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Vertebrate continental assemblage from the Last Interglacial in southern South America (Entre Ríos, Argentina). Biostratigraphy and paleoenvironment

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ABSTRACT

This contribution aims to analyse the best-known paleovertebrate records from the beginning of the Late Pleistocene in Salto Ander Egg Formation (SAEF), Argentina. This fossil assemblage allowed us to infer the paleoenvironmental conditions for these deposits, and to discuss the biostratigraphic record within a geochronological framework. Salto Ander Egg Formation (SAEF), mapped in southwestern Entre Ríos province, is composed of fluvial deposits and was dated with ages ranging from 120 to 60 ky. Three sub-sequences were identified in the succession, which suggests a transgressive cycle over the MIS5 composed of a rising trend during MIS5e, a high stand stage in MIS5c, and a minor transgressive cycle during MIS3. A quantitative analysis has shown that approximately 50% of the total richness estimated for the unit has been sampled up to the moment. Two biostratigraphic units could be discriminated based on the study of faunistic associations. One of them, with Brazilian fauna, is linked to the basal sequences of SAEF (SS1). The other, exhibiting Pampean affinities, corresponds to middle and upper levels of SAEF (SS2–SS3).

1. Introduction

The study of fossil faunas, particularly of those including late Cenozoic mammals, is a topic of interest in most countries in South America. In Argentina, this topic is more developed for Buenos Aires province as paleontological studies in other areas of the country have just recently started (Ferrero et al. 2007; Ferrero and Noriega, 2009; Zurita et al. 2004, 2014; Cruz, 2012; Cruz et al., 2012). Similarly, the best-known data about the biostratigraphic sequence of mammals are from for the Pampean region of Buenos Aires province and have been used by many authors as the basis to support a chronostratigraphical scale (Pascual et al., 1965; Cione and Tonni, 1999, 2005; Cione et al. 2007; Verzi et al., 2004, 2008; Deschamps et al., 2012). This scheme is often employed for biostratigraphic generalizations. It is also useful to determine relative chronologies and temporal correlations among distant areas of South America. Thus, it is necessary to study the paleofaunas within an accurate stratigraphic and geochronological context and to consider regional biogeographic particularities in order to enrich and enhance the discussions on chronostratigraphic/geochronological hypotheses based on biostratigraphy.

Ameghino (1885, 1891) and Ortiz (1888) were pioneers to provide information about Quaternary fauna from Entre Ríos province. A century later, Tonni (1987, 1992) published some isolated records. More recently, the first records of taxa, new taxa to science and systematic lists of taxa, were also published, but with no major revisions (Tonni et al., 2001; Carlini et al., 2002; de la Fuente et al., 2002; Noriega et al., 2004; Noriega and Tonni, 2007; Scillato-Yané et al., 2005; Vucetich et al., 2005). These contributions, though preliminary in some cases, generated valuable biogeographic and biostratigraphic hypothesis that attempted to explain the peculiarities of the faunal composition. Continuing fieldwork exploration and collection of fossils in several localities in Entre Ríos province, comparative analysis in collections, and the study of geological units in a regional context have allowed us to obtain more accurate fossil records, expand the record of taxa already known for other regions, and describe new taxa to science (Ferrero, 2005, 2007, 2008a,b, Ferrero, 2006; Ferrero et al., 2005, 2007; Alcaraz et al., 2005; Prevosti et al., 2005; Ferrero and Noriega, 2007; Noriega and Tonni, 2007; Zurita and Ferrero 2009; Gasparini and Ferrero, 2010; Alcaraz and Ferrero, 2013; Ferrero and Alcaraz, 2013).

In this contribution, we review the stratigraphic provenance of all specimens described for the study area in the light of a new geologic interpretation of the units outcropping in southwestern Entre Ríos province (Brunetto et al., 2015).

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The vertebrate fossil assemblages from fluvial valleys were formerly assigned to Arroyo Feliciano and Tezanos Pinto Formations (Noriega et al., 2004; Carlini et al., 2004; Ferrero, 2009; Ferrero and Noriega, 2009), according to Iriondo et al. (1985) and Iriondo and Kröhling (2008). The latter correlated the highest terraces of the fluvial valleys to the entire region and assigned them to the Arroyo Feliciano Formation. In addition, they hypothesized that this unit - accumulated during the Late Pleistocene - and that it belongs to MIS3 based only on a small number of fossil mammals (Iriondo et al., 1985).

Later studies integrating lithostratigraphic, biostratigraphic, and geochronological data determined that the fossil fauna described for/the Late Pleistocene from SW Entre Ríos comes from the Salto Ander Egg Formation (SAEF) and not from the Arroyo Feliciano and the Tezanos Pinto Formations as originally proposed (Brunetto et al., 2009, 2012, 2013; Ferrero, 2013; Brunetto et al., 2015).

The SAEF fossil vertebrate record is analyzed in this work considering the paleoenvironmental conditions prevailing over its deposition. Similarly, the biostratigraphic significance of this record is discussed within a geochronological framework.

2. Geologic setting

Argentinian Mesopotamia (Fig. 1A) is part of the intracratonic Chaco-Paraná basin (Chebli et al., 1999) and formed in the craton of Río de La Plata (Rapela et al., 2007), which accumulates sediments from the Neopaleozoic (Chebli et al., 1999; Reinante et al., 2014). The bedrock from this basin is composed almost entirely of rocks that constitute the Río de la Plata craton (Rapela et al., 2007). The basin surface shows a stratigraphic column ranging from Late Miocene to Holocene ages. In Entre Ríos province, the upper stratigraphic column exhibits sequences of fluvial, lacustrine and aeolian deposits from Late Pleistocene-Holocene that constitute the sedimentary fluvial valley fill (Iriondo, 1998; Brunetto et al., 2012, 2013). The SW of Entre Ríos is a geomorphological unit known as Crespo Loessic Hills (Iriondo, 1998), which is undergoing fluvial incision. Litostratigraphic units of this region have sedimentological particularities that distinguish them from those outcropping in the rest of the province (Brunetto et al., 2009; Iriondo, 2010). Particularly, the mineralogical content of the SAEF indicates that this unit had local sedimentological sources (Brunetto et al., 2009, 2012, 2013, 2015). Conversely, Arroyo Feliciano Formation (central-northern Entre Ríos) and El Palmar Formation (western Entre Ríos) display sediments from distant sources (Brunetto et al., 2012).

2.1. Salto Ander Egg Formation (SAEF) lithostratigraphy

The sediments of the SAEF belong to fluvial sequences that overlay in erosive discordance with different Neogene-Quaternary units. In some places the SAEF overlays with Paraná Formation, in others this overlays with some of the units that compose the Punta Gorda Group (Puerto General Alvear, La Juanita and Punta Gorda Formations). Originally, this geologic unit was referred to as the Arroyo Feliciano Formation (Noriega et al., 2004; Ferrero and Noriega, 2007, 2009; Ferrero, 2009), which was mapped in northern Entre Ríos province (Iriondo et al., 1985) and extended to all fluvial valleys of the province (Iriondo, 1998). However, subsequent studies based on significant sedimentological differences allowed us to recognize a new lithostratigraphic unit (Brunetto et al., 2009, 2013, 2015). The Salto Ander Egg Formation is mapped in SW Entre Ríos (Fig. 1A) outcropping on the cliff of the Doll and Ensenada creeks (Fig. 1B and C). The integrated stratigraphic column is formed by: 1) poorly structured mud facies, which can be interpreted as aggradational deposits in a low energy flow regime, both proximal to and distal from the channel; 2) cross-stratified clast-supported conglomerate facies; 3) low-angle cross-bedded sandy gravels facies; 4) low-angle stratified sandy silt facies. Lithofacies 2, 3 and 4 correspond to channel facies of a braided river (Brunetto et al., 2015). This unit is overlain by pond and aeolian facies from the Tezanos Pinto Formation (Brunetto et al., 2015).

2.2. Sequence stratigraphy

The complete sequence represents the last full Late Pleistocene interglacial-glacial cycle in the SW of Entre Ríos. This is formed by three fluvial subsequences (SS1, SS2 and SS3), and a sequence of transitional pond deposits covered by loess (SS4) (Brunetto et al., 2015). The hierarchical discontinuities of different order, which delimit these subsequences, show marked changes in the sedimentation energy conditions, controlled by climatic changes and sea level oscillations (Brunetto et al., 2015).

2.3. Geochronology

Optically stimulated luminescence (OSL) data show that most of the analyzed sediments are aged between 120 and 60 ky. The SS1 was dated close to 120 ky, whereas the SS2, to ca.100 ky and the SS3, to ca. in 60 ky (Brunetto et al., 2015). The geochronological data suggest that SS1 accumulated during MIS 5e, SS2, between MIS 5c and MIS 5a, and SS3, during the beginning of MIS 3. Another group of OSL geochronological data indicated that the SS4 subsequence is part of the Tezanos Pinto Formation, which accumulated between the end of MIS 3 and MIS 2, i.e., between 34 and 11 ky (Kröhling et al., 2010; Kruck et al., 2011; Brunetto et al., 2015).

3. Materials and methods

Most of the specimens mentioned in this work were collected by the authors and are stored at the paleontological collections of the *Centro de Investigaciones Científicas y de Transferencia de Tecnología de la Producción*, belonging to the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) (CICYTTP-M/R/A-PV), and the *David Rhys Museum*, belonging to Universidad Adventista del Plata (UAP), both in Entre Ríos (Argentina).

Fossils come from five localities of southwestern Entre Ríos province where the Salto Ander Egg Formation is exposed: Doll Creek (Fig. 1B) and Salto Ander Egg, Ensenada Creek, El Pelado Creek, Barrenechea Creek (Fig. 1C). In order to determine the stratigraphic provenance of the fossils, the architectural elements recognized in the type locality (Salto Ander Egg) and integrated to subsequences of deposition (SS1–SS3) (Brunetto et al., 2015) were extrapolated to the localities sampled (Fig. 2). The subsequences in the different sites were delimited taking into account the lithological variations and the most important discontinuities in the unit. The localities of fossil provenance were registered by GPS receiver (Table 1) and the stratigraphic levels were measured with metric tape.

The sedimentological and mineralogical studies conducted in the CICYTTP laboratories (see Brunetto et al., 2009, 2012, 2015). The Optically Stimulated Luminescence analyses were carried out in the *Luminescence Dating Laboratory* (University of Oxford) and some replications were made in the *Datação, Comércio e Prestação de Serviços Laboratory (DATAÇÃO)* of Sao Paulo, Brazil (see Brunetto et al., 2015).

For quantitative data analyses, we computed the species accumulation curve and the Chao 2 estimator of asymptotic species richness. The accumulation curve is an approach commonly used in ecology, which can also be used in paleontological studies. The collector curve simply quantifies the collecting effort against the identification of new species. Besides, the collector curve can also serve to provide an approach to assess the quality of the fossil record (Benton, 1998). The Chao 2 estimator, widely employed in ecological studies (Chazdon et al., 1998; Gotelli and Colwell, 2001), uses a non-parametric method to estimate species richness based on the concept that rare species carry the highest amount of information about the missing species. We chose Chao 2 estimator because it provides one of the least biased

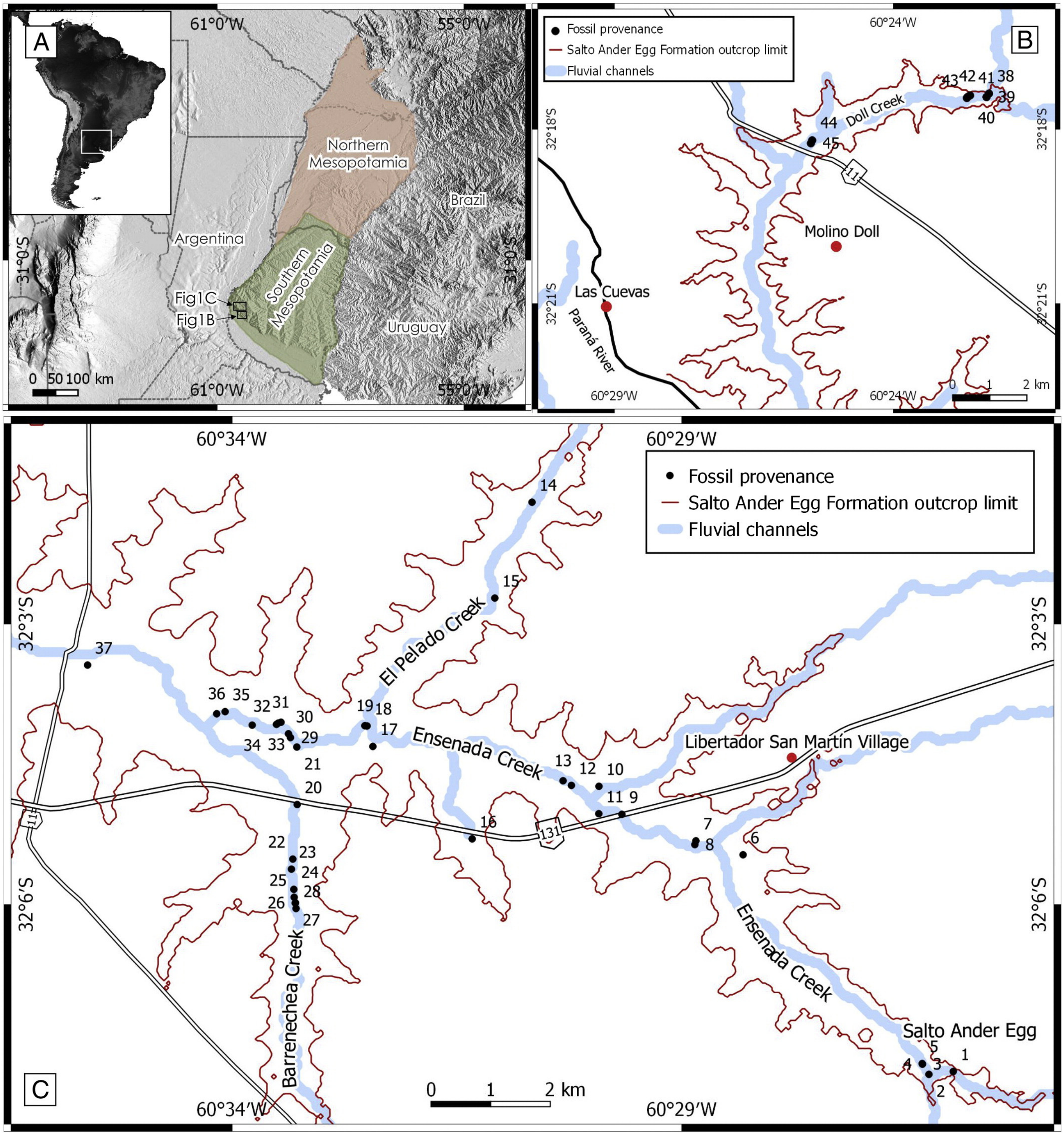

Fig. 1. A) Regional geological map of the southwestern Mesopotamia (Entre Ríos Province), B) taxa geographic provenance in Doll creek, C) taxa geographic provenance in Ensenada basin (see Table 1 for GPS references).

estimates for small sample sizes, which is particularly important for the estimation of species richness (Colwell and Coddington 1994; Chao et al., 2009). To asses completeness, we used non-parametric estimators like ICE (Incidence-based Coverage Estimator) and Chao2 with a 1000 bootstrap with EstimateS v.9 (2013). **Abbreviations** — AE + number, lithotome of Salto Ander Egg Formation; EPF, El Palmar Formation; HST, highstand systems tract; ICE, Incidence-based Coverage Estimator; LST, lowstand systems tract; MIS + number, marine isotopic stage; RST, regressive systems tract; SAEF, Salto Ander Egg Formation; SS + number, sub-sequence; TST, transgressive systems tract.

4. Results

4.1. Paleontological content

Most of the vertebrate fossils found were mammals and, in a smaller number, birds and reptiles. Their stratigraphic provenances were established according to the deposition subsequences recognized for the unit (see Fig. 2 and Background dataset for online publication).

For the first cycle of sedimentation (SS1) an unprecedented Brazilian faunal assemblage along with typical taxa from Late Pleistocene, were found in southern latitudes. The tropical fauna corresponds to the tortoise *Chelonoidis denticulata*, the mustelid *Pteronura brasiliensis*, and the tapir *Tapirus mesopotamicus*. The typical Pampean fauna was characterized by giant tortoises (?*Chelonoidis* sp.), vultures (*Geronogyps reliquus*), horses (*Equus* (*Amerhippus*) sp., *Hippidion principale*), camelids (*Hemiauchenia paradoxa*, *Lama guanicoe*), proboscideans (*Notiomastodon* (=*Stegomastodon*) sp.), and rodents (*Hydrochoerus* sp., *Lagostomus* cf. *maximus*) and some native mammals from South America, such as notoungulates (*Toxodon platensis, ?T. gracilis*), litopterns (*Macrauchenia patachonica*), sloths (*Megatherium americanum*, *Lestodon armatus*, *Glossotherium robustum*, *Glossotherium* sp.), cingulates (*Glyptodon* sp., *Neuryurus trabeculatus*) and armadillos (*Holmesina* cf. *paulacoutoi*, *Pampatherium* sp., *Propraopus* sp., *Eutatus seguini*).

For the second cycle (SS2), we noticed the absence of tropical taxa and birds. These levels were characterized by typical taxa from the Pampean area, mainly mammals. In addition to Pampean taxa from SS1, sloths (*Lestodon* sp., *Scelidodon* sp.), glyptodonts (*Glyptodon perforatus*, *Glyptodon reticulatus*, *Panochthus* cf. *tuberculatus*), armadillos (*Propraopus* cf. *grandis*), octodontids (*Ctenomys* sp.), mastodonts (*Notiomastodon platensis*), deers (*Antifer ultra*, *Morenelaphus brachyceros*, *Ozotoceros bezoarticus*), camelids (*Lama gracilis*), peccaries (*Catagonus* sp.), bears (*Arctotherium* cf. *bonariense*), cats (*Smilodon populator*), and foxes (*Pseudalopex* (=*Dusicyon*) *gymnocercus*) were found.

For the third cycle (SS3), only two taxa have been found up to the moment: cf. *Glossotherium* and *Panochthus* sp.

4.2. Species accumulation curve and sampling completeness

The estimate of vertebrate species richness according to Chao2 was 90.13 ± 37.33 taxa (Fig. 3). The effort made over more than ten years of sampling showed a survey completeness of 49.3%–38.83% (ICE = 70.99 and Chao2 = 90.13 ± 37.33 as estimators). The quantitative analyses showed that the estimated number of sampling taxa in SAEF should be between 70 and 90. In this sense, the 35 taxa sampled represent the 39% and 50% of the estimated total richness in SAEF.

5. Discussion and conclusion

The record of vertebrates in the levels studied includes extinct faunal elements (75%), which are also known from other geographic areas from the Late Pleistocene, extant taxa (25%), and some endemism (7.14%).

According to Benton (1998), when the rate of the collector curve declines markedly, it is assumed that the collector is approaching the true total diversity, and then collecting should stop at level 90% or 95%: the effort required to find the very last species in an area might well equal the effort made for finding all the others. In our results, the evaluation of sampling completeness allowed us to estimate the proportion of vertebrate taxa, mainly mammals, which were still undetected (about 60% and 50%). There are several possible explanations for the relatively low detection of taxa. One is that a higher sampling effort is necessary to find small vertebrates that are almost absent in our biostratigraphic sequences. Another explanation is that we could be underestimating the number of taxa because, in some cases, when the identification is dubious we considered the taxon only at the genus level. A third possible explanation is a poor fossil record because of the fluvial dynamic itself, as well as of the high energy of the fluvial system studied.

Discontinuities, lithostratigraphic, and geochronologic analyses in the SAEF allow us to recognize three cycles of sedimentation (SS1–SS3) accumulated during the Late Pleistocene (125–60 ky) (Fig. 2). Taking into account the sedimentological characteristics and the architecture of lower units in the type unit, AE1, AE2, AE3, and AE4, the architectural elements could be considered to be part of the same fluvial sequence. This association is formed by well-defined floodplain facies (AE1–AE3) and channel facies (AE4). Considering all the localities sampled in the integrated profile, these facies correspond to the first subsequence (SS1). According to the geochronological data obtained in the Oxford lab, the subsequence SS1 accumulated during the MIS 5 (120–

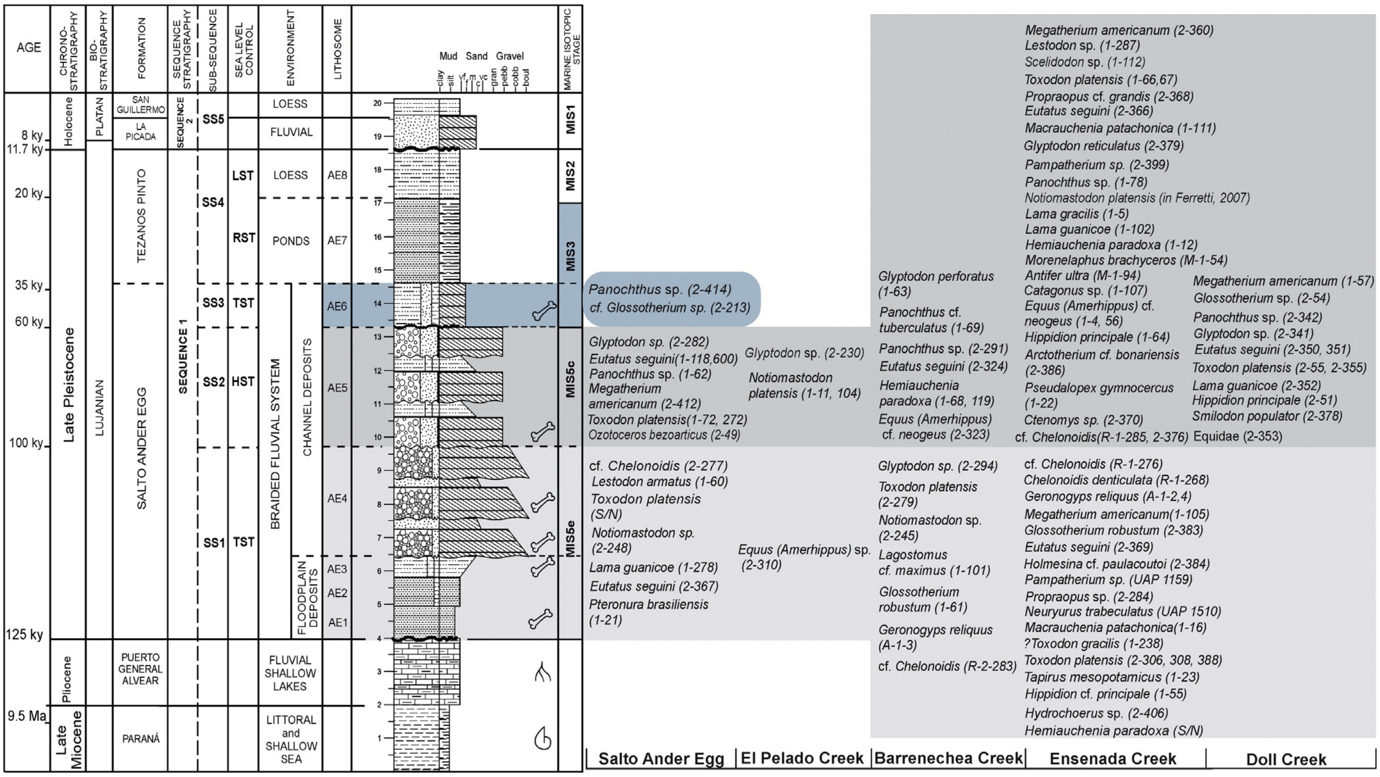

Fig. 2. Integrated stratigraphic column of the SAEF and taxa stratigraphic provenance.

Table 1
Fossils geographic location.

Site	Longitude	Latitude	Location	Description
1	60°25′ 54.21″W	32°07′ 46.96″S	Salto Ander Egg	*Toxodon platensis (1–72)*
2	60°26′ 09.79″W	32°07′ 48.7978″S	Salto Ander Egg	cf. *Chelonoidis (2–277)*, *Lestodon armatus (1–60)*, *Toxodon platensis* (S/N), *Lama guanicoe (1–278)*, *Notiomastodon* sp. *(2–248)*, *Eutatus seguini (2–367)*
3	60°26′ 13.95″W	32°07′ 42.17″S	Salto Ander Egg	*Pteronura brasiliensis (1 —21)*
4	60°26′ 13.96″W	32°07′ 42.27″S	Salto Ander Egg	*Eutatus seguini (1–118,600)*, *Toxodon platensis (1–272)*, *Panochthus* sp. *(1–62)*, *Megatherium americanum (2–412)*
5	60°26′ 14.08″W	32°07′ 41.85″S	Salto Ander Egg	*Ozotoceros bezoarticus (2–49)*, *Glyptodon* sp. *(2–282)*
6	60°28′ 08.81″W	32°05′28″S	Ensenada creek	*Megatherium americanum (2–360)*
7	60°28′ 39.01″W	32°05′ 19.05″S	Ensenada creek	*Chelonoidis denticulata (R-1-268)*
8	60°28′ 39.70″W	32°05′ 21.46″S	Ensenada creek	*Pampatherium* sp. *(2–399)*
9	60°29′ 26.42″W	32°05′ 02.04″S	Ensenada creek	*Macrauchenia patachonica (1 —111)*
10	60°29′ 41.11″W	32°04′ 44.09″S	Ensenada creek	*Pampatherium* sp. *(UAP 1159)*, *Neuryurus trabeculatus (UAP 1510)*
11	60°29′ 41.22″W	32°05′ 01.68″S	Ensenada creek	*Hemiauchenia paradoxa (1 —12)*, *Lama gracilis (1–5)*, *Equus (Amerhippus)* cf. *neogeus (1–4)*, cf. *Chelonoidis (R-1-285)*
12	60°29′ 58.76″W	32°04′ 43.50″S	Ensenada creek	*Lama guanicoe (1 —102)*, *Hippidion* cf. *principale (1–55)*, *Megatherium americanum (1–105)*, *Hemiauchenia paradoxa* (S/N)
13	60°30′ 04.09″W	32°04′ 40.52″S	Ensenada creek	*Tapirus mesopotamicus (1 —23)*
14	60°30′ 23.97″W	32°01′ 41.91″S	El Pelado creek	*Equus (Amerhippus)* sp. *(2 —310)*
15	60°30′ 47.81″W	32°02′ 43.38″S	El Pelado creek	*Notiomastodon platensis (1–11, 104)*, *Glyptodon* sp. *(2 —230)*
16	60°31′ 02.32″W	32°05′ 17.81″S	Ensenada creek	*Morenelaphus brachyceros (M-1-54)*
17	60°32′ 05.91″W	32°04′ 18.53″S	Ensenada creek	*Arctotherium* cf. *bonariensis (2–386)*
18	60°32′ 09.62″W	32°04′ 05.38″S	Ensenada creek	*Equus (Amerhippus)* cf. *neogeus (1–56)*
19	60°32′ 11.04″W	32°04′ 05.23″S	Ensenada creek	*Glossotherium robustum (2–383)*
21	60°32′ 54.61″W	32°04′ 18.90″S	Ensenada creek	*Eutatus seguini (2–366)*, *Hippidion principale (1–64)*, *Pseudalopex gymnocercus (1 —22)*, *Propraopus* cf. *grandis (2–368)*, *Scelidodon* sp. *(1 —112)*, *Catagonus* sp. *(1–107)*, *Toxodon platensis (2–306, 308, 388)*, *Panochthus* sp. *(1–78)*
20	60°32′ 54.35″W	32°04′ 55.79″S	Barrenechea creek	*Eutatus seguini (2–324)*, *Equus (Amerhippus)* cf. *neogeus (2 —323)*
22	60°32′ 57.18″W	32°05′ 30.76″S	Barrenechea creek	*Lagostomus* cf. *maximus (1 —101)*, *Glyptodon perforatus (1–63)*, *Glossotherium robustum (1–61)*
23	60°32′ 58.06″W	32°05′ 37.21″S	Barrenechea creek	*Geronogyps reliquus (A1-3)*
24	60°32′ 56.54″W	32°05′ 50.17″S	Barrenechea creek	*Panochthus* cf. *tuberculatus (1–69)*
25	60°32′ 56.32″W	32°05′ 55.25″S	Barrenechea creek	cf. *Chelonoidis* sp. *(R-2-283)*
26	60°32′ 55.46″W	32°05′ 58.81″S	Barrenechea creek	*Toxodon platensis (2–279)*, *Panochthus* sp. *(2–291)*, *Hemiauchenia paradoxa (1–68, 119)*
27	60°32′ 55.64″W	32°05′ 58.95″S	Barrenechea creek	*Glyptodon* sp. *(2–294)*
28	60°32′ 55.11″W	32°06′2.46″ S	Barrenechea creek	*Notiomastodon* sp. *(2–245)*
29	60°32′ 58.68″W	32°04′ 12.84″S	Ensenada creek	*Toxodon platensis (1–67)*, *Ctenomys* sp. *(2–370)*, *Geronogyps reliquus (A1-2.4)*, cf. *Chelonoidis (R-2-376)*, *Holmesina* cf. *paulacoutoi (2–384)*, *Toxodon gracilis (1–238)*, *Eutatus seguini (2–369)*
30	60°32′ 59.96″W	32°04′ 10.41″S	Ensenada creek	cf. *Chelonoidis (R-1-276)*, *Eira barbara (M-2-406)*
31	60°33′ 04.74″W	32°04′ 03.02″S	Ensenada creek	*Toxodon platensis (1–66)*
32	60°33′ 06.59″W	32°04′3.59″ S	Ensenada creek	*Propraopus* sp. *(2–284)*
33	60°33′ 07.65″W	32°04′ 04.36″S	Ensenada creek	*Hydrochoerus* sp. *(2–406)*
34	60°33′ 23.20″W	32°04′ 04.86″S	Ensenada creek	*Antifer ultra (M-1-94)*
35	60°33′ 40.54″W	32°03′ 56.21″S	Ensenada creek	*Macrauchenia patachonica (1–16)*
36	60°33′ 45.92″W	32°03′ 57.57″S	Ensenada creek	*Lestodon* sp. *(1–287)*
37	60°35′ 08.63″W	32°03′ 26.34″S	Ensenada creek	*Glyptodon reticulatus. (2–379)*

(continued on next page)

Table 1 (*continued*)

Site	Longitude	Latitude	Location	Description
38	60°22′ 21.14″W	32°17′ 23.15″S	Doll creek	*Eutatus seguini (2–350, 351)*
39	60°22′ 23.68″W	32°17′ 26.71″S	Doll creek	*Glyptodon* sp. *(2–341)*
40	60°22′ 23.75″W	32°17′ 26.67″S	Doll creek	*Smilodon populator (2–378)*
41	60°22′ 40.70″W	32°17′ 25.11″S	Doll creek	*Lama guanicoe (2–352), Equidae (2–353)*
42	60°22′ 43.28″W	32°17′ 26.68″S	Doll creek	*Toxodon platensis (2–355)*
43	60°22′ 44.01″W	32°17′ 27.74″S	Doll creek	*Panochthus* sp. *(2–342)*
44	60°25′ 23.72″W	32°18′ 11.40″S	Doll creek	*Hippidion principale (2–51), Megatherium americanum (1–57)*
45	60°25′ 25.07″W	32°18′ 14.44″S	Doll creek	*Glossotherium* sp. *(2–54), Toxodon platensis (2–55)*

105 ky). Discrepancies in the geochronological data for the same samples were obtained in another laboratory (Sao Pablo) (Brunetto et al., 2015). For this reason it should not be excluded that the lower levels of the SS1 (e.g. AE1–AE3 of type unit) could have accumulated during the previous interglacial period MIS 7 (178–202 ky). However, the latter exhibited some methodological problems and uncertainties (Brunetto et al., 2015).

The overlying sequence (SS2, middle levels) is represented by channel facies of lower energy (AE5 type unit) than the energy of the channel facies of SS1. The OSL dating resulted in similar ages in both labs, providing a range of ages between 96.5 and 105 ky. Hence, it accumulated probably over the MIS 5c. The upper level is SS3 (SA6 in the type profile) and is characterized by fine channel sediment deposited under a low energy regimen. The level SS3 was dated ca. 60.9 ky, which suggests that these deposits accumulated, probably, over the MIS 3.

5.1. Lower levels of the SAEF

The fossil fauna recovered from lower levels (SS1) of the unit includes elements unknown for other Late Pleistocene units from Argentina, and from the south of Brazil and Uruguay, such as *Pteronura brasiliensis*, *Tapirus mesopotamicus* and *Chelonoidis denticulata* (Fig. 4). A peculiarity of this fauna is that both *Pteronura brasiliensis* and *Chelonoidis denticulata* are extant and sympatric species, which allows us to infer the habitat conditions from the past (Fig. 5). The current geographic distributions of both taxa are associated with tropical rainforest. *Chelonoidis denticulata* inhabits exclusively tropical warm rainforest and deciduous forest, and it never moves to open areas and savannahs (Rueda-Almonacid et al., 2007). *Pteronura brasiliensis* inhabits the most important fluvial systems of South America. It is found in rivers, streams, lakes, and permanent wetlands of tropical and subtropical regions, most of them surrounded by rainforest or riparian forest (Redford and Eisenberg, 1992; Parera, 2002; Larivière and Jennings, 2009). Although *T. mesopotamicus* is an extinct and endemic species of Entre Ríos province, it can also be considered to be a good indicator of habitat conditions because it shares, at the genus level, the geographic distribution with *C. denticulata* and *P. brasiliensis*. In South America, the genus *Tapirus* is currently restricted to tropical and subtropical areas and, based on our record, this taxon did not lived further than 32°S during the Late Pleistocene. The southernmost extant species is *T. terrestris* and it inhabits lowlands, moist and swamp forests, dry and moist shrub lands, grasslands, and a wide variety of wetlands. Although its habitat varies extensively, the most frequent habitats tend to be moist, wet or seasonally flooded areas. This species has been observed in and associated with both water and salt-licks (Redford and Eisenberg, 1992; Parera, 2002; Naveda et al. 2008). Other important faunistic presence in the SAEF is the pampathere *Holmesina* cf. *paulacoutoi*. Although this species has been recorded in many areas of Argentina, such as Chaco, Corrientes and Santa Fe provinces, it is commonly supposed to have a Brazilian biogeographic origin (Scillato-Yané et al., 2005).

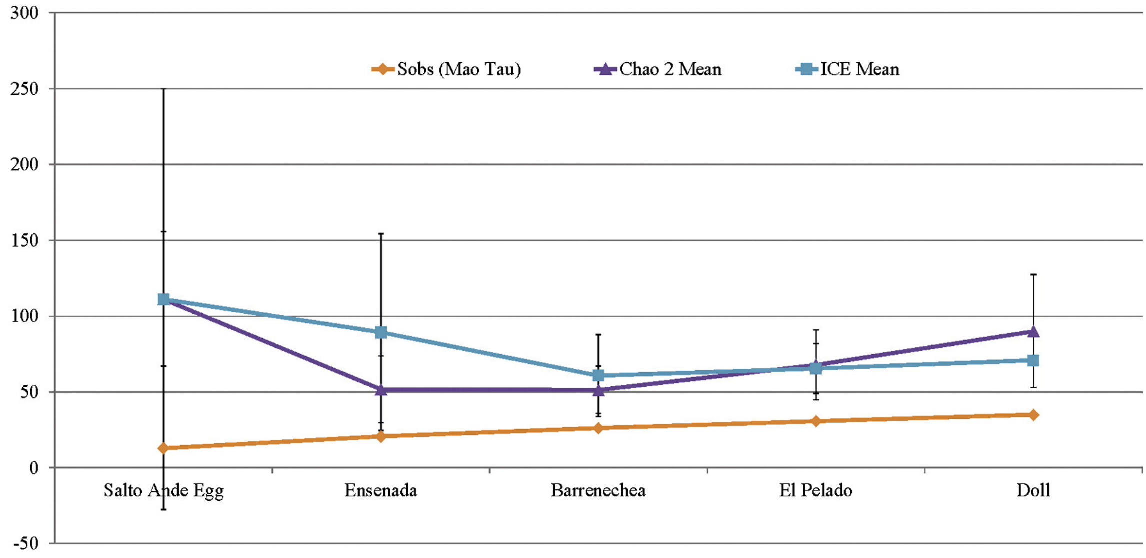

Fig. 3. Collection effort curve of each localities with EstimateS 8.2.0 (Colwell, 2013) to evaluate sampling effort using presence-absence data available and CHAO 2 as richness estimator.

Apart from the Brazilian fauna, the taxa recognized for the same basal levels of the unit are widely documented for the Pampean region and northern Mesopotamia in Argentina, southern Brazil, and northern Uruguay (Cione and Tonni, 2005; Ribeiro and Scherer, 2009; Tonni, 2009; Ubilla et al., 2009; Cruz, 2012; Cruz et al., 2012; Zurita et al., 2014) for Late Pleistocene ages. Although *N. trabeculatus* is endemic from Entre Ríos, the genus was also recorded in the areas previously mentioned.

Another taxon particularity observed in the lower levels of the SAEF is *Lagostomus* cf. *maximus* (Fig. 4). This taxon is considered to be a guide taxon of the biozone of *L. maximus* from the Platan Stage/Age (Holocene,

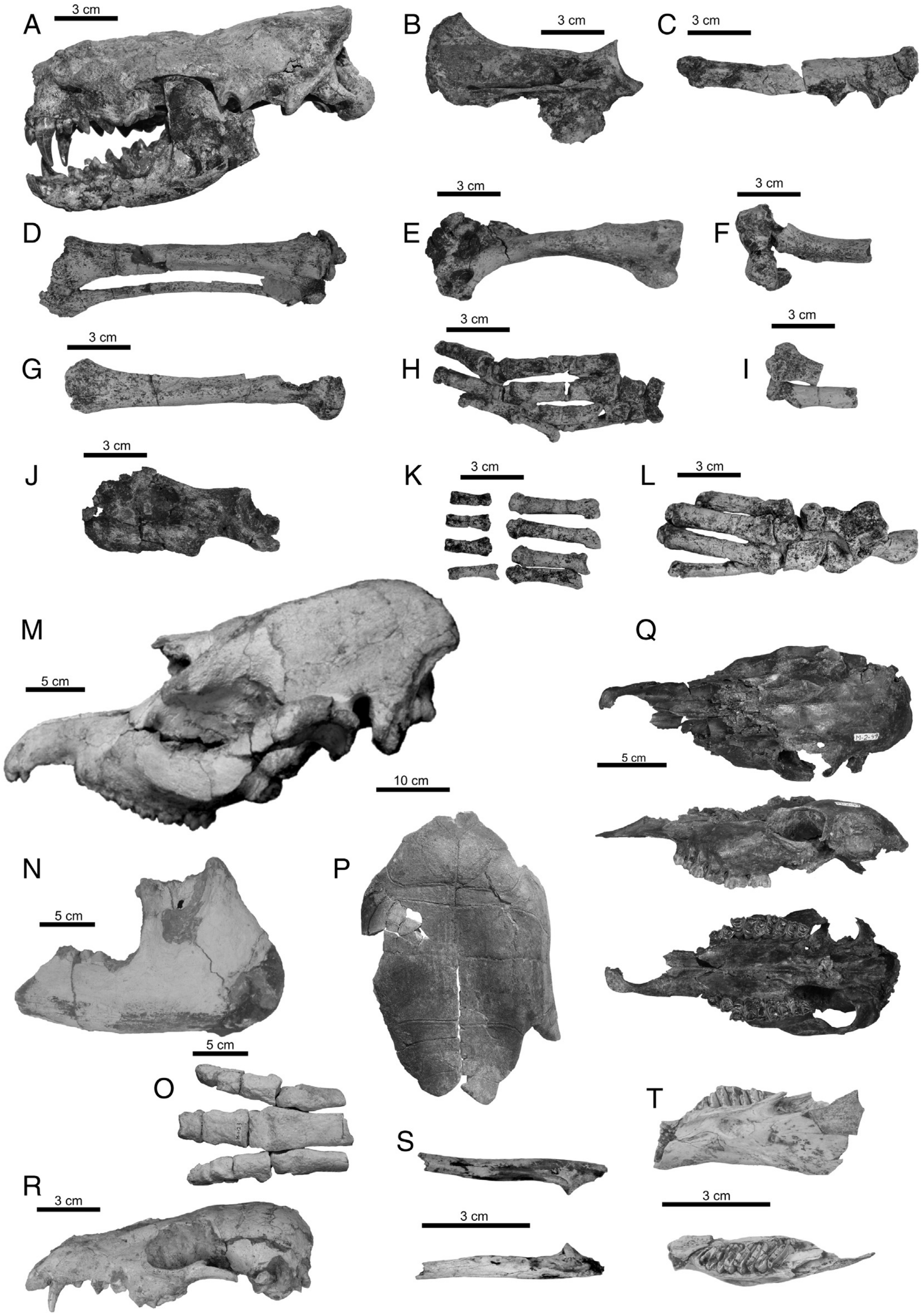

Fig. 4. Selected fossil vertebrates of SAEF. A) Skull of *Pteronura brasiliensis* (described in Prevosti and Ferrero, 2008), B) scapula, C) ulna, D) tibia and fibula, E) humerus, F) distal humerus, G) tibia, H) manus, I) distal radius and ulna, J) fragment of sacrum, K) metapods, and L) foot. M) Skull and N) mandible of *Tapirus mesopotamicus* (described in Ferrero and Noriega, 2007), and O) foot. P) Plastron of *Chelonoidis denticulata* (described in Manzano et al., 2009). Q) Skull of *Ozotoceos bezoarticus*. R) Skull of *Pseudalopex gymnocercus* (described in Prevosti et al., 2005). S) Ulna and T) mandible of *Lagostomus* cf. *maximus*.

close to 8000 ^{14}C BP in the 16th century) in the Argentinian province of Buenos Aires (Cione and Tonni, 1999; Tonni, 2009).

Regarding the chronostratigraphical and geochronological hypotheses of Cione and Tonni's (1999, 2005) scheme based on biochronological support, we find a striking difference consisting of the record of *L. maximus* in southwestern Entre Ríos province within 120 and 105 ky. The earliest occurrence of this taxon in the SW of Entre Ríos province could be explained by the biogeographic differences that could have existed between this area and the Pampean region. The distribution of taxa in time and space is uneven and, thus there may be differences in their first and last occurrences (van der Meulen et al., 2011), even in those considered to be the guide taxon of a biozone and recorded in close areas. The extrapolation of the Stage/Age scheme and their biozones (Cione and Tonni, 1999, 2005) to distant regions must be carefully made in the absence of absolute data. It is mandatory to consider regional biogeographic particularities to avoid a wrong correlation between mammal associations and time. The record of *L. maximus*, in basal levels of the SAEF, forces us to rethink the chronological calibration for the occurrence of the taxa in the fossil record of southern Entre Ríos. Additionally, *L. maximus* was registered in the late Pleistocene of southern Brazil (Kerber et al., 2011) and Uruguay (Ubilla and Rinderknecht, 2016).

5.2. Middle levels of the SAEF

In middle levels of the SAEF, dated 105.25 ± 8.73 ky and 96.5 ± 20.9 ky, megafauna typical from the Late Pleistocene were found, which was also registered in lower levels, and to which octodontids rodents (*Ctenomys* sp.), deers (*Antifer ultra*, *Morenelaphus brachyceros* and *Ozotoceros bezoarticus*), peccaries (*Catagonus sp.*), bears (*Arctotherium* cf. *bonariensis*), cats (*Smilodon populator*), foxes (*Pseudalopex gymnocercus*), and a species of camelid absent in SS1, *Lama gracilis*, are added. These taxa were also found in the Late Pleistocene in Argentina, south of Brazil and northern Uruguay (see Cione and Tonni, 2005; Vezzosi, 2008, 2011; Zurita et al., 2014; Cruz, 2012; Cruz, et al., 2012, Ubilla, et al., 2009; Ribeiro and Scherer, 2009; Scherer, 2009; Scherer et al., 2009).

In addition to the typical Late Pleistocene megafauna, taxa currently linked to open environments (pampas, savannahs, also seasonally flooded grasslands), such as *Ozotoceros bezoarticus* (Fig. 4), were recorded at the middle levels of the unit (Fig. 2). The deer *O. bezoarticus* is a mixed feeder able to tolerate a wide temperature range (Redford and Eisenberg, 1992; Mattioli, 2011). Another taxon registered is *Catagonus* sp., whose extant species is endemic from the Chacoan region and shows a reduced habitat and a limited temperature tolerance range. It is typically found in arid and dense shrublands of the Espinal under low rainfall (less than 900 mm) and high temperatures, characterized as xerophytic forest; and it is less commonly recorded in open forest areas (Redford and Eisenberg, 1992; Taber et al., 2011). Another recorded taxon which is typical of xerophytic environments is the *Lama guanicoe*. It inhabits deserts with xeric scrub, mountains and plains with grasslands, savannas and temperate forests. The guanacos are opportunistic herbivores and mixed feeders and feed on a large proportion of both grasses and shrubs (Redford and Eisenberg, 1992; Franklin, 2011). Although *Lama guanicoe* is also recorded in lower levels of SAEF, it is more frequent in middle levels of the unit. The current environmental preferences of this species seem to contradict the paleoenvironment inferred for the SAEF; however, there is strong evidence about the wide distribution of *Lama guanicoe* during the Late Pleistocene, which reached tropical environments in southern Brazil and even more in the northeastern region of that country (Scherer, 2009). The canid *Pseudalopex gymnocercus* (Fig. 4) is the only one currently distributed in Entre Ríos province. This species inhabits subtropical environments, typically linked to grasslands, in South America. It is frequently found in open habitats, tall grass plains and subhumid to dry environments, and it is also common in ridge, dry scrubs and open forests (Redford and Eisenberg, 1992; Sillero-Zubiri, 2009).

5.3. The Lujanian stage/age and the SAEF

The Late Pleistocene record of mammals from Buenos Aires province, from flood plain sediments from Guerrero Member from Luján Formation (Tonni, 2009), has been used as the biochronological support to extrapolate its relative age to other areas of Argentina and even to

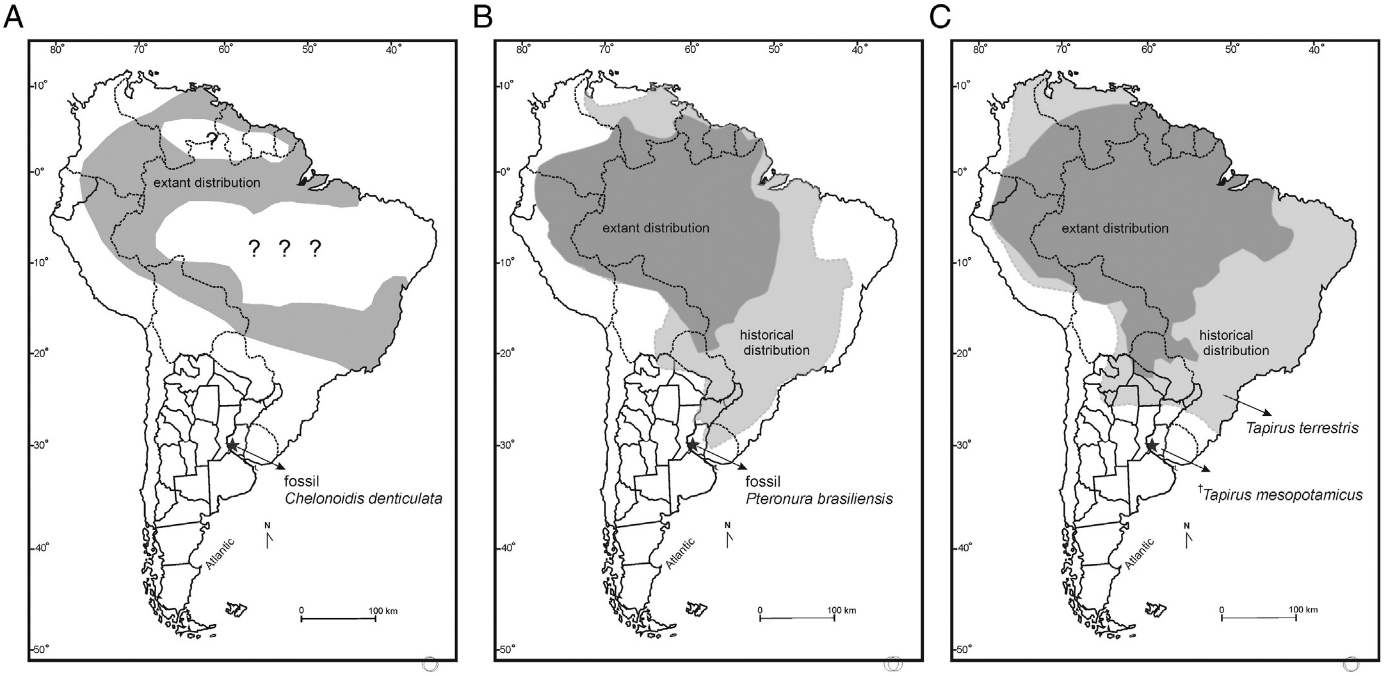

Fig. 5. Geographic distribution. A) *Chelonoidis denticulate* (Rueda-Almonacid et al., 2007), B) *Pteronura brasiliensis* (Prevosti and Ferrero, 2008; Groenendijk et al., 2015), C) *Tapirus terrestis* (Naveda et al., 2008).

other areas of South America. This unit accumulated over 21 ± 0.4 ^{14}C BP and 10.3 ± 0.1 ^{14}C BP) (Tonni et al. 2003; Tonni, 2009) and belongs to *Equus (Amerhippus) neogaeus* Biozone, which is the biostratigraphic base of the Lujanian Stage/Age (Cione and Tonni, 1999). However, the record of *E. (A.) neogaeus* in marine sediments from the Last Interglacial set the base of the biozone in 0.13 Ma (Cione and Tonni, 1999) or alternatively to MIS 3 (Tonni et al., 2010). Within the fauna of the Guerrero Member, the taxa found are characteristic from arid and cold climatic conditions and associated to the Last Glacial Maximum (Tonni and Fidalgo, 1978). The upper Lujanian Stage/Age corresponds to the lower level from La Postrera Formation in Buenos Aires province, accumulated over 10.7 ± 0.9 ^{14}C BP and 8.4 ± 0.2 ^{14}C BP. The mammals recovered are similar to those from the Guerrero Member fauna, including the last record of megaherbivores heavier than 1 tonne and typical species associations from the Patagonic and Central areas of Argentina (e.g., *Lyncodon patagonicus*, *Zaedyus pichyi* and *Dolichotis patagonum*).

In this framework, we recognized the fauna from the SAEF to be older than that characterizing the Lujanian Stage/Age in the Bonarian Pampean region. The fauna from the base of the SAEF is biostratigraphically relevant because it represents an assemblage associated to typical interglacial climatic conditions for the beginning of the Late Pleistocene. In addition, the faunistic composition from the middle levels exhibits a change marked by the lack of typical taxa from tropical environments, and the youngest limit of the uppermost stratigraphic levels from SAEF were dated to 60.93 ± 6.07 ky.

5.4. The record of MIS 5 continental fauna in Argentina

A molar (CICYTTP-PV-M-2-406) of *Eira barbara* (Carnivora: Mustelidae) was recorded in the Ensenada creek locality, but no accurate stratigraphic context could be obtained. Taking into account the taphonomic characteristics of the specimen, it is probable that it comes from the SAEF; however, this should be confirmed with new findings. In this case, the record of *E. barbara* would bring more evidence in favor of the extant taxa found in the Late Pleistocene of the southwestern Entre Ríos province and linked to tropical and subtropical rainforests.

Apart from the lower and middle levels of the SAEF, another unit linked to MIS 5 in Entre Ríos province is El Palmar Formation (EPF) dated 80.7 ± 13.4 and 88.4 ± 35.7 ky (Iriondo, 1980; Iriondo and Kröhling, 2008). A mammalian association typical of the Late Pleistocene, including xenarthrans, litopterns, notoungulates, proboscideans, deers and horses, to which the record of *T. terrestris* (Ferrero et al., 2007) is added, was recovered from EPF. In contrast with SAEF, the only taxon in EPF linked to tropical and subtropical areas is *T. terrestris*. As the richness in EPF is lower than that of the SAEF, the bias in the fossil record makes it difficult to compare the richness of these units.

Micromammals with tropical affinities were described for Constitución (southeastern Buenos Aires province), a continental sequence in the Atlantic marine cliffs. They were identified to be an interglacial association based on stratigraphic, magnetostratigraphic, and mainly faunistic evidences, but without absolute chronological data (Pardiñas et al., 2004). Other mammal association coming from Centinela del Mar (southeastern Buenos Aires Province), ca. 70 km SSW of Constitución, was suggested to be related to sediments from the Interglacial Sangamonian (Isla et al., 2000). These sediments were dated ca. 90 ky (Isla et al., 2000), what would indicate a correlation to MIS5 a or c. However, the record of taxa does not indicate a tropical environment. These results agree with the geochronological data and environmental characterization of the faunal assemblage from the SAEF SS2. Accordingly, Lujanian continental vertebrates were recorded (Tonni, 2009) in offshore deposits from Pascua Formation (Fidalgo et al., 1973).

5.5. Chronostratigraphic implications

The Last Interglacial period, Marine Isotope Stage (MIS) 5e, was characterized by global mean surface temperatures that were at least 2 °C warmer than present (Rohling et al., 2008). A global sea level peak of at least 6.6 m higher than today during the Last Interglacial, was estimated from a compilation of local sea level indicators and a statistical approach (Kopp et al., 2009). Geomorphologic and morphostratigraphic data and uranium–thorium (U/Th) ages from numerous worldwide sites reveal the relative movements of sea level during the peak of the Last Interglaciation (MIS 5e), assumed average duration between 130 ± 2 and 119 ± 2 ky (Hearty et al., 2007). These authors inferred a brief period of instability (~120 ky) characterized by a rapid rise to between +6 to +9 m and an apparently rapid descent of sea level into MIS 5d after 119 ky.

In the Southern Hemisphere, the deep-sea benthic oxygen-18 record and the δD_{ice} in East Antarctica (European Project for Ice Coring in Antarctica: EPICA) allowed the inference that the change in surface temperature (ΔT_s) range, was +4.5 °C for the warmest of MIS 5.5 (Jouzel et al., 2007).

In the Atlantic coast of Argentina, the Late Pleistocene transgression was inferred from fragmented expositions in the littoral of Buenos Aires province (Schnack, et al. 2005). The corresponding deposits assigned to the Puente de Pascua Formation, were interpreted as being from littoral and estuary environments (Fucks et al., 2010). Unfortunately, this record lacks of a solid geochronological control. Scarce correlations of these littoral deposits with the continental record have been established for the Buenos Aires province (Tófalo et al., 2011; Toledo et al., 2014).

The geochronological data from the SAEF suggests that these continental deposits from Entre Ríos province can be correlated with MIS 5. Particularly, there would be a correspondence between the sequence having vertebrate taxa with subtropical/tropical affinities and an age ca 120 ky, with the maximum peak of the Last Interglacial stage (MIS 5e). Morphostratigraphic and sequence analyses support this statement (Brunetto et al., 2015). However, more numeric ages will be necessary in order to test the current pattern.

Taking into consideration the lack of a good site as a reference of the base of Lujanian stage, we consider the SAEF section is the best place up to now reported, where the basal limit of Late Pleistocene is exposed. The use of Lujanian stage has been very extensive in southern South America as the chronostratigraphic reference for the complete Late Pleistocene, despite not having a representative type section. Furthermore, the biostratigraphic concept of the Lujanian age based on vertebrate fossils has not been an unequivocal reference of regional environmental changes for this part of the world. The finding of a distinctive tropical faunal assemblage and the correlation of the containing sediments with the Southern Hemisphere peak of MIS 5e, make SAEF (120–60 ky) an excellent chronostratigraphic reference for the Late Pleistocene of the continental record in southern South America.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.palaeo.2016.11.017.

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