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Chaetophractus vellerosus (Mammalia: Dasypodidae) in the Ensenadan (Early – Middle Pleistocene) of the southeastern Pampean region (Argentina). Paleozoogeographical and paleoclimatic aspects

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With 4 figures

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Abstract: The xenarthran fauna recognized for the Ensenadan age is particularly abundant; Dasypodidae comprise approximately 20 % of this fauna. *Chaetophractus vellerosus* is recorded in the Pampean region from the Bonaerian-Lujanian (Middle Pleistocene – Late Pleistocene/Early Holocene) to the present, with a current disjunct distribution (a continuous main area comprising the Gran Chaco and central Argentina, and a secondary area in the coastal region of Buenos Aires Province) attributed to a wider paleodistribution. The materials presented here are from Ensenadan sediments outcropping at Punta Hermengo (General Alvarado County, Buenos Aires Province), that would have been deposited under arid to semiarid climate conditions. These allow extension of the temporal distribution of the species to the Ensenadan in the Pampean region, as well as representing new evidence to test hypotheses of distributional changes related to global climatic variations recognized for the Quaternary. In this sense, the current disjunct distribution can be interpreted as the result of fundamentally humid recent conditions that resulted in a relict occurrence of the species in coastal areas.

Zusammenfassung: Die Xenarthriden-Fauna aus dem Ensenandense (Unter-Pleistozän) ist sehr divers, davon machen die Dasypodidae etwa 20 % der gesamten Artenzahl aus. *Chaetophractus vellerosus* kommt im Pampa-Gebiet vor, vom

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Bonaerense (Mittel-Pleistozän) bis rezent, mit einer heutzutage disjunkten geographischen Verbreitung und einer weiteren Verbreitung in der erdgeschichtlichen Vergangenheit. Die hier beschriebenen Funde stammen von Punta Hermengo (General Alvarado County, Bundesstaat Buenos Aires), aus Schichten des Ensenandense, die in einer trockenen Umwelt abgelagert wurden. Die Fossilien belegen eine größere zeitliche Verbreitung dieser Art im Pampa-Gebiet (Unter-Pleistozän). Die heutige disjunkte Verbreitung von *C. vellerosus* korreliert mit einer klimatischen Änderung (höhere Feuchtigkeit), wodurch die Verbreitung auf trockene Gebiete eingeschränkt wurde.

1. Introduction

Xenarthrans are particulary abundant among the middle- to large-sized mammals recorded in the Ensenadan (Early – Middle Pleistocene). Within this group, the family Dasypodidae, represented by 8 genera and 20 species or 21 in the living mammalian fauna (Wetzel 1982; Nowak 1999 and others), comprise 20 % of the total Ensenadan xenarthrans, with 5 genera and at least 7 recognized species (Carlini & Scillato-Yané 1999). Among the Euphractinae Euphractini, *Chaetophractus villosus* is recorded from the Chapadmalalan (Pliocene) and *C. vellerosus*, from the Bonaerian-Lujanian (Middle Pleistocene – Late Pleistocene-Early Holocene) to the present (Scillato-Yané 1982; Carlini & Vizcaíno 1987; Carlini & Scillato-Yané 1999).

The current distribution of *C. vellerosus* is disjunct, with a main continuous area extending over the Gran Chaco and central Argentina, and a secondary area in central latitudes of the coastal region in Buenos Aires Province (Carlini & Vizcaíno 1987) (Fig. 1). Carlini & Vizcaíno have explained this disjunct distribution as a relict of a more widespread distribution that comprised a larger part of the territory currently included in Buenos Aires province, during the Late Pleistocene and part of the Holocene.

The local edaphic characteristics in the coastal region of the Buenos Aires Province (Bahía Samborombón), determine more xeric conditions respect to the regional soils ones (Murriello et al. 1993). The local soils are covered by xerophytic trees known collectively as "Talares" (*Celtis tala* xeric forests). These "Talares" develop on elevated shell-beds ("albardones"), covered by markedly sandy soils; the ensemble forms a system that is extremely permeable to water. These deposits/beds originated during Holocene marine

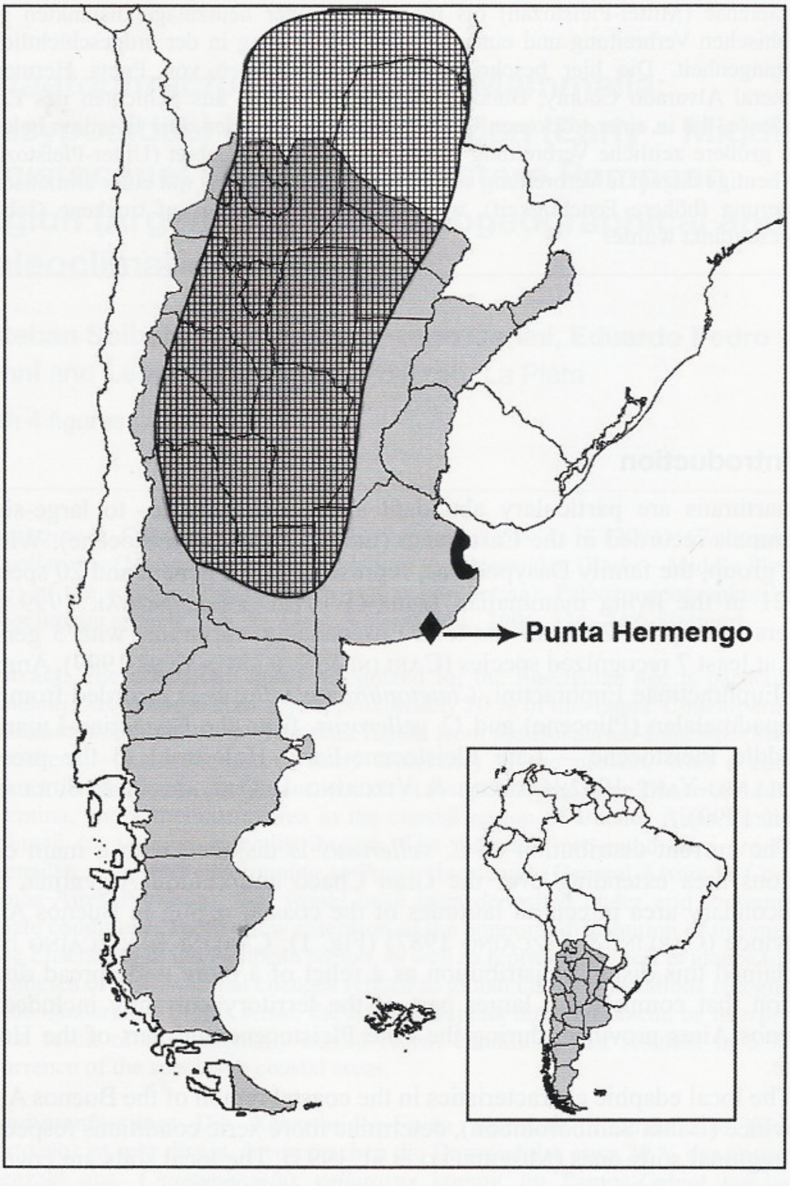

Fig. 1 (Legend see p. 737)

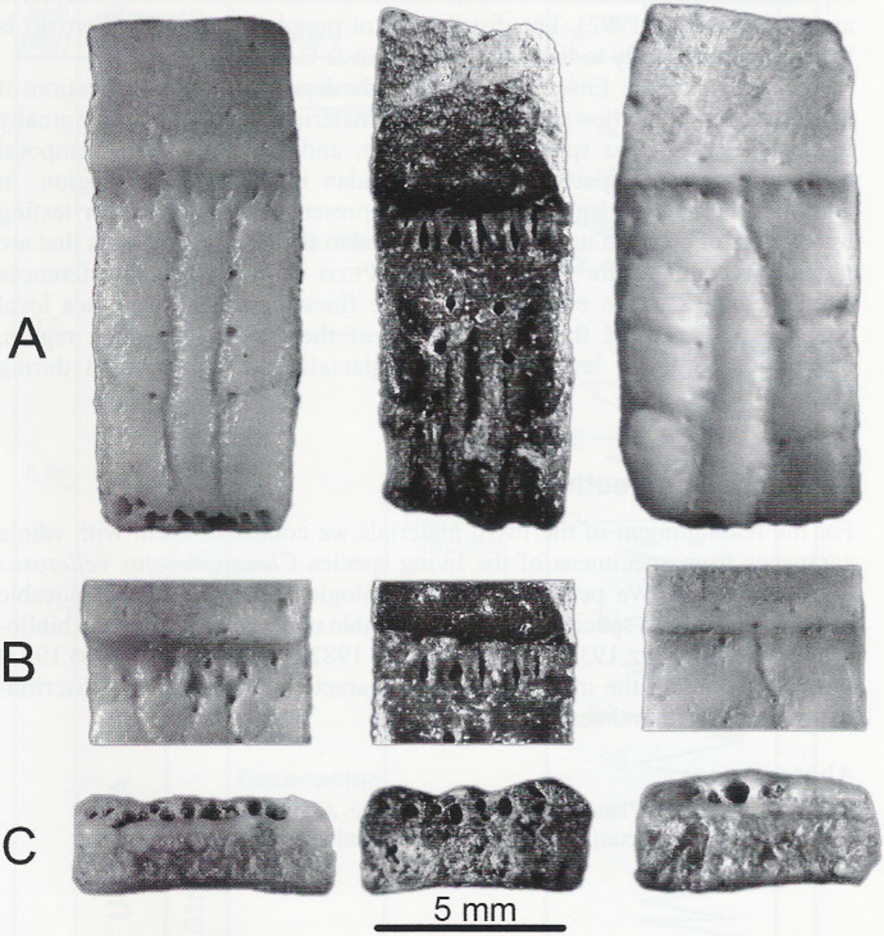

Fig. 2. A – Dorsal view of movable osteoderms of: *Chaetophractus vellerosus*; † *C. vellerosus* (MLP, 94-I-1-22) and *Zaedyus pichiy*; **B** – Detail of area between articulation zone and posterior zone of the osteoderm; **C** – Posterior view of the osteoderms and location of the piliferous foramina.

Fig. 1. Approximated current distribution of *C. vellerosus,* in squared the main area and in black the relictual area in Buenos Aires. Black diamond shows the provenance of fossil remains.

ingressions and represent elevations of 1 to 2 m above the level of adjacent areas (Goya et al. 1992). The distribution of populations of *C. vellerosus* is restricted specifically to these sectors (Glaz & Carlini 1999).

A revision of the Ensenadan dasypodids deposited in the collection of Museo de La Plata allowed us to reassign materials that had been originally identified as *Zaedyus* sp. to *C. vellerosus*, and thus extend the temporal distribution of this species to the Ensenadan in the Pampean region. In addition, the newly identified materials represent new evidence for testing hypotheses of changes in distribution related to the climatic changes that are globally recognized for the Quaternary (Petit et al. 1999 and references cited therein; Zachos et al. 2001). These fluctuations produced sea level changes that affected the continentality of the current Pampean region, bringing it to lower levels during interglacials and increasing it during glacials.

2. Material and methods

For the reassignment of the fossil materials we compared them with whole carapaces from specimens of the living species *Chaetophractus vellerosus* and *Zaedyus* sp. We performed a morphological analysis of the movable osteoderms of both species (using the available materials and specific bibliography [Fernández 1931; Scillato-Yané 1982; Vizcaíno & Bargo 1993] in order to obtain the more significant characters for taxonomic discrimination (see Fig. 2 and descriptions below).

Abbreviations:

MLP: Museo de La Plata, Buenos Aires province, Argentina.
BMNH: British Museum of Natural History, London.

Fig. 3. Chronostratigraphic time scale for the Quaternary of the Pampean region according to Cione & Tonni (1999), $\delta^{18}O$ curve for benthic forams, modified from Shackleton (1995), G: Patagonian glaciation, from Rabassa et al. (2005).

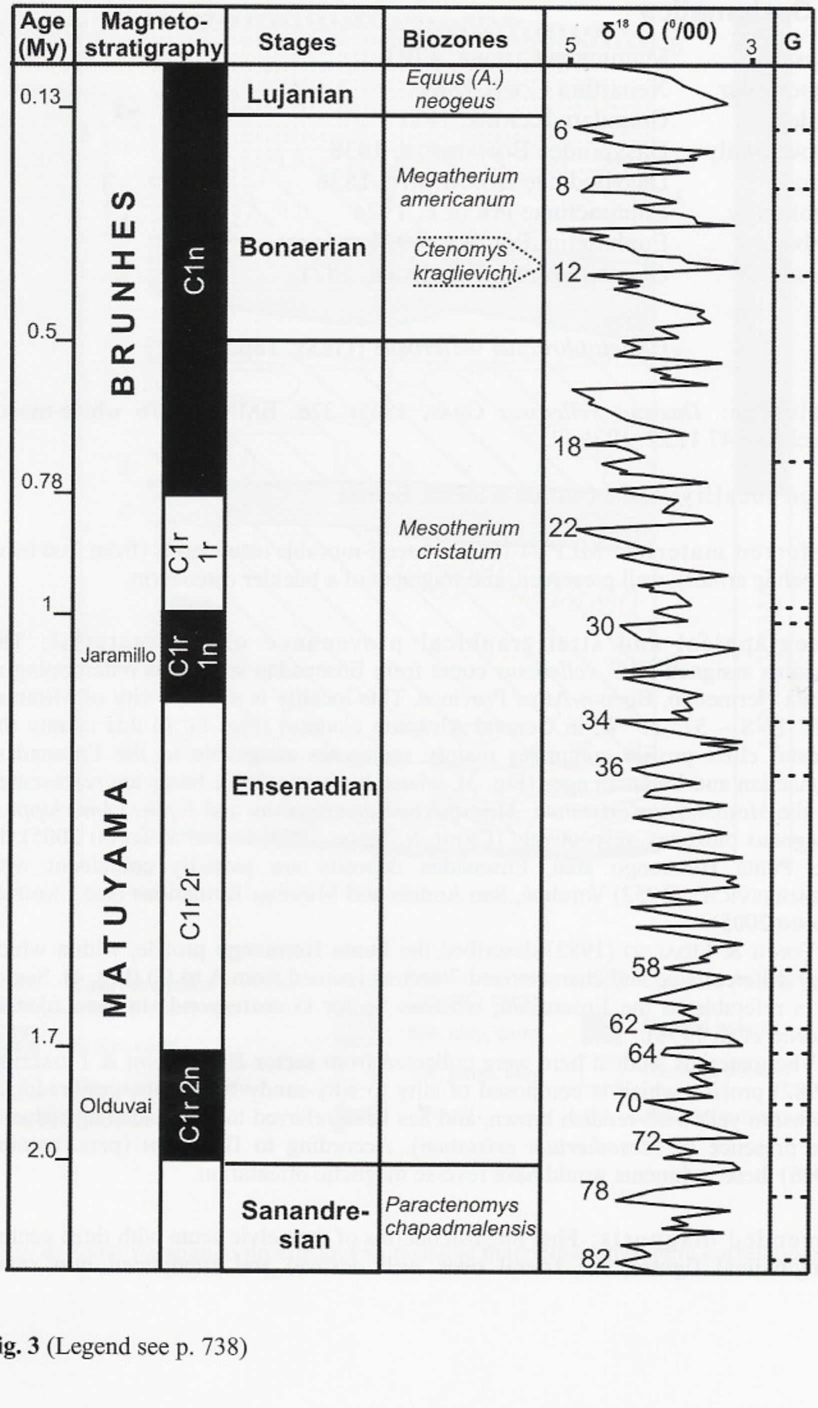

Fig. 3 (Legend see p. 738)

3. Systematics

Class	Mammalia Cuvier, 1793
Superorder	Xenarthra Cope, 1889
Order	Cingulata Illiger, 1811
Superfamily	Dasypoidea Bonaparte, 1838
Family	Dasypodidae Bonaparte, 1838
Subfamily	Euphractinae Pocock, 1924
Tribe	Euphractini Pocock, 1924
Genus	*Chaetophractus* Fitzinger, 1871

Chaetophractus vellerosus (Gray, 1865)

Holotype: *Dasypus vellerosus* Gray, 1865: 376. BMNH 1376 whole-mount specimen; 47.11.22. 10 skull.

Type locality: Santa Cruz de la Sierra, Bolivia.

Referred material: MLP 94-I-1-22: 4 semi-movable osteoderms (from first band of pelvic armor), well preserved, and fragment of a buckler osteoderm.

Geographical and stratigraphical provenance of the material: The remains assigned to *C. vellerosus* come from Ensenadan sediments outcropping at Punta Hermengo, Buenos Aires Province. This locality is near the city of Miramar (38° 17'S – 57° 50' W, in General Alvarado County) (Fig. 1). In this county the coastal cliffs profile comprises mainly sediments assignable to the Ensenadan, Bonaerian and Lujanian ages (Fig. 3), whose biostratigraphic bases are represented by the *Mesotherium cristatum, Megatherium americanum* and *Equus* (*Amerhippus*) *neogaeus* biozones, respectively (Cione & Tonni 1999; Cione & Tonni 2005). In the Punta Hermengo area, Ensenadan deposits are partially coincident with Kraglievich's (1952) Vorohué, San Andrés and Miramar formations (see Cione & Tonni 2005).

Tonni & Fidalgo (1982) described the Punta Hermengo profile, within which they differentiated and characterized 7 sectors (named from A to G) (Fig. 4). Sector A is referable to the Ensenadan, whereas Sector G corresponds to the Lujanian (Tonni et al. 1998).

The materials studied here were collected from sector B of Tonni & Fidalgo's (1982) profile, which is composed of silty to silty-sandy sediments, gray-reddish-brown to yellowish-reddish brown, and has been referred to Ensenadan age (due to the presence of *Mesotherium cristatum*). According to Bidegain (pers. comm., 2006) these sediments would have reverse magnetic orientation.

Emended diagnosis: First line osteoderms of the pelvic scute with three central longitudinal figures, the lateral ones well defined and subdivided into small

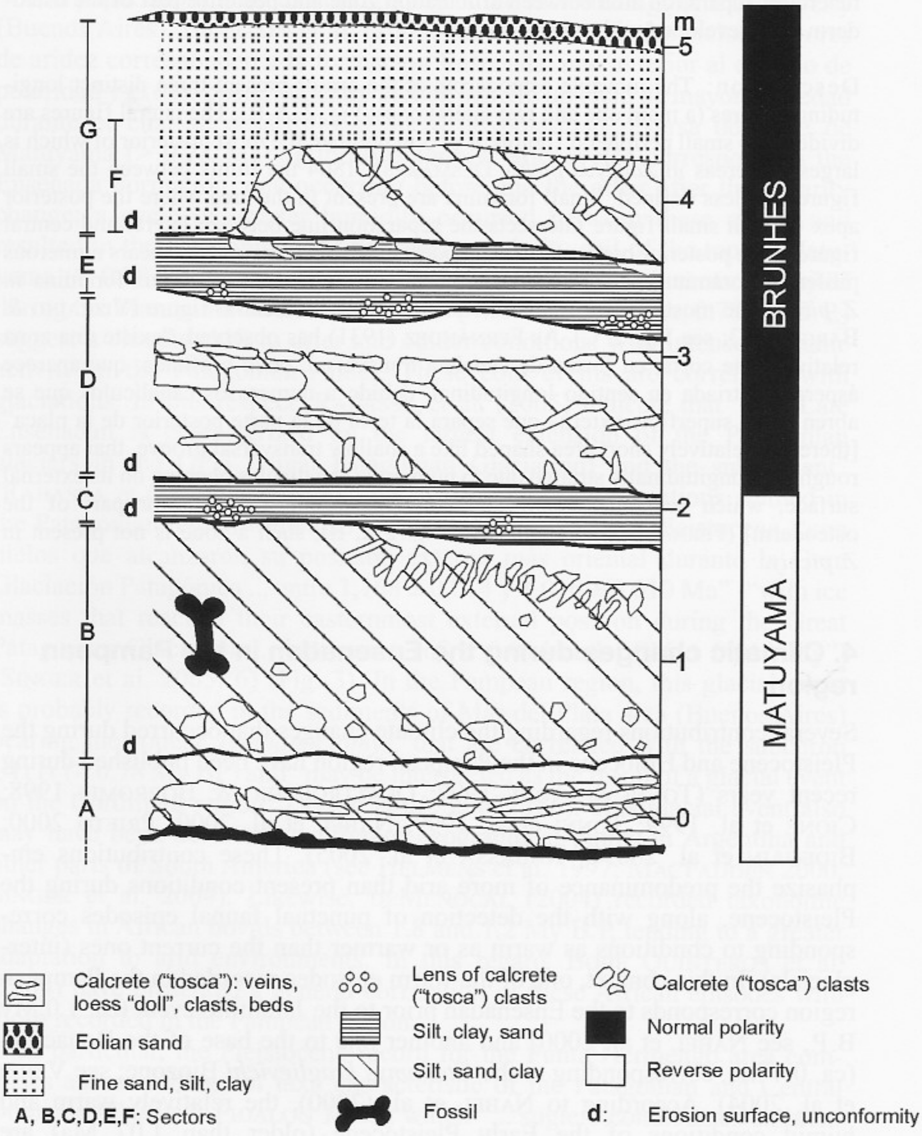

Fig. 4. Punta Hermengo profile and its possible magnetostratigraphic correlations.

tubercles; separation area between articulation zone and posterior part of the osteoderm well developed with rugose surface.

Description: The movable osteoderms of the armor present three distinct longitudinal figures (a main one and two lateral ones; Fig. 2. A-B). The lateral figures are divided into small peripheral figures, 4 or 5 in number, the most posterior of which is largest, whereas in *Zaedyus pichiy* DESMAREST, 1804 the limits between the small figures are less defined. Small foramina are present in the area where the posterior apex of each small figure intersects the separation line between lateral and central figures. The posterior border of the osteoderms is rather straight and bears numerous piliferous foramina, whereas it is very thin and has scarce piliferous foramina in *Z. pichiy*; the most evident foramen coincides with the central figure (VIZCAÍNO & BARGO 1993; see Fig. 2. C). As FERNÁNDEZ (1931) has observed, "existe una zona relativamente corta, en forma de canaleta transversal, poco profunda, que aparece áspera y estriada en sentido longitudinal, debido a numerosos canalículos que se abren en su superficie externa que separa la tecla de la parte posterior de la placa" [there is a relatively short area shaped like a shallow transversal groove, that appears rough and longitudinally striated due to numerous canalicules opening on its external surface, which separates the articulation zone from the posterior part of the osteoderm] (FERNÁNDEZ 1931: 64; see Fig. 2 A, B); such a zone is not present in *Z. pichiy*.

4. Climatic changes during the Ensenadan in the Pampean region

Several contributions regarding the climate changes that occurred during the Pleistocene and Holocene in the Pampean region have been published during recent years (TONNI & CIONE 1997; QUATTROCCHIO & BORROMEI 1998; CIONE et al. 1999; TONNI et al. 1999, NABEL et al. 2000; PRIETO 2000; BIDEGAIN et al. 2005b; RABASSA et al. 2005). These contributions emphasize the predominance of more arid than present conditions during the Pleistocene, along with the detection of punctual faunal episodes corresponding to conditions as warm as or warmer than the current ones (interglacials). In this context, one of the warm episodes recorded in the Pampean region corresponds to the Ensenadan prior to the Jaramillo event (ca. 1.0 My B.P., see NABEL et al. 2000) and another one to the base of the Bonaerian (ca. 0.4 Ma, corresponding to the *Ctenomys kraglievichi* Biozone; see VERZI et al. 2004). According to NABEL et al. (2000), the relatively warm and humid conditions of the Early Pleistocene (older than 1.07 Ma) are evidenced by both faunal remains (Tapiridae, Procyonidae and Echimyidae) and lithology.

In a paper about magnetostratigraphy in the surroundings of La Plata city (Buenos Aires), BIDEGAIN et al. (2005c) stated that "los dos ciclos mayores de aridez corresponden a la formación Ensenada, uno anterior al cambio de polaridad y el otro posterior, entre ambos ocurrió un ciclo de mayor humedad durante el cual se desarrolló el suelo de polaridad reversa del tope de Matuyama (> 0.78 Ma)" ["the two longest arid cycles correspond to the Ensenada Formation, one occurring before and the other after the polarity change; a cycle of greater humidity occurred between these cycles and resulted in the development of the reverse polarity soil of the top of Matuyama (> 0.78 My)"] (BIDEGAIN et al. 2005c: 7). The sediments deposited during the Matuyama-Bruhnes transition (Middle Pleistocene, 0.78 My B.P.) suggest a climate shift to drier and colder conditions with intense volcanic activity in the Patagonian Andes. These cold events are correlated with glaciations. In this respect, RABASSA et al. (2005) indicate that "The Late Ensenadan is characterized by the largest extension of the Patagonian glaciers in the GPG [Great Patagonian Glaciation] and the subsequent" (RABASSA et al. 2005: 99). It is noteworthy that the glaciations studied in the Patagonian region were also frequent during the early Pleistocene, "con hielos que alcanzaron su posición externa más oriental durante la Gran Glaciación Patagónica ... entre 1,168 ± 0,014 y 1,016 ± 0,010 Ma" ["with ice masses that reached their easternmost external position during the Great Patagonian Glaciation ... between 1.168 ± 0.014 and 1.016 ± 0.010 My"] (SINGER et al. 2005: 6) (Fig. 3). In the Pampean region, this glacial event is probably recorded in the sediments of Mar del Plata area (Buenos Aires) bearing the rodent *Tympanoctomys,* that are correlated with the subchron C1r1r (> 0.78 My BP) and "may be interpreted as the result of a glacial event on the Cordillera region" (VERZI *et al.*, 2002: 156). This glacial event also may have been detected at different geographical points in Argentina and other parts of South America (see HELMENS et al. 1997; MACFADDEN 2000; SINGER et al. 2004). Likewise, DEMENOCAL (2004) recorded taxonomic changes in African bovids between 1.8 and 1.2 My B.P, tending to a greater adaptation to arid environments. In this regard, BOBE QUINTEROS et al. (2004) have presented a general correlation of these African episodes with those recorded in the Pampean region.

In particular, the Pleistocene record for the Punta Hermengo area comprises an assemblage of taxa characteristic of the Patagonian and Central Domains (TONNI & FIDALGO 1982); which "... sugiere condiciones ambientales de menor temperatura y humedad que las registradas actualmente en el área de estudio" [suggests environmental conditions with lower temperature and humidity than those currently recorded in the study area"] (TONNI et al. 1998: 78).

5. Results and discussion

5.1. Chronological aspects

The preliminary magnetostratigraphic studies performed by BIDEGAIN (pers. comm., 2006) at Punta Hermengo yielded reverse magnetic orientation for the sediments bearing the *Chaetophractus* remains. The native ungulate, *Mesotherium cristatum,* has only been recorded in the C1r sector, at least at those sites where the records have been associated with magnetostratigraphic profiles (TONNI et al. 1999; BIDEGAIN et al. 2005c). This ungulate is characteristic of the Ensenadan and was found in the B sector of Punta Hermengo. Consequently, the B sector of Punta Hermengo profile can be referred to the chron C1r, probably subchron C1r1r (0.90-0.78 Mμ) (Fig. 3A, B).

5.2. Paleoenvironmental aspects

Even though the extant mammal species prevailing in Punta Hermengo correspond to the Subtropical Domain, no remains of these taxa have been recorded in any of the sectors in the profile described by TONNI & FIDALGO (1982), and thus these authors indicate that the deposit would have occurred under arid to semiarid climatic conditions, with predominant presence of Patagonian and Central fauna. These climatic conditions are related to the global changes of the glacial Pleistocene (SHACKLETON 1995) that generated several glacial advances in the Patagonian region (SINGER et al. 2004; RABASSA et al. 2005).

These arid or semiarid conditions favored the expansion of Patagonian and Central faunal elements (i.e., *Tolypeutes matacus, Dolichotis patagonum, Zaedyus pichiy, Microcavia australis, Lyncodon patagonicus, Lestodelphys halli*); *C. vellerosus* belongs to the latter. In this context, its current disjunct distribution may be interpreted as the result of warm and fundamentally humid recent and extant interglacial conditions that have led to the relictic presence of the species in non-climaxic areas and, following CARLINI & VIZCAÍNO (1987) and GLAZ & CARLINI (1999), the edaphic characteristics (well-drained sandy sediments of Bahía de Samborombón).

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