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ORIGINAL PAPER

Mammals in Last 30 to 7 ka Interval (Late Pleistocene-Early Holocene) in Southern Uruguay (Santa Lucía River Basin): Last Occurrences, Climate, and Biogeography

Martín Ubilla[1] · **Andrés Rinderknecht**[1,2] · **Andrea Corona**[1] · **Daniel Perea**[1]

Abstract Fossiliferous Quaternary sedimentary beds in the Santa Lucía Basin (southern Uruguay) are potentially useful for the study of the last occurrences of extinct taxa, as well as the environmental and climatic patterns in the late Pleistocene to the early Holocene. They have provided a chronological framework (AMS ^{14}C and Optically Stimulated Luminescence dates), a mammalian diversity and interpretations of last occurrence, the climatic-environmental setting, and some associated biogeographic processes. The ages produced encompass the last 30 to 7 ka interval (latest Pleistocene-early Holocene). The mammalian assemblage (36 genera, 24 species) includes typical South American late Pleistocene mammals, extinct species of extant genera, and some extant species that still exist elsewhere on the continent. The preservation pattern includes articulated and semi-articulated skeletons of large and small mammals. The presence in the southern Uruguayan Pampean area of some mammals currently inhabiting Patagonia, northwest and central Argentina (*Dolichotis*, *Galea*, *Microcavia*, *Chaetophractus*, *Lagostomus*, and *Vicugna*) is explained by the predominance of open areas and cold climates associated with the Last Glacial Maximum. The mammalian record depicts local extinctions or shifting ranges occurring in latest Pleistocene or early Holocene. The sedimentary chronological framework and taphonomic features suggest the persistence into the early Holocene of *Eutatus seguini*, *Morenelaphus brachyceros*, *Equus neogeus*, *Hemiauchenia* sp., *Lama* sp., and *Vicugna* sp. *Glyptodon* and *Glossotherium* seem to persist at least to the latest Pleistocene. This pattern can substantiate the hypothesis that some megafauna and large mammals persisted for some millennia alongside people with extinction occurring before, during, and after human colonization.

Keywords Late Pleistocene · Early Holocene · Uruguay · Mammals

Abbreviations

AA	NSF-Arizona AMS Laboratory, USA
AMS	Accelerator Mass Spectrometry
BETA	Beta Analytic: radiocarbon dating, Miami AMS lab, USA
LP	LATYR Laboratorio de Radiocarbono, Centro de Investigaciones Geológicas, La Plata, Argentina
OSL	Optically Stimulated Luminescence
UIC	Luminescence Dating Research Laboratory of the University of Illinois, USA

Introduction

According to ice core studies performed in the Antarctic area, the last glacial cycle experienced millennial-scale alternating climatic episodes, lesser-marked than those in the Northern Hemisphere, along with warm peaks identified as the Antarctic Isotopic Maximum (AIM) (Blunier and Brook 2001; EPICA 2006; Jouzel et al. 2007; Buiron et al. 2012; Bradley 2015). The Last Glacial Maximum (LGM) related to the Marine Isotopic Stage 2 (ca. 27 to 11.7 ka) was associated with severe

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✉ Martín Ubilla
martinubilla@gmail.com

[1] Departamento Paleontología, ICG, Facultad de Ciencias, Udelar, Iguá 4225, 11400 Montevideo, Uruguay

[2] Paleontología, Museo Nacional de Historia Natural de Montevideo, 25 de mayo 582, 11000 Montevideo, Uruguay

global temperature declination and marine regression (ca. 120 to 130 m below current sea level) (Murray-Wallace and Woodroofe 2015; Lowe and Walker 2015). In the Argentinian and southern Uruguayan Pampean areas, the LGM favored the presence of mammalian taxa adapted to cold and arid conditions, whereas these species are currently mainly distributed in Patagonia and central Argentina (Tonni et al. 1999; Ubilla and Rinderknecht 2014, 2016; Cione et al. 2015).

In the Southern Hemisphere, the LGM was followed by a long-term warming from 18 ka to the Holocene. This trend was interrupted by ca. 1700 years of temperature decline between ca. 14.4 to 12.7 ka and was recognized as the Antarctic Cold Reversal period (ACR) (Jouzel et al. 1995; Orombelli et al. 2010; WAIS 2015 and references therein). There is evidence that following this cold episode, a rapid warming occurred after 12.7 ka (AIM 1) with one or two peaks around 11.5 (Orombelli et al. 2010; WAIS 2015; Lowe and Walker 2015). In Patagonia, after the ACR and during the warming phase ca. 12 ka, various mammalian taxa, including some representatives of megafauna, went extinct (Metcalf et al. 2016). However, in the Argentinian Pampas, some mammalian taxa that are currently extinct persisted into the early Holocene (Barnosky and Lindsey 2010; Prates et al. 2013; Prado et al. 2015; Barnosky et al. 2016).

Fossiliferous Quaternary sedimentary beds occur in the Santa Lucía Basin (southern Uruguay) and are potentially useful for the study of the last occurrences of extinct taxa, as well as the environmental and climatic patterns in the late Pleistocene to the early Holocene (Fig. 1). In the XIX century and first half of the XX century, few mammals including some representatives of the megafauna (*Glyptodon* sp., *Megatherium americanum* Cuvier, 1796, *Macrauchenia* sp., *Glossotherium* sp., *Lama gracilis* Gervais and Ameghino, 1880, *Toxodon* sp., and *Doedicurus* sp.) and few freshwater mollusks were referred from this area (Vilardebó and Berro 1838; Devincenzi 1927; Kraglievich 1937; Jones 1956; Méndez-Alzola 1950). Recently, knowledge of the fossil content and stratigraphic units has increased (Spoturno et al. 2004, 2013; Ubilla et al. 2009; Ubilla and Martínez 2016 and references therein). However, a detailed taxonomic update linked to a more precise chronological framework is necessary.

This contribution provides: a) a chronological framework of fossiliferous beds (the last 30 to 7 ka interval based on radiocarbon and optically stimulated luminescence ages), b) a mammalian diversity summary highlighting the most significant records and interpretations of last occurrence of mammals (in particular mega and large mammals), and c) the climatic and environmental setting involved and some associated biogeographic processes.

Fig. 1 **a-b**, geographic locations of Quaternary beds in the Santa Lucía River basin and ^{14}C and OSL dating; **c**, close-up of samples for OSL dating on the Pilatos creek. **CA**: Paso Barrancas, **CB**: Paso Cuello, **CC**: Paso Pache, **CD**: Vejigas creek; **CE-G**: Pilatos creek

Geographic and Geological Setting

The sedimentary beds analyzed in this study are located in the Santa Lucía River basin, in southern Uruguay. In this area, the fossiliferous outcrops appear on the Santa Lucía River side, which is the principal watercourse in the region. Outcrops also appear in various secondary watercourses, the Vejigas, Pilatos, and Aparicio creeks (Fig. 1). This area is an agricultural region and the sediments offer a variety of economic uses. Because of the removal of the native riparian forests that has occurred over the last few decades, erosive processes occur along the side of the watercourses, allowing for the extraction of different fossil types, primarily mammals and woods.

The most common Quaternary strata (Online Resource 1) include the following sedimentary facies: orange to red fining up conglomerates; coarse to fine sandy beds; and occasionally thin paleosoils on the top. These beds are up to 13 m in height (including the subsurface) and exhibit horizontal stratification to tabular and sigmoidal cross-stratification with bars and channelized facies. They usually overlie Proterozoic, Cretaceous, or Tertiary beds. A meandering and anastomosed fluvial environment of deposition related to Quaternary episodes of the current Santa Lucía River system has been interpreted (Spoturno et al. 2004, 2013). The paleontological content is scarce, mostly restricted to few, but well-preserved, mammalian bones. In addition, there are facies up to 2–3 m high including light brown to green grayish sand, clayey silt and sandy silt with reworked loess occurring along with some paleosoils (Spoturno et al. 2004). There are also lenses of less than 1 m high with dark clay and fine to medium sand, predominantly green in color with fine parallel stratification (Online Resource 1). The paleontological content is rich and includes woods (many in living positions) (Online Resource 1), mammals, pollen into the lenses, and trace-fossils in paleosoils (de Oliveira et al. 2011; Corona et al. 2013; Verde et al. 2013; Ubilla and Rinderknecht 2014, 2016). The continental deposition was believed to be associated with gravitational and alluvial processes, including small lakes and ponds, under arid to semi-arid climate (Spoturno et al. 2004). In general, these beds overlie Tertiary units and the aforementioned conglomerates and sandy levels. However, these clastic facies occasionally intercalate or laterally substitute the clayey and sandy silt beds.

According to Spoturno et al. (2004, 2013), the conglomerates and sandy beds are the Barrancas Formation and the clayey and silty beds are the Dolores Formation (Online Resource 1). Following the stratigraphic criteria and mammalian biostratigraphic information, the Dolores Formation has been considered late Pleistocene in age (Ubilla et al. 2009).

Materials and Methods

The ^{14}C dates (conventional and AMS) were summarized from previous reports on wood, organic soil, bones, and teeth (Table 1). However, the calibrated ages provided here were calculated for this study, following Calib (2013) (http://calib.qub.ac.uk/calib/), and included the SHCal-13 option (Stuiver et al. 2013; Hogg et al. 2013). According to the aforementioned sedimentary features, these samples belong to the Dolores Formation. The OSL samples taken from the sandy and sandy silt levels belong to the Barrancas and Dolores formations (Table 2, Online Resource 2) and were collected following the lab requirements (http://www.uic.edu/labs/ldrl/). Most dated samples included in Table 1, and all samples included in Table 2, have GPS location data associated with them, but are not provided here to preclude fossiliferous sites depredation.

According to Barnosky and Lindsey (2010), last occurrences interpreted as survival of a taxon based on dates obtained directly from the specimen sample using AMS (bone, tooth, hair, etc.) are more confident. One AMS taxon date is provided here (Table 1; Ubilla and Rinderknecht 2016). Many previous efforts to obtain taxon date information from bones and teeth of large and megafauna have failed (*Glyptodon* bones, Meneghin personal communication; *Equus* and *Hemiauchenia* bones, Lindsey personal communication). Therefore, taphonomic features were considered to evaluate the possible reworking processes of the material. Taphonomic features are significant to interpret the last records of extinct taxa in this context. In this sense, the interpretation of the "last occurrence or record" in this work could not mean survival because dates were not obtained directly from bones or teeth, rather by the sedimentary context or surrounding wood. However, the indicated last occurrence of taxa could possibly indicate its last survival and more empirical studies should be conducted. Information available from the literature at the continental and regional scales is considered to evaluate the consistency of the results.

The mammal fossils belong to the Andrés Sanchez collection (San Ramón), Federico López Collection (Canelones), Paleontological Collection of the Museo Nacional de Historia Natural de Montevideo, and the Paleontological Collection of the Facultad de Ciencias. The updated taxonomic list (Table 3) follows Rego et al. (2007), Bostelmann et al. (2008), Ubilla et al. (2009), López Romanelli (2012), Corona et al. (2013), Ubilla and Rinderknecht (2014, 2016), and this paper. The pollen information included in the Discussion is from de Oliveira et al. (2011). The taxonomy of South American camelids lacks consensus, in particular regarding the extant and extinct relative medium to small laminii

Table 1 ^{14}C conventional and AMS^{+} ages from Quaternary beds of the Santa Lucía Basin (southern Uruguay)

Lab ID	Taxon Sample	Material	Sample Location	^{14}C age BP	Cal BP age 2S
Beta 289761^{+}	–	wood	Vejigas creek	**9,560 ± 60**[1]	**11,117–11,121**
Beta 289760^{+}	–	charcoal	Vejigas creek	**9,690 ± 60**[1]	**11,045–11,198**
Beta301006^{+}	–	organic soil	Paso Barrancas (Santa Lucía river)*	**10,140 ± 50**[2]	**11,857–11,960**
LP1110	*Salix humboldtiana*	wood	Paso Cuello (Santa Lucía river)*	**10,480 ± 105**[3]	**11,982–12,647**
LP1143	–	wood	Paso Pache (Santa Lucía river)	**10,500 ± 110**[3]	**11,992–12,656**
Beta283303^{+}	–	organic soil	Vejigas creek*	**10,550 ± 50**[1]	**12,383–12,649**
Beta 282856^{+}	*Phyllostylon rhamnoides*	wood	Vejigas creek*	**10,780 ± 80**[1]	**12,549–12,769**
LP1268	*Prosopis* sp.	wood	Vejigas creek	**11,090 ± 110**[4]	**12,722–13,090**
Beta 278336^{+}	*Gleditsia amorphoides*	wood	Vejigas creek	**11,222 ± 80**[1]	**12,811–13,203**
LP1283	–	wood	Paso Barrancas (Santa Lucía river)*	**11,150 ± 120**[4]	**12,725–13,169**
Beta 281079^{+}	–	organic soil	Vejigas creek	**11,770 ± 50**[1]	**13,657–13,715**
AA104910^{+}	*Lagostomus maximus*	bone	Pilatos creek**	**11,879 ± 95**[5]	**13,898–13,941**
AA91726^{+}	*Equus* sp.	enamel	Pilatos creek**	**21,530 ± 140**[6]	**25,525–26,037**
AA99845^{+}	Deer	enamel	Pilatos creek**	**22,450 ± 400**[7]	**25,934–27,436**

In bold are highlighted numeric values of dates obtained

*Beds with extinct mammals

** Beds with extinct and extant mammals in South America

[1] Meneghin (2016)

[2] Meneghin (2011)

[3] Ubilla (1999)

[4] Martínez and Ubilla (2004)

[5] Ubilla and Rinderknecht (2016)

[6] Ubilla and Martínez (2016)

[7] Ubilla and Rinderknecht (2014)

(Cajal et al. 2010 and references therein). Molecular studies support that the extinct *Lama gracilis* Gervais and Ameghino, 1880, is similar to the extant *Vicugna vicugna* (Molina, 1782) (Weinstock et al. 2009). On the contrary and based on molecular analysis, Metcalf et al. (2016) recognized *Lama gracilis* as the sister-taxon of *Vicugna vicugna*. At face value, the small laminii included in this paper are referred to as *Vicugna* sp. because they are morphologically indistinguishable from the extant taxon at the generic level. The datasets analyzed during the current study are available in the repository mentioned above and are available from the corresponding author on reasonable request.

Results

Chronology

The latest Pleistocene is substantiated by eight OSL samples and 12 calibrated radiocarbon ages and includes sedimentary beds referred to as the Dolores and Barrancas formations (Tables 1 and 2, Online Resource 1). In particular, the OSL samples ranging from 23 to 12 ka belong to the Barrancas Formation.

The early Holocene is supported by two radiocarbon and seven OSL ages (Tables 1 and 2). These samples also include sediments from the Barrancas Formation, and some were collected from beds underlying the Dolores Formation strata (in particular OSL 11,910 ± 1,040, 9,330 ± 670, and 8,760 ± 965 years) (Online Resource 1).

There is one radiocarbon age of 21,530 ± 140 year BP (cal BP 25,525–26,037) (enamel sample AA91726) based on reworked material from older beds. This sample belongs to a lens delimited by an underlying bed of OSL 12,855 ± 1,110 and 11,910 ± 1,040 years and by an overlying bed of OSL 8,760 ± 965 and 9,330 ± 670 years (Online Resource 1).

A radiocarbon age of 11,650 ± 130 year BP (cal BP 13,187 – 13,731) from the Río Negro department (southwestern Uruguay) (Ubilla 1999) and two OSL ages of 15,730 ± 925 and 16,070 ± 930 years from Colonia department (southwestern Uruguay) (Corona et al. 2013) were provided for the Dolores Formation and are congruent with the current results.

Mammal Content

As a result of the continuous fieldwork performed in the area, 36 genera and 24 species of mammals were identified (Table 3

Table 2 Optically Stimulated Luminescence (OSL) ages from Quaternary beds of the Santa Lucía Basin (southern Uruguay)

ID Lab	Sample	Sample Location	OSL Age (yr)
			Early Holocene
UIC3450	coarse sand	OSL 22 Paso Cuello*	**7,070** ± **520**
UIC2823	medium sand	OSL 1 Pilatos creek*	**8,760** ± **965**
UIC3067	medium sand	OSL 5 Pilatos creek*	**9,330** ± **670**
UIC3069	fine-medium sand	OSL 9 Pilatos creek	**>10,050**
UIC3052	medium-coarse sand	OSL 11 Vejigas creek	**10,570** ± **990**
UIC3044	fine-medium sand	OSL 2 Pilatos creek*	**10,925** ± **1,020**
UIC3333	fine sand	OSL 13 Santa Lucia river Viejo*	**11,620** ± **990**
UIC3460	medium sand	OSL 21 Pilatos creek	**11,910** ± **1,040**
			Late Pleistocene
UIC3045	medium sand	OSL 10 Vejigas creek	**12,270** ± **900**
UIC3326	medium sand	OSL 14 Pilatos creek*	**12,855** ± **1,110**
UIC3054	medium sand	OSL 8 Pilatos creek	**13,820** ± **1,050**
UIC3068	fine-medium sand	OSL 6 Pilatos creek	**17,090** ± **1,430**
UIC-3053	fine sand	OSL 7 Pilatos creek	**23,785** ± **2,990**
UIC-2822	fine sand	OSL 3 Pilatos creek*	**30,855** ± **2,370**[1]
UIC-2826	fine sand	OSL 4 Aparicio creek*	**31,160** ± **2,285**[1]
UIC-3302	silty sand	Aparicio creek*	**32,230** ± **2,640**[2]

In bold are highlighted numeric values of dates obtained

* Ages with mammal fossil content associated

[1] Ubilla and Rinderknecht (2014)

[2] Corona et al. (2013)

and references therein). This assemblage, aside from typical South American late Pleistocene mammals, included extinct species of extant genera and some extant species that still exist elsewhere on the continent. The preservation pattern included articulated and semi-articulated skeletons, usually very well preserved, of both large and small mammals (Corona et al. 2013; Ubilla and Rinderknecht 2014, 2016). Marks, likely produced by felid predators, were observed on a few bones.

Among xenarthrans, an almost complete skull of the ground-sloth *Mylodon darwini* Owen, 1839, from the late Pleistocene strata was found, the only skull of this taxon found in Uruguay. It is a rarely represented species in the Quaternary of Uruguay, only exemplified by a few fragmented materials (Mones and Francis 1973; Perea 2011; Fariña et al. 2013). In addition, remains of *Doedicurus* cf. *D. clavicaudatus* (Owen, 1847) (mandibles and osteoderms) were recovered, which is also a very rare xenarthran species from the Quaternary of Uruguay. The osteoderms were unearthed from beds of OSL 12,270 ± 900 years; however, the possibility of reworking should not be disregarded (Online Resource 1). In the Argentinian Pampa, the last occurrence of this species was verified from archaeological sites from the interval 11 to 7.5 ka (Barnosky and Lindsey 2010; Prado et al. 2015 and references therein). Both genera are notably absent from the rich paleontological levels of the late Pleistocene Sopas Formation in northern Uruguay, which encompass more than 45 genera (Ubilla et al. 2016). The rareness of these species may be related to its solitary behavior or very small populations. The ground-sloth *Glossotherium robustum* (Owen, 1842) was found in beds with radiocarbon ages of 10,140 ± 50 year BP (cal BP 11,857–11,960). This megamammal has been registered at archaeological sites in the Argentinian Pampa over the ^{14}C 11–10 ka (cal BP 12,800–11,400) interval (Prates et al. 2013; Prado et al. 2015). Barnosky and Lindsey (2010) indicated that the last occurrence of the species in South America was likely between cal BP 12,400 and 11,900.

Glyptodon clavipes Owen, 1839, was recovered from beds overlying strata of OSL 8760 ± 965 and 9330 ± 670 years (osteoderms), in beds of 10,480 ± 180 year BP (cal BP 11,982–12,647) (wood associated with most part of carapace; Online Resource 1) and 10,550 ± 50 year BP (cal BP 12,383–12,649) (organic soil below an almost complete carapace and caudal tube, Meneghin 2016). It should be stressed that the osteoderms could have been reworked from older beds. *Glyptodon* sp. has been recorded at archaeological sites in the ^{14}C 11–10 ka (cal BP 12,800–11,400) interval in the Argentinian Pampa (Prates et al. 2013) as well from northern Uruguay in Pay Paso 1 cal BP 11,081 and 9093 (Suárez 2015a, b, 2016). This taxon occurred in the sedimentary beds of 12,502 ± 55 years BP (cal BP 14,234–15,001) in northern Uruguay (Sopas Formation, Rio Negro Department) (Ubilla and Martinez 2016). In Brazil, this species has been found in beds with non-calibrated radiocarbon ages of 8 to 6 ka (Faure et al. 1999; Turkey 2009). Nevertheless, until dates based on

Table 3 Mammals of Quaternary sedimentary beds of the Santa Lucía river Basin (southern Uruguay) and ages of the sedimentary context

TAXA	NUMERICAL AGES
XENARTHRA	
Catonyx cuvieri	OSL 32,230 ± 2,640; OSL 31,160 ± 2,285
Catonyx tarijensis	
Mylodon darwini	
Glossotherium robustum	^{14}C 11,150 ± 120 (cal 12,725–13,169); ^{14}C 10,140 ± 50 (cal 11,857–11,960)
Megatherium americanum	
Propraopus sp.	
Pampatherium typum	
Eutatus seguini	OSL 8,760 ± 965; OSL 9,330 ± 670
Chaetophractus villosus	
Glyptodon clavipes	OSL 8,760 ± 965; OSL 9,330 ± 670; ^{14}C 10.480 +/− 100 (cal 11,982–12,647)
Panochthus tuberculatus	
Doedicurus clavicaudatus	OSL 12,270 ± 900
Neuryurus cf. *N. rudis*	
RODENTIA	
cf. *Holochilus*	
Cavia sp.	
Galea ortodonta	OSL 30,855 ± 2,370
Microcavia criolloensis	OSL 30,855 ± 2,370
Dolichotis cf. *D. patagonum*	OSL 8,760 ± 965; OSL 11,910 ± 1,040
Hydrochoerus sp.	
*Lagostomus maximus**	^{14}C 11,879 ± 95 (cal 13,898–13,941)
Myocastor sp.	
CARNIVORA	
Dusicyon sp.	
Arctotherium cf. *A. tarijensis*	
Smilodon populator	
PERISSODACTYLA	
Equus cf. *E.*(*A.*) *neogeus*	OSL 11,910 ± 1,040; ^{14}C 10,480 ± 105 (cal 11,982–12,647)
Hippidion sp.	
ARTIODACTYLA	
Tayassu cf. *T. pecari*	OSL 30,855 ± 2,370
cf. *Catagonus*	
Morenelaphus brachyceros	^{14}C 11,150 ± 120 (cal 12,725–13,169); ^{14}C 10,140 ± 50 (cal 11,857–11,960)
Morenelaphus sp.	OSL 10,925 ± 1,020; OSL 8,760 ± 965
Antifer ultra	
Hemiauchenia sp.	OSL 11,620 ± 990
Lama sp.	OSL 8,760 ± 965; OSL 9,330 ± 670
Vicugna sp.	OSL 10,925 ± 1,020; OSL 8,760 ± 965
PROBOSCIDEA	
Notiomastodon sp.	
NOTOUNGULATA	
Toxodon platensis	
LITOPTERNA	
Macrauchenia patachonica	
cf. *Neolicaphrium*	

* Taxon-date. See explanation in text

bones are available, Barnosky and Lindsey (2010) estimated a last appearance earlier than 18 ka for *Glyptodon* in South America. The giant armadillo *Eutatus seguini* Gervais, 1867, occurs in beds overlying those with OSL ages between 8760 ± 965 and 9330 ± 670 years (Online Resource 1). This matches with the information provided by archaeological evidence from Argentina. In the Argentinian Pampa area, this large armadillo persisted into the early Holocene (10 to 7 ka) at many sites (Mazzanti and Quintana 1997; Prates et al. 2013; Prado et al. 2015; Cione et al. 2015). *Chaetophractus villosus* (Desmarest, 1804) is the only extant xenarthran registered in the late Pleistocene beds of Santa Lucía Basin and currently lives outside of Uruguay. Recently, Francia and Ciancio (2013) described the occurrence of *C. villosus* in the late Pleistocene in Corrientes (Argentina) in older beds referred to the MIS-3 interval of time.

All rodents found belong to extant genera and four of them occur elsewhere in South America today (*Galea*, *Microcavia*, *Dolichotis*, and *Lagostomus*). The record of *Dolichotis* cf. *D. patagonum* (Zimmermann, 1780) in early Holocene beds should be taken with caution, because this record is based on a fragmented skull that could have been reworked from older beds (Table 3; Online Resource 1) (Ubilla et al. 2009). Both caviine species, *Galea ortodonta* Ubilla and Rinderknecht, 2001, and *Microcavia criolloensis* Ubilla et al., 1999, are represented by articulated and well-preserved skeletons (Ubilla 2008; Ubilla and Rinderknecth 2014). Notably, remains of lagostomines are frequent and in one particular instance, an almost complete articulated skeleton of *Lagostomus maximus* (Desmarest, 1817) was found with a taxon-date of cal BP 13,982–13,941, suggesting the last appearance of this taxon in this area (Ubilla and Rinderknecht 2016).

Horse genera (*Equus* and *Hippidion*) are also common in these beds. Records of *Equus* cf. *E.* (*A.*) *neogeus* Lund, 1840 (almost complete skull) were collected from sediments with OSL 11,910 ± 1040 years and radiocarbon 10,480 ± 180 year (cal BP 11,982–12,647) (wood; Online Resource 1). In the Argentinian Pampa, the last occurrence is in the ^{14}C 11–10 ka (cal BP 12,800–11,400) interval (Prates et al. 2013). Steele and Politis (2009) and Prado et al. (2015) interpreted a window for *Equus* restricted to the 13–10 ka interval in the Pampean region. *Equus* sp. is found in cal BP 11,081 and 9093 and cal 12,802 and 12,470 at the Pay Paso 1 archaeological site of northern Uruguay (Suárez 2015a, b, 2016). In Brazil, it is found in beds with non-calibrated radiocarbon ages of 8 to 6 ka (Faure et al. 1999; Turkey 2009). Barnosky and Lindsey (2010) proposed the last occurrence of *Equus* on the continental scale between 12.4 and 11.9 ka.

Laminii are frequently found in outcrops and include large extinct taxa (*Hemiauchenia* Gervais and Ameghino, 1880) and medium to small specimens similar to guanaco and vicugnas *s.l.*, taxa extant elsewhere in South America. An articulated and well-preserved skeleton of a juvenile of *Hemiauchenia* was found in OSL 11,620 ± 990 years bed. *Vicugna* sp. was found in an OSL 10,925 ± 1,020 years bed and in strata with ages between OSL 8,760 ± 965 and 12,855 ± 1,110 years, which yields material similar to *Lama* sp. (Online Resource 1). According to Prates et al. (2013), *Hemiauchenia* and a small laminii identified as *Lama gracilis* Gervais and Ameghino, 1880, occurred in the ^{14}C 11–10 ka (cal BP. 12,800–11,400) interval in the Pampean area. Metcalf et al. (2015) calibrated the extinction of *Lama gracilis* in Patagonia at approximately 12 ka. Deer were relatively frequent in the beds and in particular *Morenelaphus brachyceros* (Gervais and Ameghino, 1880) (complete antlers) was found in the sedimentary context of 10,140 ± 50 year BP (cal BP 11,857–11,960), *Morenelaphus* sp. in OSL 10,925 ± 1,020 years and in beds overlying strata with OSL ages between 8,760 ± 965 and 9,330 ± 670 years (Online Resource 1). There is little evidence available in literature regarding the last occurrence of this taxon along the late Pleistocene-early Holocene boundary.

In late Pleistocene strata, a complete skull of *Arctotherium* cf. *A. tarijense* Ameghino, 1902, is under evaluation. The Tremarctinae bear was also found in radiocarbon beds of 11,650 ± 130 year BP (cal BP 13,187–13,731) (Dolores Formation, Río Negro department, southwestern Uruguay) (Ubilla 1999; Ubilla and Perea 1999). At the southernmost South American sites (Chile, Cueva Chimbúes, and Cueva del Puma), bones of *Arctotherium* provided non-calibrated radiocarbon taxon dates of 11 to 10 ka (Soibelzon et al. 2005; Prevosti and Martin 2013). Metcalf et al. (2015) estimated that the extinction of *Arctotherium* in Patagonia occurred approximately in the 12 ka.

Discussion and Conclusion

According to the ^{14}C and OSL ages produced, the Quaternary sedimentary beds of the Santa Lucía Basin roughly encompass the last 30 to 7 ka time interval (latest Pleistocene to the early Holocene). As there are no stratigraphic alterations, this chronological framework is considered reliable at face value. However, as previously mentioned, there is one radiocarbon dating more reasonably considered as reworked sample. The geological mapping of the area (Spoturno et al. 2004, 2013) revealed that the Barrancas Formation is putatively considered a Quaternary sensu lato unit. The set of ages includes the first numerical ages (OSL) for the sedimentary facies of this formation. In addition, a larger sample of dates than previously reported for the Dolores Formation is included. In the numerical set, some ages are around the late Pleistocene/early Holocene boundary and, in fact, sedimentary facies of both lithostratigraphic units reach the early Holocene.

At the regional scale, the late Pleistocene of Argentinian Pampas of Buenos Aires Province was dominated by a dry climate and arid conditions (Prado et al. 2015 and references). A sub-humid to cold-temperate and dry climate was described for the interval 30 to 11 ka in eastern Argentinian Pampean area (Blasi et al. 2010). Palynological records indicate dry to semiarid conditions in the 16 to 12 cal interval and a change to a sub-humid to humid climate during the Pleistocene-Holocene transition and early Holocene (Tonello and Prieto 2010). Concomitantly, mammals adapted to cold, dry climates and open to semi-open habitats inhabited the Argentinian Pampean area during LGM (Tonni et al. 1999; Cione et al. 2015).

The mammalian record, and other associated information found in the Santa Lucía beds, includes taxa reflecting the possible effect of last phases of the MIS-3 but particularly the LGM. It is in part congruent with the pattern observed in the Argentinian Pampas. The presence of some mammals currently inhabiting Patagonia, northwestern and central Argentina, and the southern Uruguayan Pampean area is explained by the predominance of cold climates associated with open areas promoted in particular under the last phases of MIS-3 and especially by the LGM. In particular, *Chaetophractus villosus*, *Galea*, *Microcavia*, *Dolichotis* cf. *D. patachonica*, *Lagostomus maximus*, and *Vicugna* sp. are widespread elsewhere in South America in areas of open grasslands and arid to semiarid climates (Soibelzon et al. 2013; Patton et al. 2015; Cione et al. 2015). Some extinct mammals such as glyptodonts, *Equus* (*A.*) *neogeus*, and *Macrauchenia*, are usually linked to open environments. The record of capybaras (*Hydrochoerus* sp.) and coypus (*Myocastor* sp.) indicates the presence of watercourses (Patton et al. 2015). Although, *Tayassu pecari* (Link, 1795) is well adapted to the tropical and subtropical rainforest, it can be present in arid environments such as savannas and the Chaco forest near watercourses (Gasparini et al. 2014). The palynological record comes from greenish argillaceous and sandy lenses mostly aging with the post ACR interval (four sites with radiocarbon encompassing the 13 to 11.9 cal interval and one site delimited between OSL 12 and 8 ka) (Fig. 2). The composition of the lenses suggests the dominance of herbs (with trees and shrubs scarce) and the presence of water bodies probably related to abandoned paleochannels (de Oliveira et al. 2011). The presence of *Salix humboldtiana* indicates water bodies and *Prosopis* is adapted to live in arid to semi-arid soils. The mammalian fauna found in this study concurs with this pattern.

According to the current geographic distribution of some extant genera of mammals in South America, the record in the aforementioned assemblage indicates that local extinctions or shifting range occurred in latest Pleistocene or early Holocene (Soibelzon et al. 2013; Ubilla and Rinderknecht 2014, 2016, and references therein). Barnosky and Lindsey (2010) proposed that taxon-dates, among other information, are required to establish a more confident linkage between the last occurrences and survival. The taxon-date of cal BP 13,898–13,941 of *Lagostomus maximus* concurs with the ACR (14.4 to 12.7 ka) and was interpreted as the last occurrence of this taxon in this area (Table 3; Fig. 2) (Ubilla and Rinderknecht 2016). The incorporation of *L. maximus* from the Argentinian Pampas was probably facilitated, if not before, by the aforementioned lower sea level in LGM. The severe sea level retraction significantly reduced the Rio de la Plata estuary and Uruguay River system, thereby connecting lands currently

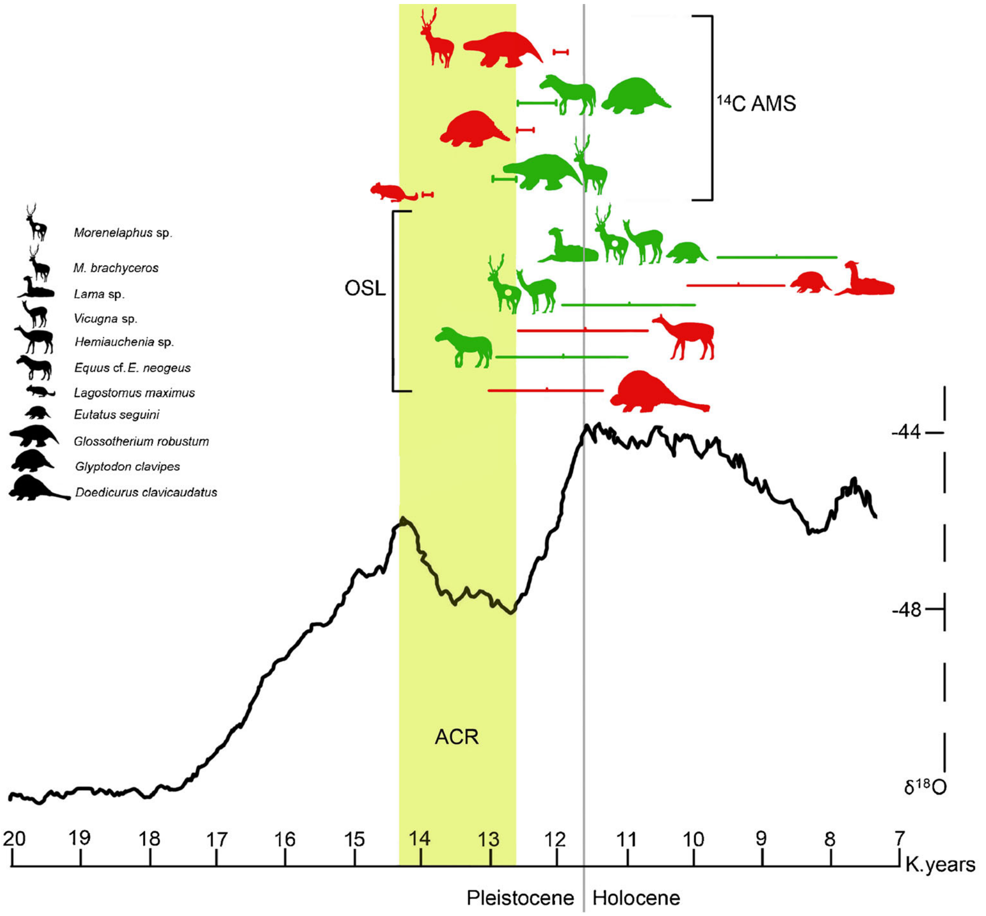

Fig. 2 Last records of mammals in late Pleistocene to early Holocene in Santa Lucía Basin, southern Uruguay. AMS ^{14}C cal age and OSL age ranges and taxa recorded are depicted. AMS ^{14}C cal age taxon-date of *L. maximus* is included. The Antarctic isotopic curve modified from Matrat et al. (2014). ACR: Antarctic Cold Reversal. Colors in taxon silhouettes are for aesthetic purposes

segregated (Violante and Parker 1999; Ubilla and Rinderknecht 2016 and references therein). *Lagostomus maximus* is absent in Holocene archaeological sites from Uruguay and its disappearances from this country, in fact, is better explained by the climatic amelioration posterior to the ACR, particularly in the early Holocene (Fig. 2). This could also be the case of the disappearance of the genera *Microcavia* and *Galea* but not for the genus *Cavia*, which persists in current mammalian communities (Ubilla and Rinderknecht 2014). The co-occurrence of these three genera of cavine requires further explanation.

Although no additional taxon-date is yet available, the sedimentary chronological framework and taphonomic features of the fossil record (articulated material such as almost complete skeletons, a complete carapace associated with caudal tube, very well-preserved skulls, etc.) allow us to take at face value the persistence into the early Holocene in southern Uruguay of the following taxa: *Eutatus seguini*, *Morenelaphus brachyceros*, *Equus* (*A.*) *neogeus*, *Hemiauchenia* sp., *Lama* sp., and *Vicugna* sp. (Table 3; Fig. 2). *Glyptodon* and *Glossotherium* seem to persist at least to the latest Pleistocene (Table 3; Fig. 2). According to Suárez (2015a, b, 2016), both *Equus* and *Glyptodon* are registered in the early Holocene in northern Uruguay. It is an expected pattern considering the many Argentinian sites in the Pampas with evidence of persistence into the 11–10 ka period or later (Pratt et al. 2013; Prado et al. 2015). According to our dates, the estimation of the last appearance of *Glyptodon* of no earlier than 18 ka (Barnosky and Lindsey 2010) seems to be unrealistic.

Finally, it should be noted that no human evidence was found in the outcrops. However, lithic artifacts related to the paleoindians were previously found in the area, especially in the Vejigas and Pilatos creeks (Meneghin 2016 and references therein). Except for one (López Romanelli 2012), these artifacts lack stratigraphic context and are considered to be reworked. According to regional evidence, early human colonization in the Pampean region occurred ca. 12 ka (Prates et al. 2013; Suárez 2016). If the faunal records related to latest Pleistocene and early Holocene in southern Uruguay are in fact evidence of extinction in the area, they should be considered to substantiate the hypothesis that some megafauna and large mammals persisted for some millennia alongside people, with extinction occurring before, during, and after human colonization (Prado et al. 2015 and references therein). The proposal that environmental changes associated with climate and collateral human influence could be the trigger of faunal extinctions, rather than the proposal of the overkill hypothesis

(Barnosky and Lindsey 2010; Cione et al. 2015; Prado et al. 2015).

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