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New Late Pleistocene megafaunal assemblage with well-supported chronology from the Pampas of southern South America

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ABSTRACT

Late Pleistocene outcrops exposed in Buenos Aires province, Argentina, represent one of the most informative sources about the paleoecology of South American megafauna. However, there are no records of an accurately dated carnivore–herbivore taphocenosis. This paper presents preliminary results of a recent excavation at the margins of the Salado River, on sediments attributed to the Luján Formation (Late Pleistocene–Early Holocene). The fossiliferous strata consist of greenish brown sandy-clays deposited in a small paleopond environment that was filled by fluvial sediments, exhibiting abundant organic matter, gypsum and carbonate concretions. Fieldwork yielded an association of extinct large-sized mammals that include the horse *Hippidion principale*, the saber-tooth cat *Smilodon populator* (at least one adult and one juvenile associated specimen), a giant ground sloth *Megatherium americanum*, and the glyptodont *Doedicurus clavicaudatus*. Four ^{14}C dates were performed on organic matter (12,100 ± 100 ^{14}C BP), a femur of *S. populator* (13,400 ± 200 ^{14}C BP), and a cervical vertebra of *Hippidion principale* (12,860 ± 120 ^{14}C BP), and a pelvis of *D. clavicaudatus* (12,380 ± 190 ^{14}C BP) situating the site within 12,500 and 13,500 years, approximately. Remarkably, some of the recovered specimens exhibit conspicuous bone modifications (furrows, pits, punctures, striations and crenulated margins) attributed to the activity of a medium-large carnivore. The association between bones of herbivore mammals with conspicuous modifications produced by a large carnivore, and the presence of cub and adult remains of *Smilodon*, link this felid with at least part of the excavated association.

1. Introduction

The Pampean region of Buenos Aires province (Argentina) contains one of the best records of climatic fluctuations and biological events in South America at the end of the Pleistocene, triggering a large amount of multidisciplinary analyses (e.g. Politis et al., 1995; Tonni et al., 1999, 2003; Cione et al., 2003; Prieto et al., 2004; Prevosti and Vizcaíno, 2006; Quattrocchio et al., 2008). Extinct large-sized mammals (megafauna) have been recovered in the numerous outcrops exposed along many rivers of this region, showing that an impressive mammal community inhabited in this region during the late Pleistocene, not comparable with any modern or extinct mammalian fauna (Patterson and Pascual, 1972; Simpson, 1980). Some mammal species recovered have been useful as climatic proxies (Tonni and Fidalgo, 1978; Tonni, 1992; Tonni and Cione, 1994, 1995; Tonni et al., 1999; Vizcaíno, 2000; Vucetich and Verzi, 2002; Voglino and Pardiñas, 2005), and recent discoveries indicate the potential of other unexpected tetrapod records as possible environmental indicators (Tambussi and Acosta Hospitaleche, 2003; Báez et al., 2008).

Despite the relevance of this fauna, the chronology of Pleistocene paleontological sites in the Pampean region was historically delineated through biostratigraphic studies without numerical ages. However, recent efforts to acquire more accurate chronological dates have been successful, obtaining chronological data (Bonadonna et al., 1999; Tonni et al., 1999; Gentile and Ribot, 2000; Tonni et al., 2003). Nearly all of the radiocarbon dates were obtained from organic matter and molluscan shells, but there are a few ^{14}C taxon dates based on megafauna taxa from the Pampean region (see Table 1). Due to the scarcity of taxon dates and lack of taphonomic-controlled excavations in the paleontological sites in this region, these vital tools needed to test previously proposed

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Table 1
^{14}C taxon dates from the Pampean region of Buenos Aires province.

	Taxon	Age ^{14}C BP	Locality	Reference
1	*Pseudolestodon* sp. (LP-152)	10,710 ± 90(standard)	Arroyo Tapalqué	Figini et al., 1998
2	*Glossotherium robustum* (CI OXA-4591)	12,240 ± 110 (AMS)	Arroyo Seco II	Politis and Beukens, 1990; Politis et al., 1995*
3	*Glossotherium robustum* (AA-9049)	10,500 ± 90 (AMS)	Arroyo Seco II	Politis and Beukens, 1990; Politis et al., 1995*
4	*Megatherium americanum* (AA-55117)	7750 ± 250 (AMS)	Campo Laborde	Politis and Messineo, 2008
5	*Megatherium americanum* (AA-55118)	8080 ± 200 (AMS)	Campo Laborde	Politis and Messineo, 2008
6	*Megatherium americanum* (AA-39363)	10,440 ± 100 (AMS)	Paso Otero 5, Río Quequén Grande	Martínez, 2000, 2001
7	*Megatherium americanum* (LP-174b)	13,070 ± 120 (standard)	Campo de Arce, Río Quequén Chico	Tonni et al., 2003
8	*Megatherium americanum* (LP-53)	8390 ± 140 (standard)	Arroyo Seco II	Fidalgo et al., 1986
9	*Megatherium americanum* (CAMS-58182)	12,200 ± 170 (AMS)	Arroyo Seco II	Politis and Beukens, 1990; Politis et al., 1995
10	*Megatherium americanum* (TO-1506)	7320 ± 50 (AMS)	Arroyo Seco II	Politis and Beukens, 1990; Politis et al., 1995*
11	*Equus* (*Amerhippus*) *neogeus* (AA-7965)	11,250 ± 105 (AMS)	Arroyo Seco II	Politis and Beukens, 1990; Politis et al., 1995
12	*Equus* (*Amerhippus*) *neogeus* (TO-1504)	8890 ± 90 (AMS)	Arroyo Seco II	Politis and Beukens, 1990; Politis et al., 1995
13	*Equus* (*Amerhippus*) *neogeus* (OXA-4590)	11,000 ± 100 (AMS)	Arroyo Seco II	Politis and Beukens, 1990; Politis et al., 1995
14	*Equus* (*Amerhippus*) *neogeus* (LP-1235)	10,290 ± 130 (standard)	Zanjón Seco, Río Quequén Grande	Tonni et al., 2003
15	*Toxodon platensis* (CAMS-16389)	11,750 ± 70 (AMS)	Arroyo Seco II	Politis and Beukens, 1990; Politis et al., 1995*
16	*Toxodon platensis* (AA-7964)	11,590 ± 90 (AMS)	Arroyo Seco II	Politis and Beukens, 1990; Politis et al., 1995*
17	*Doedicurus clavicaudatus* (TO-1507-1)	7010 ± 100 (AMS)	La Moderna	Politis and Beukens, 1990; Politis and Gutiérrez 1998; Politis et al. 2003
18	*Doedicurus clavicaudatus* (TO-2610)	7460 ± 80 (AMS)	La Moderna	Politis and Beukens, 1990; Politis and Gutiérrez 1998; Politis et al., 2003
19	*Doedicurus clavicaudatus* (TO-1507-2)	7510 ± 370 (AMS)	La Moderna	Politis and Beukens, 1990; Politis and Gutiérrez 1998; Politis et al., 2003
20	*Doedicurus clavicaudatus* (TO-1507)	12,330 ± 370 (AMS)	La Moderna	Politis and Beukens, 1990; Politis and Gutiérrez 1998; Politis et al., 2003
21	*Glyptodon clavipes*	4300 ± 90	Río Luján, Mercedes	Rossello et al., 1999; Discussed by Cione et al., 2001
22	*Doedicurus clavicaudatus* (LP-2568)	12,380 ± 190 (standard)	La Chumbiada, Rio Salado	This paper
23	*Smilodon populator* (LP-2140)	13,400 ± 200 (standard)	La Chumbiada, Rio Salado	This paper
24	*Hippidion principale* (LP-2259)	12,860 ± 120 (standard)	La Chumbiada, Rio Salado	This paper

hypotheses about paleoecological issues as well as macroevolutive events (e.g. extinctions) are lacking. Moreover, the few available numerical ages preclude the correlation of lithostratigraphic units distributed in several localities of the Pampean region.

Late Pleistocene deposits exposed along the cutbanks of the Salado River are one of the most important sources for megafaunal remains, exploited since the XIXth Century. Nevertheless, numerical chronologies of the different deposits of the río Salado basin have been scanty. Recent field trips carried out in several localities along the Salado resulted in the discovery of a small paleopond that yielded well-preserved remains of both herbivore and carnivore components of the megafauna. This paper reports the geological features of the new locality, as well as chronological and taphonomical analyses of the recovered specimens, representing the first megafauna assemblage with taxon dated chronological information discovered in this relevant region of South America.

2. Results

2.1. Geological setting and landscape

Pleistocene deposits that characterize the Pampean region are in general brownish silts associated with loess and reworked loess with concretions of calcium carbonate. These deposits bear most of the megafauna remains, and are distributed through the Chaco-Pampean Plain and part of the neighboring countries (Teruggi, 1957; Sayago, 1995; Iriondo, 1990, 1999; Zárate, 2003; Fucks and Deschamps, 2008, among others). The thickness of these sediments and the plain morphology of the landscape suggest an environment subject mostly to semiarid to arid conditions. Paleosols, fluvial sequences and faunal changes have been identified within these deposits as a response to more humid climatic conditions (González Bonorino, 1965; Tonni and Fidalgo, 1978; Teruggi and Imbellone, 1987; Kemp et al., 2006; Fucks et al., 2007).

The studied outcrops are located along the Salado River, in the vicinity of La Chumbiada, General Belgrano town, and flanked to SE by broad depressions representing either temporary ponds or scattered areas with small depressions (Fig. 1). All these geomorphological traits are generated by deflation processes, and are today occupied temporarily by water, suggesting dominant deflation processes with scarce sedimentation that models a plane landscape with both positive and negative irregularities.

Fossil specimens were found in cutbanks of the Salado River, in levels attributable to the Luján Formation (Fidalgo et al., 1973). From a sedimentological point of view, the sequences (Fig. 2) are fluvial and fluvio-lacustrine in origin. From the bottom of the channel and up to 2 m height on the left cutbank, the sediment is a brown diamicton, tough but friable, with smooth stratification. Clasts are irregular and composed of sediments from the underlying Pampeano Formation, with scarce $CaCO_3$. The incipient rounding and resistance, and the similarity with the sediments of the Pampeano Formation suggest little transport. Overlying these levels, a clayey sand facies can be observed, dark grey to black, 0.5 m thick, and continues downward at least 0.50 m, loose and homogeneous. Over this level, 0.40 m of brownish-green sand with lenses of the underlying facies is present, with the upper part mixed. Above, approximately 4 m of sediments are divided into three sections. The lower section is sandy silt, brown to yellowish red, with concentrations of carbonate concretions, equidimensional in shape, 3–5 cm in diameter, and situated in different levels. Sediments of the intermediate section (0.50 m thick), are silty, gray and very friable. The highest concentration of carbonates is in the upper part. Overlying a discontinuity, there are 0.50 m of dark gray silts, friable and structureless, with the lowest 0.10 m semicircular in section. The modern soil is formed on these deposits. Five hundred meters upstream, over the aeolian deposits there is 1.5 m of clayey silty sediments, yellowish grey, with a large amount of the freshwater gastropod *Heleobia*.

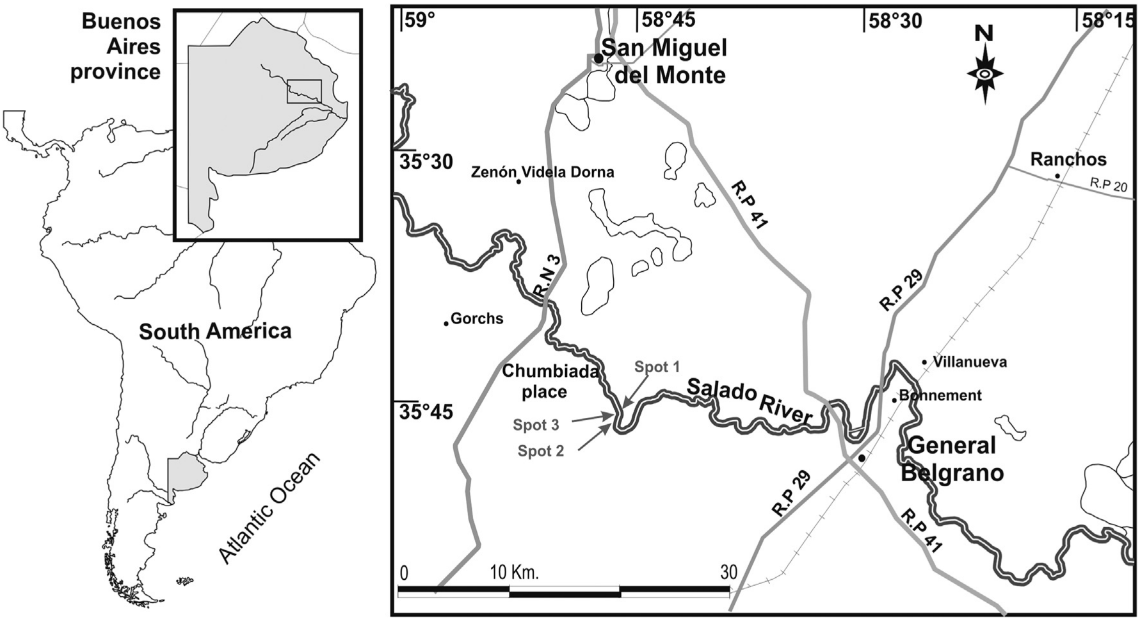

Fig. 1. Geographic location of the studied locality, Salado River, Buenos Aires province, Argentina.

Sedimentary exposures of the studied area suggest that channel deposits settled over the Pampean loess in the fluvio-lacustrine sedimentation. Over these deposits, a small pond was developed, represented by black to green muddy textures in which megafaunal remains were found, as well as a large amount of rhizoconcretions that suggest favorable environmental conditions. Afterwards, this environment became altered, and between 12 and 9.5 ka fluvial accumulation occurred, documented by horizontally and trough stratified. This process produced the filling of the paleopond.

2.2. Dating

The dates were obtained by radiocarbon analysis of bone collagen, molluscan shells and organic matter (Fig. 2). One sample obtained from the *Hippidion* skull is currently being processed by AMS. Bone material was pretreated using the collagen extraction method of Longin (1971), with slight modifications. The dating of ^{14}C was done at the Laboratorio de Tritio y Radiocarbono (LATyR, La Plata), by synthesis of samples to benzene. The ^{14}C activity of

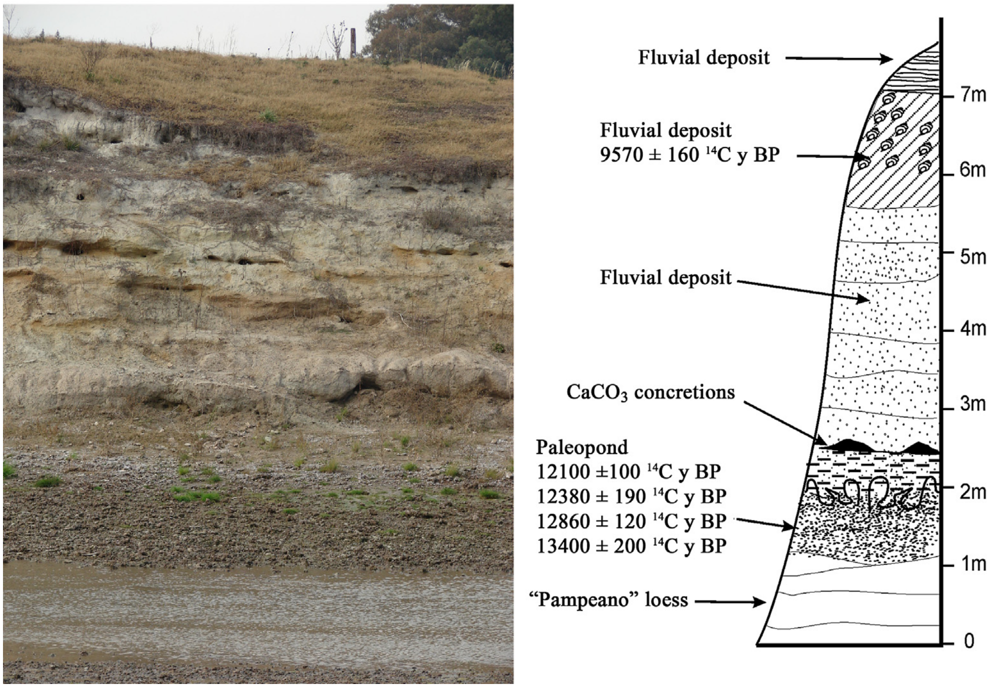

Fig. 2. Stratigraphic section at the studied locality, near to the "La Chumbiada" location, Salado River, Buenos Aires.

synthesized benzene was measured using liquid scintillation counting (LSC) on a Packard Tri-Carb in low 40K, borosilicate glass vials. Age calculations are based on the Libby half-life of 5568 y and reported in ^{14}C years before 1950. Errors quoted refer only to the standard deviation (7 1s) calculated from a statistical analysis of sample, background, and standard count rates. None of the ^{14}C ages were corrected by ^{13}C or for any “reservoir effect”.

The following ^{14}C ages were obtained from the site (see Fig. 2): 12,100 ± 100 ^{14}C BP (LP-2184; organic matter), 12,860 ± 120 ^{14}C BP (LP-2259; cervical vertebra of *Hippidion principale*), 12,380 ± 190 ^{14}C BP (LP-2568; pelvis of *Doedicurus clavicaudatus*), and 13,400 ± 200 ^{14}C BP (femur of *Smilodon populator*). Additionally, 500 m upstream of the locality, samples of the gastropod *Heleobia parchappei* were extracted, which yielded an age of 9570 ± 160 ^{14}C BP (LP-2299). The studied samples yielded ^{14}C ages consistent with its stratigraphic position.

2.3. Fossil sample

Up to now, 29 bone specimens were collected in three distinct fossiliferous spots separated by 50 m (Fig. 1), within the boundaries of the small paleopond (see geological setting). Four extinct large mammal species are among this bone assemblage (Fig. 3), the saber-toothed cat *S. populator* (left radius and scapula in Location 1; left maxilla of a juvenile, and right femur, calcaneus and astragalus of an adult in Location 2), the giant ground sloth *Megatherium americanum* (right mandible in Location 1), a large glyptodont *D. clavicaudatus* (incomplete carapace and pelvis in Location 2), and the extinct horse *H. principale* (nearly complete skull, four cervical vertebrae and left ulna in Location 3). Several undetermined bones were found in close association with specimens in Location 1 and 2, as well as coleopteran elytra and plant debris associated with the *Hippidion* specimen in Location 3.

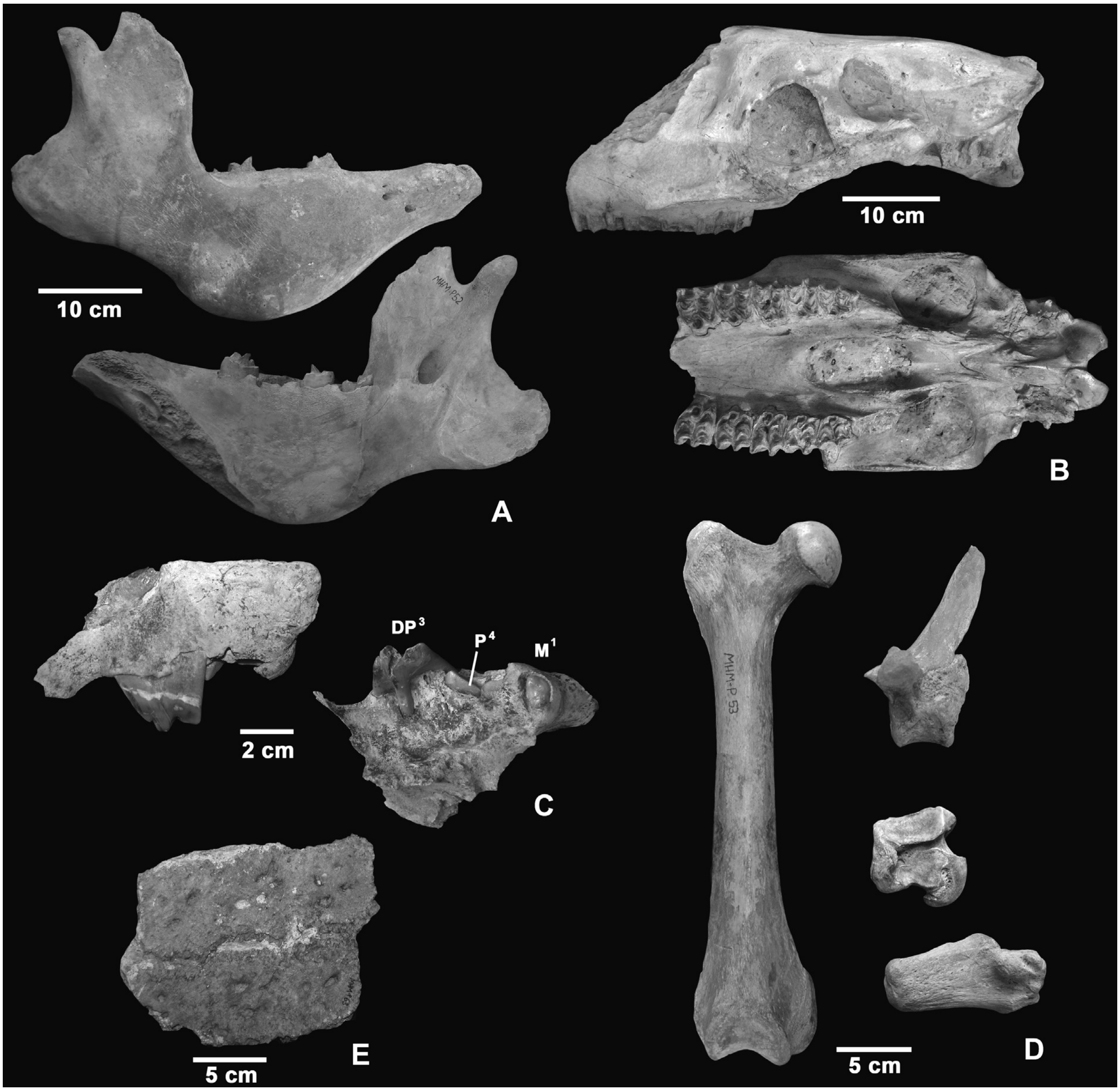

Fig. 3. Recovered specimens from the Salado River locality. A, Right hemimandible of the ground sloth *Megatherium americanum* in lateral and medial view; B, incomplete skull of extinct horse *Hippidion principale* in lateral and ventral (palatal) view; C, left maxilla corresponding to a juvenile saber-toothed cat *Smilodon populator* in lateral and ventral (palatal) view; D, bones of an adult individual of *Smilodon populator* (dorsal vertebra, left Femur, left astragalus and left calacaneum); E, fragment of carapace of the large-sized glyptodont *Doedicurus clavicaudatus*.

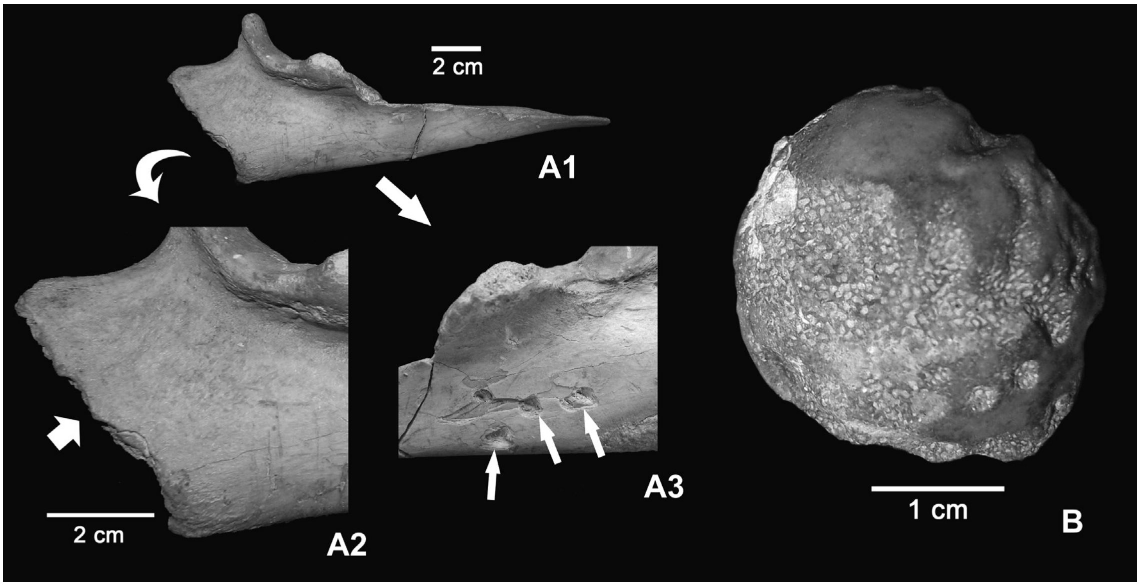

Fig. 4. Bone modifications exhibited by specimens collected in the studied locality. A, Right ulna in lateral view (A1), with details of the crenulated rim presents in the olecraneal region (A2) and pits and scores located above the articular region in medial view (A3); B, long bone epiphysis strongly damaged, with scooping out and several punctures.

2.4. Taphonomy

All the recovered bones were found disarticulated but closely associated. Bones corresponding to both juvenile and adult specimens of *Smilodon* were found in close association in Location 2, together with remains of the glyptodont *Doedicurus* and some indeterminate bone specimens that show conspicuous surface modifications (e.g. Fig. 4B). Also, elements recovered of the *Hippidion* individual (skull, cervical vertebrae and ulna) were found together in an area no larger than 1 m^2.

In general, the preservation of the recovered bones is excellent, with low weathering ($\leq$1 sensu Behrensmeyer, 1978), and containing high amounts of preserved collagen (Huarte and Carbonari, pers. comm.). In terms of their organic content, this condition is rare in Pleistocene remains of the Pampean region, allowing for optimism for the recovery of ancient molecules.

The site assemblage exhibits a high frequency of bone modifications as fractures, punctures, furrows and pits. Strikingly, the great number and types of modifications are rare in relation to the sparse number of collected bone specimens. *Smilodon* bone specimens do not show any kind of mark or modification.

Two of these recovered specimens exhibit conspicuous marks, compared with the bone modifications observed by Marean and Ehrhardt (1995), Pickering et al. (2004), and Martín (2008) produced by carnivore activity. A femoral head epiphysis of an indeterminate mammal (Fig. 4B) was found in close association with both juvenile and adult specimens of *Smilodon* and *Doedicurus* in Location 2. This bone specimen bears conspicuous pits and furrows, with deep impressions in cancelous bone that could be attributed to a medium-large carnivore. Also, there are numerous bone fragments on the border of the femur epiphysis, with polished and rounded edges. Another remarkable specimen consists of a right ulna (Fig. 4A1) of *H. principale* (recovered in spot 3), which also preserves marks of intense carnivore activity. This bone specimen shows profuse crenulated marks on the posterior edge of the preserved portion of the diaphysis (Fig. 4A2). As a result of the gnawing activity, the olecraneal epiphysis and part of the proximal end of the ulnar diaphysis are absent. Also, punctures, scores and drag marks can be observed in the medial surface of the ulna, close to the ventral edge and below the articular surface (Fig. 4A3).

3. Discussion

The Guerrero Member, named by various authors (e.g. Tonni et al., 1999) as “sector verde” for its greenish color, is one of the subunits of the Luján Formation, composed by fluvial deposits (Ameghino, 1880; Fidalgo et al., 1973; Dangavs and Blasi, 1995; Isla, 2002). The deposition of this subunit appears to have been started around the Last Glacial maximum (ca. 21 ka BP) and continued until at least ca. 10 ka BP (Tonni et al., 2003). According to previous chronological data of this subunit, new taxon dates obtained suggest that the paleopond deposits, that contain the recovered megafauna assemblage studied here, correspond to the Guerrero Member time span recognized for other Pampean localities (e.g. Tapalqué, Tonni et al., 2003). However, the sedimentological features observed in the locality contrast with the typical traits that exhibits the Guerrero Member deposits along the Salado River and other localities, calling into account of the variability or instability of the macroscopic characteristics of this subunit of the Lujan Formation, as was pointed out previously in another locality within the Pampean region (Fucks and Deschamps, 2008: 336).

Several ^{14}C dates have already served to fill the lack of numerical chronologies in the geological units present in the Pampean region (Politis and Beukens, 1990; Carbonari et al., 1992; Figini et al., 1995, 1998; Tonni et al., 2003; Fucks et al., 2007). These dates were performed mainly on charcoal, molluscan shells, $CaCO_3$ clasts, and organic matter, with very few radiocarbon analyses based on bone collagen, due mainly to the inadequate collagen fraction present in nearly all bones recovered from this region of Argentina. Also, nearly all of the taxon date analyses obtained in the Pampean region were made on specimens recovered from archaeological sites (see Table 1), with Tapalqué and Paso Otero the two most accurately dated paleontological localities of the Pampean region according to Cione et al. (2003). These localities are several kilometers from the Salado river basin, and their chronologies were obtained on samples extracted from isolated bones of three different sites (Tonni et al., 2003). Due to this scarcity, the new ^{14}C taxon dates presented in this study are relevant and, moreover, the recovered mammal association constitutes the first paleontological megafaunal assemblage with a well-supported numerical chronology for the rio Salado basin. Additionally, ^{14}C dates obtained from *H. principale* constitute the first chronological age for this extinct horse species, and the *S. populator* date represents the first numerical chronological information of this saber-toothed cat for Argentina.

Several proxies utilized for the study of Pleistocene paleoclimate indicated arid environmental conditions in the Pampean region during the deposition of the Guerrero Member of the Luján Formation (ca. 21,000–13,000 BP), associated with more continental conditions and environments related to a lower sea level (Clapperton, 1993a, 1993b; Prieto, 1996; Tonni et al., 1999; Quattrocchio et al., 2008; Tonello and Prieto, 2010). However, the fossil record and the assemblage here reported indicate that megafauna succeeded in this environment in the Pampean region, at least in the Salado river basin. How this arid environment may have supported this spectacular fauna of large mammals is still under intense debate (e.g. Tonni et al., 1999; Vizcaíno, 2000; Prevosti and Vizcaíno, 2006; Bargo and Vizcaíno, 2008). Nevertheless, it is important to note that the predominance of fluvial and fluvio-lacustrine deposits recognized in the new locality indicates that around 14 ka more humid conditions prevailed in the Salado river basin than previously suggested.

Although physical hydraulic processes cannot be ruled out, the presence of at least two *Smilodon* individuals in different ontogenetic stages in close association with marked bone specimens suggest that at least part of the bone assemblage could be controlled by this large carnivore. Interestingly, paleoecological studies propose bone consumption capabilities for other saber-toothed cats. Binder and Van Valkenburgh (2010), based in tooth wear and high breakage frequency, suggested that the late Pleistocene species *Smilodon fatalis* could have consumed bone at least under environmental stress, and Marean and Ehrhardt (1995) inferred that saber-toothed cat *Homotherium* had carcass consumption abilities. Moreover, a recent study about cranial morphology of sabertooth cats (Prevosti et al., 2010) indicates that derived forms of these large felids (including *Smilodon*) were capable of hunting and consuming large mammals. These observations can be used as arguments to indicate that the saber-toothed cat *S. populator* was involved in the formation of the studied taphocenosis. However, the significant differences between the obtained ages of *Smilodon* and the recovered herbivore mammals (see Table 1) indicate that this hypothesis should be applied with certainty only in Location 2, where the two *Smilodon* remains were found in close association with marked bones. Gnawing damage on the bones collected, remains of cubs, juvenile-adult associated specimens, and the proximity of a water body appears to be signatures of a den-like assemblage as was pointed out by some authors (e.g. Brain, 1981) for other carnivores. Relatively little is known about the paleoecology of this sabertooth cat in South America. Hopefully, future discoveries in the Pampean region will provide new information about this interesting subject.

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