
- MERCERAT, A., 1891. Caracteres diagnósticos de algunas especies de Creodonta conservadas en el Museo de La Plata. *Revista del Museo de La Plata* 2, 51–52.
- MERRIAM, J.C. & STOCK, C., 1925. Relationships and structure of the short-faced bear, *Arctotherium*, from the Pleistocene of California. *Contributions to palaeontology from the Carnegie Institution of Washington. Papers concerning the palaeontology of the Pleistocene of California and the Tertiary of Oregon, Part 1*, 1–35.
- NELSON, R.A., FOLK, G.E., PFEIFFER, E.W., CRAIGHEAD, J.J., JONKEL, C.J. & WELLIK, D.L., 1980. Behaviour, biochemistry, and hibernation in black, grizzly, and polar bears. *International Conference on Bear Research and Management* 4, 284–290.
- NOWAK, R.M., 1999. *Walker's Mammals of the World*, 5th ed, Vol. II. John Hopkins University Press, Baltimore, MD, 1936 pp.
- OWEN, R., 1838. Note on the *Glyptodon*. In *Buenos Aires and the Provinces of the Rio de La Plata*, W. PARISH, ed., John Murray, London, 1–178.
- OWEN, R., 1840. Fossil Mammalia (4). In *Zoology of the Voyage of H.M.S. Beagle*, C. DARWIN, ed., Smith, Elther & Co. London, 81–111.
- PREVOSTI, F., 2006. Grandes cánidos (Carnivora, Canidae) del Cuaternario de la República Argentina. Sistemática, filogenia, bioestratigrafía y paleoecología. PhD Thesis, Universidad Nacional de La Plata, 501 pp. (unpublished).
- PREVOSTI, F.J., SOIBELZON, L.H., PRIETO, A., SAN ROMAN, M. & MORELLO, F., 2003. The Southernmost Bear: *Pararctotherium* (Carnivora, Ursidae, Tremarctinae) in the latest Pleistocene of Southern Patagonia, Chile. *Journal of Vertebrate Paleontology* 23, 709–712.
- QUINTANA, C., 1992. Estructura interna de una paleocueva, posiblemente de un Dasypodidae (Mammalia, Edentata) del Pleistoceno de Mar del Plata (Provincia de Buenos Aires, Argentina). *Ameghiniana* 29, 87–91.
- RABASSA, J., CORONATO, A.M. & SALEMME, M., 2005. Chronology of the Late Cenozoic Patagonian glaciations and their correlation with biostratigraphic units of Pampean Region (Argentina). *Journal of South American Earth Sciences* 20, 81–103.

- RIGGS, E.S., 1933. Preliminary description of a new marsupial saber-tooth from the Pliocene of Argentina. *Field Museum of Natural History Geological series* 6, 61–66.
- SCHUBERT, B.W. & KAUFMANN, J.E., 2003. A partial short-faced bear skeleton from an Ozark cave with comments on the paleobiology of the species. *Journal of Cave and Karst Studies* 65, 101–110.
- SOIBELZON, E., 2008. Los Mamíferos del Ensenadense (Pleistoceno Inferior-Medio) del Este de la Región Pampeana, con énfasis en los Xenarthra. Bioestratigrafía, Diversidad y Correlaciones Biogeográficas. PhD thesis, Universidad Nacional de La Plata, 304 pp. (unpublished).
- SOIBELZON, E., ZURITA, A. & CARLINI, A., 2006. *Glyptodon munizi* Ameghino (Mammalia, Cingulata, Glyptodontidae): redescipción y anatomía. *Ameghiniana* 43, 377–386.
- SOIBELZON, L.H., 2002. Los Ursidae (Carnivora, Fissipedia) fosiles de la Republica Argentina. Aspectos sistematicos y paleoecologicos. PhD thesis, Universidad Nacional de La Plata, 238 pp. (unpublished).
- SOIBELZON, L.H., 2004. Revisión sistemática de los Tremarctinae (Carnivora, Ursidae) fósiles de América del Sur. *Revista del Museo Argentino de Ciencias Naturales* 6, 107–133.
- SOIBELZON, L.H. & PREVOSTI, F., 2007. Los carnívoros (Carnivora, mammalia) terrestres del Cuaternario de América del Sur. In *Geomorfología Litoral i Quaternari. Homenatge a D. Joan Cuerda Barceló*, G.X. PONS & D. VICENS, eds, Monografies de la Societat d'Història Natural de les Balears Special Volume 14, Palma de Mallorca, 49–68.
- SOIBELZON, L.H. & RINCÓN, A., 2007. The fossil record of the short-faced bears (Ursidae, Tremarctinae) from Venezuela. Systematic, biogeographic, and paleoecological implications. *Neues Jahrbuch für Geologie und Paläontologie* 245, 287–298.
- SOIBELZON, L., ISLA, F.I. & DONDAS, A., 2001. Primer registro de tres individuos asociados de *Arctotherium latidens* (Ursidae: Tremarctinae). Presentado en la Reunión Anual de Comunicaciones de la Asociación Paleontológica Argentina, Diamante. *Ameghiniana* 38, 40R.
- SOIBELZON, L.H., TONNI, E.P. & BOND, M., 2005. The fossil record of South American short-faced bears (Ursidae, Tremarctinae). *Journal of South American Earth Sciences* 20, 105–113.
- SOIBELZON, L.H., ROMERO, M.R., HUZIEL AGUILAR, D. & TARTARINI, V.B., 2008. A new finding in the Blanco of the El Salvador indicates the probable dating of the Tremarctinae's (Ursidae, Carnivora) entrance to South America. *Neues Jahrbuch für Geologie und Paläontologie* 250, 1–8.
- STINER, M.C., 1998. Cave bear ecology and interactions with Pleistocene humans. *Ursus* 11, 41–58.
- TORRES, T., 1988. Osos (Mammalia, Carnivora, Ursidae) del Pleistoceno de la Península Ibérica (*U. deningeri* von Reichenau, *U. spelaeus* Rösenmüller Heinroth y *U. arctos* Linneo). *Boletín Geológico y Minero, Instituto Geológico y Minero de España* 49, 1–316.
- TRAJANO, E. & FERRAREZZI, H., 1994. A fossil bear from northeastern Brazil, with a phylogenetic analysis of the South American extinct Tremarctinae (Ursidae). *Journal of Vertebrate Paleontology* 14, 552–561.
- VIZCAÍNO S.F. & LOUGHRY, W.J., 2008. Xenarthran biology: Past, present, and future. In *The Biology of the Xenarthra*, S.F. VIZCAÍNO & W.J. LOUGHRY, eds, University Press of Florida, Florida, 1–10.
- VIZCAÍNO, S., ZÁRATE, M., BARGO, S. & DONDAS, A., 2001. Pleistocene burrows in the Mar del Plata area (Argentina) and their probable builders. *Acta Paleontologica Polonica* 46, 289–301.
- WOODBOURNE, M.O., CIONE, A.L. & TONNI, E.P., 2006. Central American provincialism and the Great American Biotic Interchange. In *Advances in Late Tertiary Vertebrate Paleontology in Mexico and the Great American Biotic Interchange*, O. CARRANZA-CASTAÑEDA & E.H. LINDSAY, eds, *Instituto de Geología y Centro de Geociencias Special Volume 4*, Universidad Nacional Autónoma de México Press, México, 73–101.
- ZÁRATE, M., BARGO, S., VIZCAÍNO, S., DONDAS, A. & SCAGLIA, O., 1998. Estructuras biogénicas en el Cenozoico tardío de Mar del Plata (Argentina) atribuibles a grandes mamíferos. *Revista Asociación Argentina de Sedimentología* 5, 95–103.