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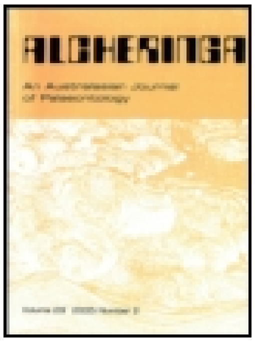

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Lagostomus maximus (Desmarest) (Rodentia, Chinchillidae), the extant plains vizcacha in the Late Pleistocene of Uruguay

MARTÍN UBILLA and ANDRÉS RINDERKNECHT

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The extant plains vizcacha, *Lagostomus maximus*, is described from the Late Pleistocene (Dolores Formation) of Uruguay based on an almost complete articulated skeleton. It is compared with the nominally extinct Pleistocene species of the genus. An AMS ^{14}C taxon-age is determined for *L. maximus* at 11 879 ± 95 years BP (cal. BP 13 898–13 941). *Lagostomus maximus* is absent from modern mammal communities in Uruguay, and no Holocene evidence is available. Because *L. maximus* exhibits remarkable sexual and ontogenetic dimorphism, we examined a range of juvenile, sub-adult and adult male and female specimens. It is not possible to differentiate the articulated Pleistocene fossil from sub-adult specimens of *L. maximus* based on this sample. Moreover, the skull characteristics, including a broad vertical ramus of the zygomatic arch, semi-circular temporal crest and short robust sagittal crest, most closely resemble extant female individuals. Molar size is non-predictive for ontogenetic stage or body mass because it reaches stability during early adulthood. Other fragmentary skull remains are herein assigned to *L.* sp. cf. *L. maximus*. *Lagostomus cavifrons* from the Pleistocene of Argentina is considered synonymous with *L. maximus*. Its character states concur with the range of intraspecific variability and it has been established on a young adult or adult male individual. Likewise, the other Argentinean Pleistocene species based on incomplete mandibles, *L. angustidens*, *L. striatus*, *L. heterogenidens*, *L. egenus*, *L. minimus* and *L. debilis*, concur with ontogenetic morphs and are here assigned to *Lagostomus* sp. The ecological preferences of extant *L. maximus* infer open arid or semi-arid landscapes for the latest Pleistocene of southern Uruguay. This hypothesis is reinforced by the coeval presence of *Microcavia*, *Galea* and small camelids in the same strata. The Last Glacial Maximum likely promoted this environmental setting. Latest Pleistocene or early Holocene climatic change might have facilitated local extinctions and/or range shifts among this mammal fauna.

Martín Ubilla [martinubilla@gmail.com], Facultad de Ciencias, Universidad de la Republica, Iguá 4225, 11400, Montevideo, Uruguay; Andrés Rinderknecht [apaleorinder@yahoo.com], Museo Nacional de Historia Natural, Paleontología, 11000, Montevideo, Uruguay. *Received 13.4.2015; revised 9.11.2015; accepted 12.1.2016.*

Key words: Pleistocene, *Lagostomus maximus*, Uruguay, taxon-age.

THE extant plains vizcacha, *Lagostomus maximus* (Desmarest, 1817), is a member of Chinchillidae, which according to current molecular studies is closely related to Dinomyidae (Huchon & Douzery 2001, Spotorno *et al*. 2004, Opazo 2005, Upham & Patterson 2012 and references therein) and first recorded in the Oligocene (Kramarz *et al*. 2013). The modern geographic distribution of *L. maximus* includes central and northern parts of Argentina (Llanos & Crespo 1952, Jackson *et al.* 1996, Ojeda & Bidau 2013a), southeastern Bolivia and southern Paraguay (Jackson *et al.* 1996, Anderson 1997, Morales 2007; Fig. 1). Examples of the Chinchillidae are recorded in Uruguay from the late Miocene (Francis & Mones 1965, 1966, Perea *et al*. 2013) until the group's final disappearance after the Late Pleistocene. It is absent from Uruguay today, but was reintroduced by farmers in 1889 in western Uruguay (Salto department) and exterminated by the government in 1920 after being declared noxious (Vaz-Ferreira 1969). *Lagostomus maximus* is gregarious and fossorial, being found primarily in subtropical humid to semi-arid grasslands and dry thorn to desert scrub (Llanos & Crespo 1952, Jackson *et al*. 1996, Patton *et al*. 2015). *Lagostomus maximus* is one of the most sexually dimorphic rodents, especially in relative body size (Llanos & Crespo 1952). Notable ontogenetic differences also exist between males and females (Llanos & Crespo 1952, Rasia *et al*. 2011).

The fossil record of *Lagostomus* (including the subgenus *Lagostomopsis*) extends from the late Miocene, but a species-level taxonomic review is necessary (Kerber *et al*. 2011, Rasia & Candela 2013, Patton *et al*. 2015 and references therein). Molecular clock estimates suggest divergence in the early or middle Miocene (Rowe *et al*. 2010, Upham & Patterson 2012). Remains of the extant *L. maximus* have been identified from the Middle to Upper Pleistocene and Holocene in Argentina, but much of this material is fragmentary (e.g., Tonni & Fidalgo 1982, Prado *et al*. 1987, Tonni *et al*. 1988, Gómez *et al*. 1999, Gutierrez & Martínez 2008, Politis & Messineo 2008, Quintana & Mazzanti 2011, Cruz 2013, Vezzosi 2014). *Lagostomus* is also a biostratigraphical marker of the Platan Stage/Age in Buenos Aires Province, Argentina (Cione & Tonni 1999, 2005). Mandibular elements of *L.* sp. cf.

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Fig. 1. Current geographic distribution of extant *Lagostomus maximus* (based on Llanos & Crespo 1952, Anderson 1997, Morales 2007, Jackson *et al*. 1996, Ojeda & Bidau 2013a) and the location of the Pleistocene specimen in Uruguay.

L. maximus have been found in Upper Pleistocene strata in southern Brazil (Kerber *et al*. 2011). Several Pleistocene species of *Lagostomus* were also described from Argentina based mostly on mandible components and other incomplete material (Burmeister 1866, Ameghino 1889, 1891a, b). In Uruguay, *Lagostomus* sp. has been reported from Pleistocene beds (Calcaterra 1972, Ubilla & Perea 1999), and Jones (1956) identified two incisors and a left femur as *Lagostomus maximus* from the Pleistocene 'Pampeana' Formation in Canelones Department. Unfortunately, these specimens could not be relocated for this study, thus, their taxonomic assignment can not be confirmed. *Lagostomus maximus* is absent from Holocene archaeological sites in Uruguay (Duran & Bracco 2000 and references therein).

This paper describes the first incontrovertible record of *Lagostomus maximus* in the Pleistocene of Uruguay, based on a well-preserved skeleton comprising the skull, mandible and partially articulated postcranial skeleton. An AMS ^{14}C taxon-age has also been determined, and a revision of other Pleistocene species is included along with a discussion of the palaeobiogeographical and palaeoenvironmental significance.

Material and methods

Institutional abbreviations. AA, NSF-Arizona AMS Laboratory, USA; BRA, Centro Investigaciones Paleontológicas San Ramón (Andrés Sánchez collection), San Ramón, Uruguay; NHMUK, Mammal Section, The Natural History Museum, London, UK; MACN-Ma, sección Mamíferos, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MACN-Pv, Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MACN-A, Ameghino collection, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MNHN, Museo Nacional de Historia Natural, Montevideo, Uruguay; MLP-M, Mastozoología, Museo de La Plata, La Plata, Argentina.

Measurements (Tables 1 and 2). Cranium and upper dentition: TL, total length; CBL, condylobasilar length; CBaL, condylobasal length; PL, palatal length; NL, nasal length; NW, nasal width; FL, frontal length; IC, interorbital constriction; PaL, parietal length; PaW, parietal width; BZW, zygomatic width; BMW, mastoid width; PW, palatal width; RW, rostral width; DL, upper diastema length; P4–M3L, upper check-teeth length; M1–M3L, upper molars length; ItW, upper incisor transverse width; ApIW, upper incisor anteroposterior width; Hsk, height of skull; P4L, upper P4 length; P4W, upper P4 width; M1, M2 and M3 L, upper molars length; M1, M2 and M3 W, upper molars width; UA, upper angle of tooth laminae with respect to sagittal plane. Mandible and lower dentition: tl, total length; dl, lower diastema length; p4hm, height of mandible at p4; condyhm, height of mandible at condyle; p4–m3l, lower check-teeth length; m1–m3l, lower molar series length; itw, lower incisor transverse width; atpw, lower incisor anteroposterior width; p4w, lower p4 width; m1, m2 and m3 l, lower molars length; m1, m2 and m3 w, lower molars width; La, lower angle of tooth laminae with respect to the sagittal plane (Fig. 2). Postcranium: TL, total length; PTW, proximal transverse width; TDW, transverse diaphysis width; DTW, distal transverse width; Appw, anteroposterior proximal width of humerus; Apdw, anteroposterior distal width of humerus; OPL, olecranon process length; DLH, deltoid length of humerus; Tfw, trochlear fossa width of humerus (Table 3).

The calibrated age of *L. maximus* was calculated using Calib 2013 and included the SHCal-13 option (Stuiver *et al*. 2013, Hogg *et al*. 2013). The specimens and quantitative comparisons of extant *Lagostomus maximus* are listed in the Online Supplementary Data 1–5. Because of marked sexual and ontogenetic dimorphism in this species (Llanos & Crespo 1952, Rasia *et al*. 2011, Rasia & Candela 2013), a segregated set of 35 male and 39 female individuals was compiled. Multiple ontogenetic stages (juvenile, sub-adult and adult) were also discriminated following Llanos & Crespo (1952) and Rasia *et al*. (2011), to accommodate for size variation and incremental modifications in the skull, especially the temporal and parietal crests and the vertical ramus of the zygomatic arch. The term 'young adult' is used herein to define specimens that have achieved adult-stage morphologies but are not yet fully grown. Our fossils from Uruguay (Figs 3–5, Online

	L. maximus		***L.* sp. cf. *L. maximus***		
	BRA-2-993	**BRA-3-933**	**BRA-879**	**BRA-958**	**BRA-547**
TL	104.6			88.5	
CBL	91.8			77.4c	
CBaL	92.9			79c	
PL	52.1		45.0	44c	
NL	46.2	40c	39c		
NW	20.5	18.3	16.7		
FL	33.2	31.6	29.0		
IC	30.0	28.2	26.6	24.6	
PaL	24.9				
PaW	38.3				
BZW	64.8	52.3	55.6		
BMW	42.4			39.8	
PW	26.	24.6	23c	24.7	
RW	23.4	20.0	17.0	19.7	
DL	31.4	27.9	26.0	27c	
P4-M3L	25.4	21.9	19.2	20.0	18.6
M1-M3L	19.0	16.8	14.9	15.1	
ItW	4.6	3.9	3.9	3.9	
ApIW	4.5	3.7	3.6	3.9	
Hsk	29.4	25.2	23.4	26.7	
P4L	4.5	4.3	3.6	4.1	
P4W	7.2	6.6	6.5	7.5	
M1L	4.4	4.2	3.9	3.8	3.4
M1W	7.5	6.7	6.7	7.5	6.2
M2L	4.3	4.9	3.8	4.5	
M2W	6.8	6.8	6.3	7.3	
M3L	9.2	7.8	7.4	6.6	
M3W	8.4	6.3	6.6	7.2	
UA	49°	56°	52°		

Table 1. measurements (mm) of skull and upper teeth of fossil material of *Lagostomus* from the Late Pleistocene of Uruguay. Abbreviations in Material and Methods.

	L. maximus	***L.* sp. cf. *L. maximus***	
	BRA-2-993	**BRA-961**	**BRA-2-713**
tl	92.1		
dl	20.5		
p4hm	17.3	14.8	
condyhm	34.5	27.0	
p4-m3l	26.0		19.7
m1-m3l	14.0		13.9
itw	4.3		4.5
atpw	4.5		
p4l	4.0		4.3
p4w	8.8		8.3
m1l	4.2	3.9	4.9
m1w	10.3	8.8	11.1
m2l	4.2	3.7	3.9
m2w	11.2	9.9	9.8
m3l	4.2		4.9
m3w	11.4		11.8
La	20°		

Table 2. Measurements (mm) of mandible and lower teeth of fossil material of *Lagostomus* from the Late Pleistocene of Uruguay. Abbreviations in Material and methods.

Supplementary Data 8) were also compared with the Pleistocene species (Online Supplementary Data 1): *Lagostomus angustidens* Burmeister, 1866, non-Moreno, 1888 (Late Pleistocene); *L. debilis* Ameghino, 1889 (Late Pleistocene); *L. minimus* Ameghino, 1889 (Middle Pleistocene); *L. heterogenidens* Ameghino, 1889 (Late Pleistocene); *L. egenus* Ameghino, 1891a (Pleistocene); *L. striatus* Ameghino, 1891b (Pleistocene); and *L. cavifrons* Ameghino, 1889 (Late Pleistocene). All of these nominal species are based on mandible components, except for *L. cavifrons*. We also examined *L. crassus* Thomas, 1910 considered an extinct species from Peru (Online Supplementary Data 1).

Anatomical terminology follows Cooper & Schiller (1975), Elissamburu & Vizcaíno (2004), Rose (2006) and Rasia & Candela (2013). Because the osteology of extant *L. maximus* is well documented, our description emphasizes contrasting characteristics of size, ontogeny and sex. Biplots (Fig. 6) and additional quantitative comparisons (Online Supplementary Data 9) were generated using PAST 2.17 (Hammer *et al.* 2012) (http://folk.uio.no/ohammer/past/). All measurements (Online Supplementary Data 2–7) were taken using a Digimatic-Mitutoyo digital caliper. The angle of tooth laminae with regard to the sagittal plane was measured following Rasia & Candela (2013). Functional indices were calculated according to Elissamburu & Vizcaíno (2004): EI (epicondyle index) for relative insertion area of the forearm muscles; IFA (fossorial ability index), measuring mechanical advantage relative to elbow

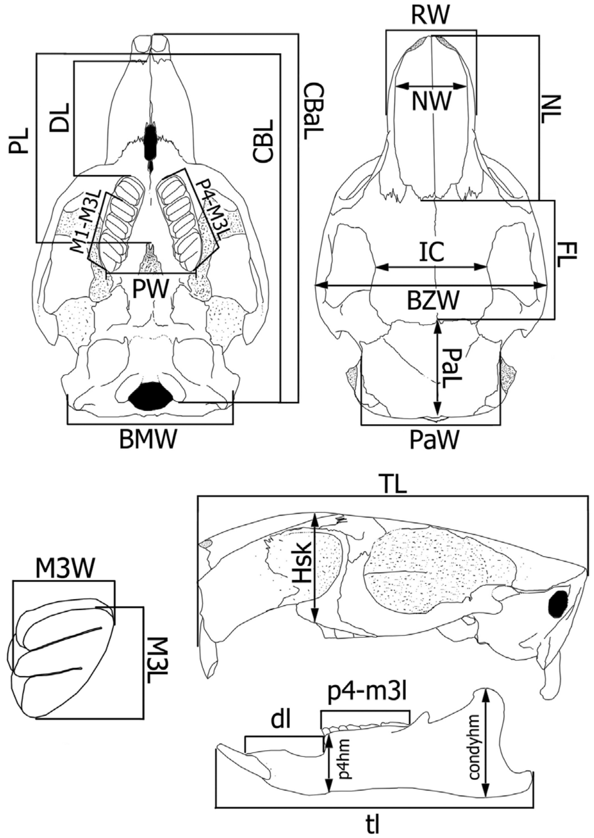

Fig. 2. Measurements used in the comparative study. Abbreviations in Material and methods.

	L. maximus BRA-2-993
Humerus	
TL	57.0
PTW	12.6
Appw	14.4
TDW	6.0
DTW	14.5
Tfw	7.5
Apdw	8.2
DLH	30.3
EI	25.4
SMI	53.15
Ulna	
TL	71.9c
OPL	15.8
TDW	4.1
IFA	27.9
Femur	
TL	87.0
PTW	22.2
TDW	8.8
DTW	16.8
Tibia	
TL	108.3
PTW	16c
TDW	8.8c
DTW	9.5

Table 3. Measurements (mm) of postcranial bones of fossil material of *Lagostomus maximus* from the Late Pleistocene of Uruguay. Abbreviations in Material and methods.

extension; and SMI (shoulder moment index), estimating mechanical advantage of muscles acting on the shoulder joint.

Geological setting

The material described here was collected from the Dolores Formation (Upper Pleistocene) exposed along the Pilatos (34°17′30.45″S, 55°55′57.16″W) and Aparicio Creek beds (34°16′12.23″S, 55°59′35.82″W) in the Santa Lucía River basin of southern Uruguay (Fig. 1; Online Supplementary Data 8). The Dolores Formation is a continental unit characterized by brown mudstones that include sandy layers (Spoturno *et al*. 2004). This unit is considered Late Pleistocene in age based on lithostratigraphical relationships, and correlates biostratigraphically with the Lujanian Stage/Age of the Buenos Aires Province (Late Pleistocene–early Holocene *sensu* Cione & Tonni 2005), using the key marker taxon *Equus neogeus* (Ubilla *et al*. 2009). Three optically stimulated luminescence dates taken along the base of the outcrops yield ranges from 31 160 ± 2 285 to 32 230 ± 2 640 years for Aparicio Creek, and 30 855 ± 2 370 years for Pilatos Creek (Corona *et al*. 2013, Ubilla & Rinderknecht 2014). An AMS ^{14}C date of 22 450 ± 400 years BP (cal. BP 25 934–27 436) was also obtained from overlying strata at Pilatos Creek (Ubilla & Rinderknecht 2014). A *Lagostomus maximus* taxon-age of 11 879 ± 95 years BP (cal. BP 13 898–13 941) was specifically calculated for this study (bone sample AA104910 from BRA-2-933, $^{\delta13}$C -9.9 and 2 sigma cal. BP). We consider this to be the last appearance datum (LAD) for *L. maximus* in this area. The associated mammal fauna is typical for the South American Late Pleistocene (Ubilla *et al*. 2009, Corona *et al*. 2013). Coeval occurrences of locally extinct modern taxa include *Microcavia*, *Galea*, *Dolichotis* sp. cf. *D. patagonum*, *Chaetophractus villosus* and *Vicugna* sp. (Rego *et al*. 2007, Ubilla 2008, Ubilla *et al*. 2009, Ubilla & Rinderknecht 2014).

Systematic palaeontology

Class MAMMALIA Linnaeus, 1758
Order RODENTIA Bowdich, 1821
Suborder HYSTRICOGNATHI Tullberg, 1899
Family CHINCHILLIDAE Bennet, 1833

Lagostomus Brookes, 1828

Lagostomus maximus (Desmarest, 1817)

Referred material. BRA-2-993: Largely articulated skeleton comprising cranium, left mandible, axis, atlas, three cervical vertebrae, scapulae, right humerus and ulna, left ulna, radius, ribs, right astragalus and left hind limb with femur, tibia, astragalus, calcaneus, tarsus, metatarsals and phalanges (Figs 3–5, Online Supplementary Data 8).

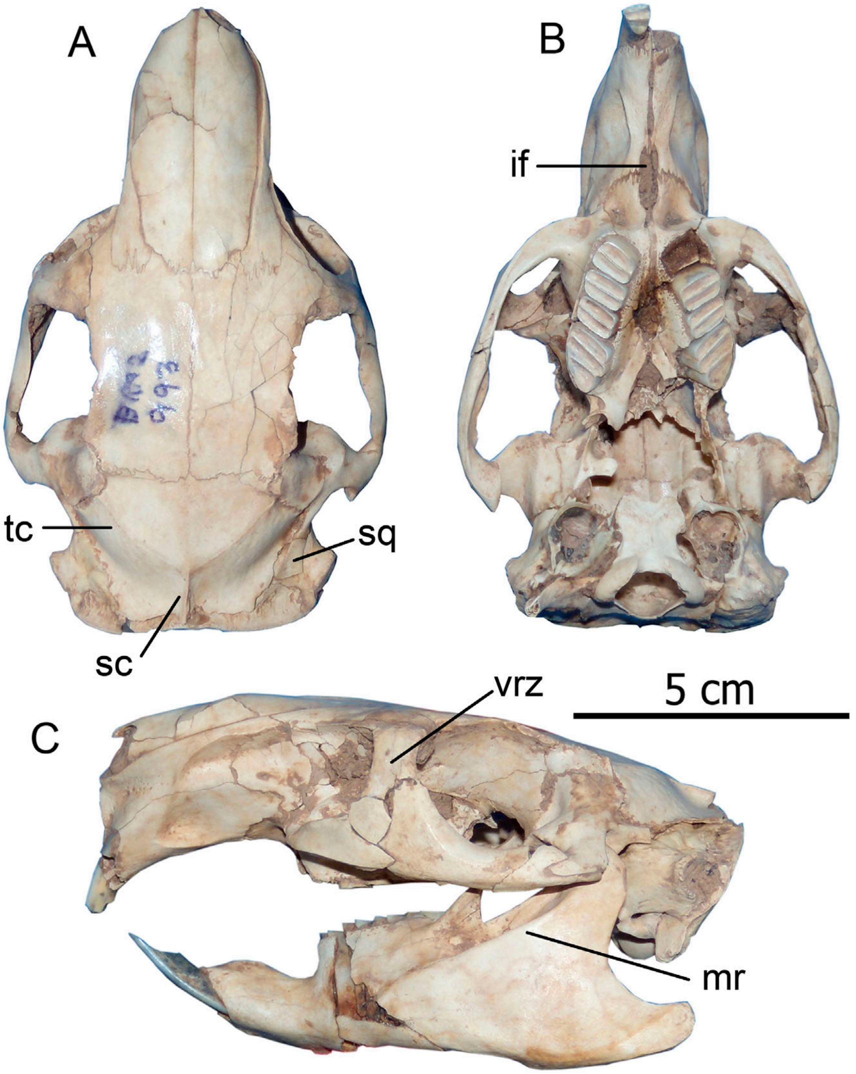

Fig. 3. Upper Pleistocene material of *Lagostomus maximus* from Uruguay (BRA-2-993). Skull: **A**, dorsal view; **B**, palatal view; **C**, lateral view of skull and mandible. Abbreviations: if, incisive foramen; mr, masseteric ridge; sc, sagittal crest; sq, squamosal; tc, temporal crest; vrz, vertical ramus of the zygomatic arch.

Locality, unit and age. Pilatos Creek, Canelones Department, Uruguay. Dolores Formation (Upper Pleistocene). *Lagostomus maximus* taxon-age of 11 879 ± 95 years BP (cal. BP 13 898–13 941).

Description

Cranium and upper dentition. The cranium of BRA-2-993 is morphologically indistinguishable from those of other *Lagostomus maximus*, and is proportionally most similar to sub-adult/young adult female and sub-adult male individuals. It is demonstrably smaller than the extinct *L. cavifrons*, which is similar to adult females and young adult males of *L. maximus*. The nasals of BRA-2-993 are slightly shorter than the premaxillae. The posterior process of the premaxilla does not extend beyond the anterior edge of the dorsal zygomatic root, as in *L. maximus* and *L. cavifrons*. The frontals are shorter than the nasals, resembling *L. maximus*. The frontals are otherwise longer than the parietals and slightly depressed along the midline. The temporal crest is weakly developed and semi-circular. The sagittal crest is relatively short and strong, and the vertical ramus of the zygomatic arch is thick as in some sub-adult *L. maximus*. The caudal portion of the squamosal extends dorsally to the external auditory meatus. The posterior palatine apophyses on the premaxillae are weakly developed. The interpremaxillary foramen is absent like some specimens of *L. maximus*. The incisive foramen is also longer than wide with subparallel external borders. The posterior process of the palatines appears to be absent, but this structure is broken in BRA-2-993. The tympanic bullae are likewise damaged but appear to have been antero-internally to postero-externally elongate. The angle of tooth laminae with respect to the sagittal plane (49°) is similar to that of *L. maximus* and most extinct vizcachas (>45°). The upper teeth series is morphologically similar to *L. maximus* and *L. cavifrons*; the

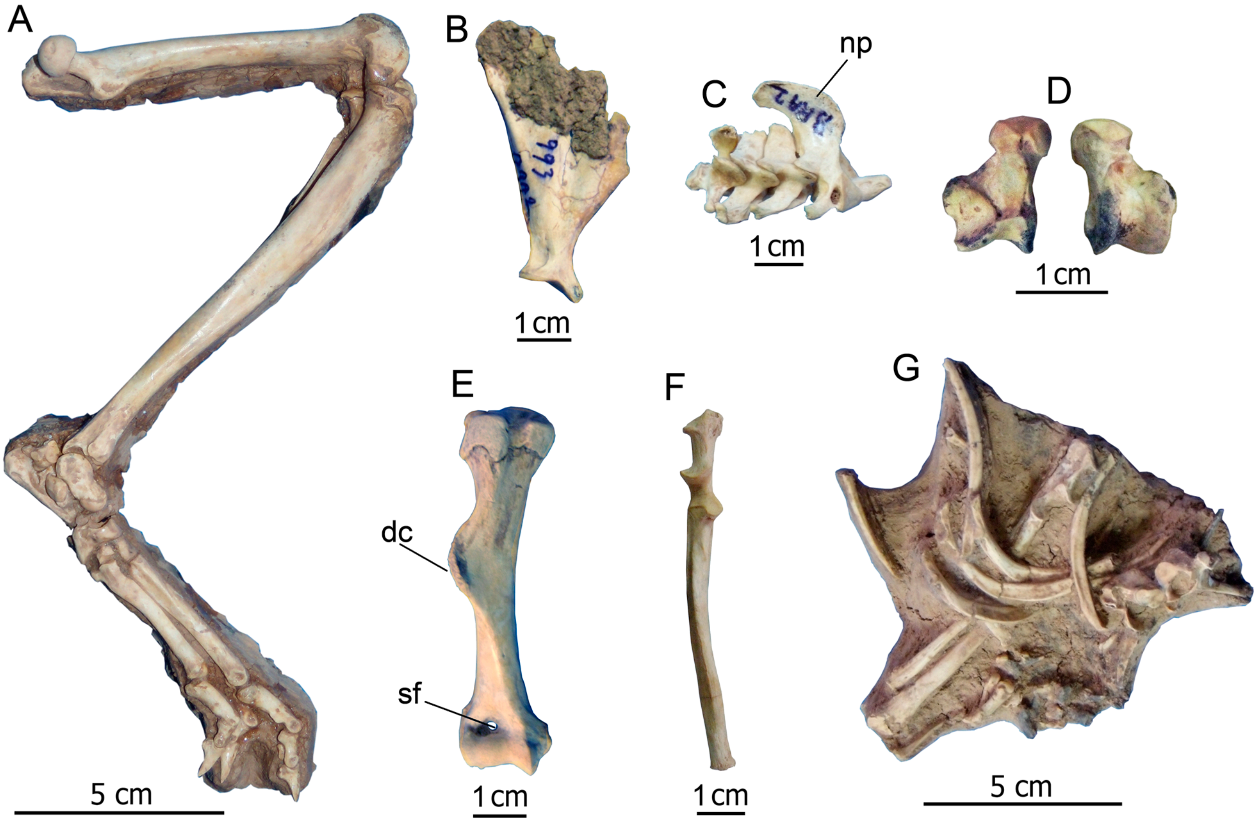

Fig. 4. Postcranial bones of Upper Pleistocene *L. maximus* (BRA-2-993) from Uruguay: **A,** left articulated hind leg; **B**, left scapula; **C**, atlas and 3–5 cervical vertebrae; **D**, right astragalus (calcaneal view in left and tibial view in right); **E**, right humerus; **F**, right ulna; **G**, articulated and semi-articulated bones including ulna, radius, some phalanges, vertebrae and ribs. Abbreviations: dc, deltoid crest; np, neural process; sf, supratrochlear foramen. Scales in cm.

M3 dimensions are compatible with many sub-adult and adult *L. maximus* (Table 1, Online Supplementary Data 2).

Mandible and lower dentition. The mandible and lower teeth are of similar size to sub-adult/young adult females, and sub-adult males of *Lagostomus maximus*, and to the extinct *L. angustidens* and *L. debilis*; they are demonstrably smaller than those of *L. cavifrons*. The masseteric ridge is well developed, and the masseteric notch is very deep. The mandibular foramen is dorsally located and posteriorly to the m3. The coronoid process is long and pointed, as occurs in a few male and female *L. maximus* (it is otherwise typically shorter and more rounded). The lower cheek teeth are anteroposteriorly compressed like those of *L. maximus*. The angle of tooth laminae (20°) is similarly compatible.

Postcranial skeleton. The postcranial elements of BRA-2-993 are identical to those of *Lagostomus maximus*, although our sample was limited to adult specimens. As a descriptive summary, the atlas has sub-rhombic condyloid facets and a low spinous process. The transverse processes are robust and laterally projecting; the articular facets for the axis are semi-circular in outline. The axis has a well-developed anterodorsally projecting odontoid process. The articular facets for the atlas are sub-triangular. The neural spine is large and posteriorly projecting; the transverse processes are short and posterolaterally directed.

The scapula has an ovoid glenoid fossa, constricted neck and basal sulcus on the coracoid process. The caudal margin is straight, and both the supraspinous and infraspinous fossae are slightly excavated. The scapular tuberosity is broken off in BRA-2-993. The proximal epiphysis of the humerus is not fused (denoting osteological immaturity), and both a well-developed deltoid crest and a supratrochlear foramen are visible on the diaphysis. The condition of the supratrochlear foramen is highly variable in *Lagostomus maximus*. The olecranon process on the ulna forms a short peak, and the anconeal process is well defined. The trochlear notch is evident and the diaphysis is curved with a weak interosseous crest. The distal epiphysis of BRA-2-993 is missing.

The femur is shorter than the tibia and has a laterodorsally oriented condylar head. The greater trochanter lacks a fused distal epiphysis. The trochanteric fossa is very deep. The accompanying tibia likewise lacks fused proximal epiphyses and possesses a prominent tibial crest. A constricted neck demarcates the convex navicular facet on the astragalus. The trochlear articulation forms a deep valley. The anterior calcaneal facet is longer than wide and is separated from the posterior calcaneal facet by a deep *sulcus tali*. The associated metatarsals are long and the phalanges (especially the second and unguals) are short and robust.

Remarks. Articulated skeletons like that of BRA-2-993 (Figs 3, 4, Online Supplementary Data 8) are common in these outcrops of the Dolores Formation (Ubilla 2008, Ubilla *et al*. 2009, Corona *et al*. 2013, Ubilla & Rinderknecht 2014). Although burrow traces were not observed, this taphonomy is consistent with preservation of small mammal skeletons. *Lagostomus maximus* is certainly a fossorial caviomorph (Elissamburu & Vizcaíno 2004), with EI, IFA and SMI values of BRA-2-993 approximating those typical for the species *L. maximus* (Table 3; Elissamburu &Vizcaíno 2004).

Lagostomus sp. cf. **L. maximus** (Desmarest, 1817)

Referred material. BRA-547, fragmentary skull with P4–M3 and articulated right mandible; BRA-879: cranium lacking postorbital region; BRA-958: fragmentary cranium lacking zygomatic arches (encrusted by carbonate matrix); BRA-3-933, cranium lacking postorbital region.

Locality and horizon. BRA 958 and BRA-879 derive from Aparicio Creek, BRA-3-933 and BRA-547 from Pilatos Creek, both in the Canelones Department of Uruguay; Dolores Formation, Upper Pleistocene.

Remarks. These specimens are tentatively referred to *L.* sp. cf. *L. maximus*. These are similar to *L. maximus*, and proportionately they resemble sub-adult individuals. These fragmentary materials lack the posterior part of the skull, which is, according to our comparative analysis, necessary to evaluate their taxonomic status in more detail.

Discussion

Morphological and taxonomic implications

Llanos & Crespo (1952) demonstrated sexual dimorphism through ontogeny in the cranium and mandible of *Lagostomus maximus*. Males were found to be larger in most dimensions, which was most pronounced in adults (see also Rasia & Candela 2013, fig. 7). Following these parameters, BRA-2-993 resembles, in selected dimensions, the sub-adult male and sub-adult or young adult female individuals (Fig. 6A, C, D; Tables 1, 2). We also obtained similar results for other cranium and mandible proportions (Online Supplementary Data 9; Tables 1, 2).

Llanos & Crespo (1952) further proposed that the total length of the molar series relative to length of the cranium increased the masticatory surface area in immature animals. Additionally, the M3 width versus total cranium length reaches its maximum during early ontogeny, becoming relatively constant after cranial length plateaued at *ca* 100 mm long in sub-adults specimens (Fig. 6B). Not surprisingly, molar size has, thus, a poor predictive characteristic of sub-adult and adult ontogenetic stages for body mass calculations or taxonomic assessments. In the case of BRA-2-993, its molar width and length values are coherent with some sub-adults, and adult males and females of *L. maximus*.

Recently, Rasia *et al*. (2011) and Rasia & Candela (2013) identified sexual and ontogenetic differences in the temporal and parietal region of *L. maximus*. BRA-2-993 accordingly has a relatively short but well-defined sagittal crest associated with weakly curving temporal crests that are reminiscent of those in sub-adult and young adult females of *Lagostomus maximus* (Fig. 5). Males with similar skull sizes (here termed sub-adults: Fig. 6) have low and less developed sagittal crests and posteriorly poorly defined converging temporal crests (Fig. 5). BRA-2-993 also displays a robust descending ramus of the zygomatic arch, a characteristic of sub-adult females.

According to Ameghino (1889), *Lagostomus cavifrons* (the only Pleistocene species described based on a skull), differs from *L. maximus* in having a more horizontal cranial roof, and a depression in the nasal-frontal region. However, these traits do not significantly depart from the range of variability we observed within our sample of extant *L. maximus*. Furthermore, *L. cavifrons* is of comparable size to adult females and young adult males of *L. maximus* (Fig. 6A, C, D, Online Supplementary Data 9). We also suggest that the nasal-frontal depression might be either taphonomic/diagenetic, or similar to structures found in some *L. maximus* specimens (Fig. 7). The holotype has a temporal region with long sagittal crest and posteriorly converging temporal crest similar to males of *L. maximus*.

Other purported fossil species of *Lagostomus* described based on mandibles also conform to the range of intraspecific variability observed in extant *L. maximus* (Fig. 7). For example, the transverse width of the lower incisor, height of the mandible at the p4, and length of the p4–m3 in *L. angustidens* and *L. debilis* are similar to BRA-2-993, and to young adult females and sub-adult males of *L. maximus* (Fig. 6D, Online Supplementary Data 9). *Lagostomus egenus* is likewise compatible with adult males of *L. maximus*, whereas *L. heterogenidens* and *L. minimus* are closer to sub-adults (Fig. 6D, Online Supplementary Data 9, Table 2). *Lagostomus egenus* is peculiar in having a longitudinal sulcus on the labial face of its incisor. This was not observed in our sample and might represent individual variation or a pathological/diagenetic fracture. The longitudinal striations on the labial face of the incisors of *L. striatus* occur in some specimens of *L. maximus*. Taking into account the variability evident in extant species, we regard these fossils (Fig. 7) as more appropriately assigned to *Lagostomus* sp. Preliminary

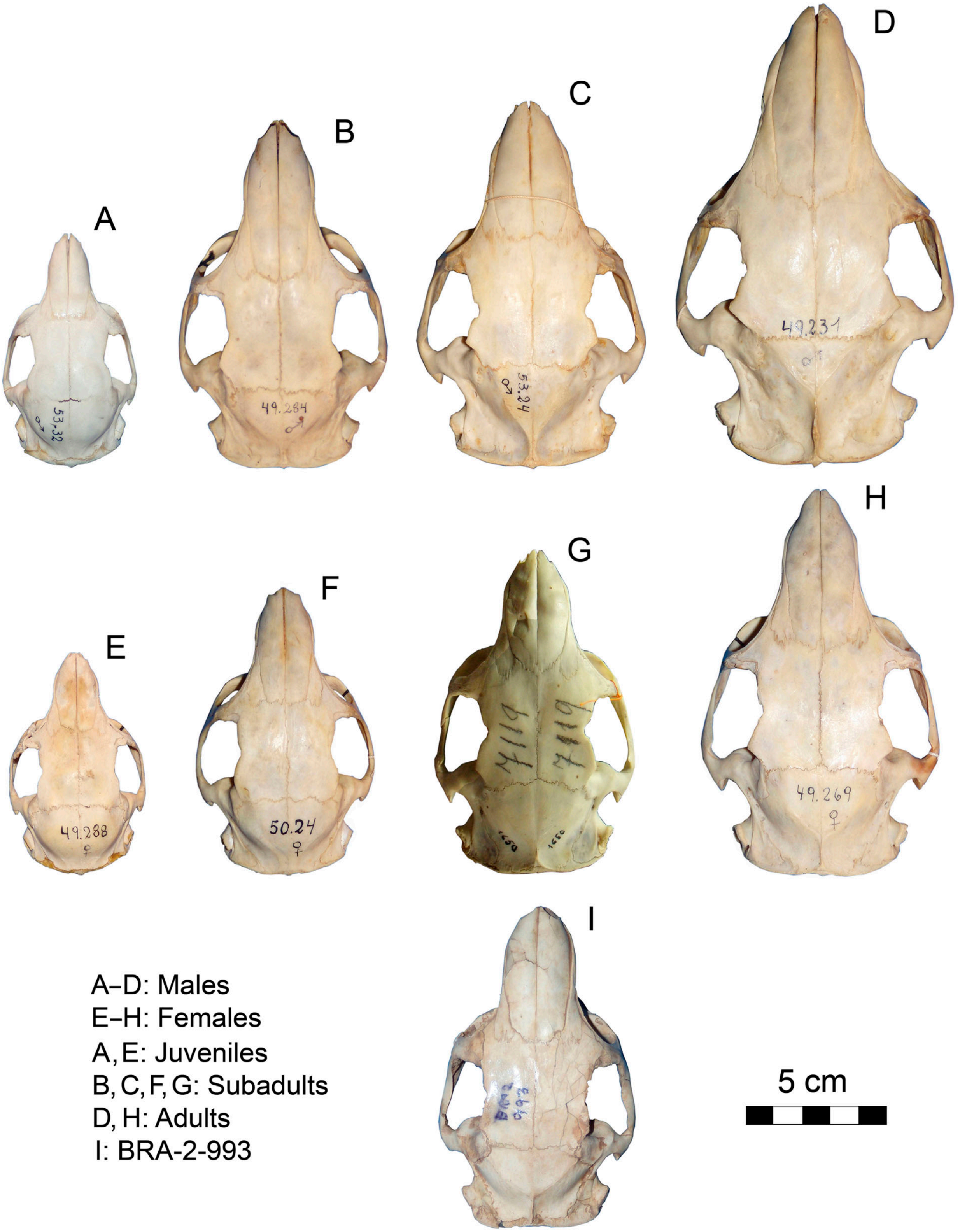

Fig. 5. Dorsal view of selected comparative specimens of extant *Lagostomus maximus*: **A**–**D**, males; **E**–**H**, females; **A**, **E**, juveniles; **B**, **F**, **C**, **G**, sub-adults; **D**, **H**, adults. **I**, *L. maximus* (BRA-2-993) from the Late Pleistocene of Uruguay.

comparisons with *L. crassus* (Thomas 1910, Ojeda & Bidau 2013b) concur with referral to *L. maximus* (Cabrera 1960, Jackson *et al*. 1996), but this material is more robust than BRA-2-993 and might be a male.

Biogeographical and palaeoenvironmental implications

According to Upham & Patterson (2012), *Lagostomus* belongs to a clade that probably originated in a

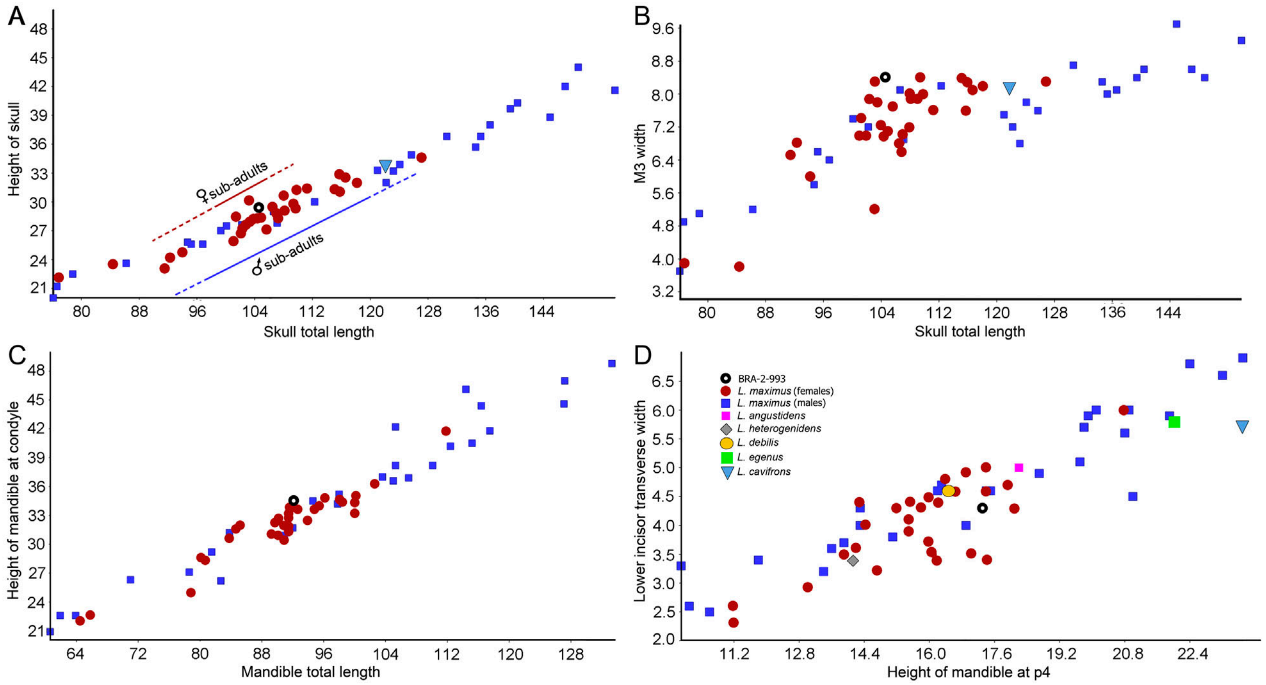

Fig. 6. Biplots that include males and females of extant *L. maximus*, the Pleistocene material from Uruguay (BRA-2-993) and the Pleistocene nominal taxa of Argentina.

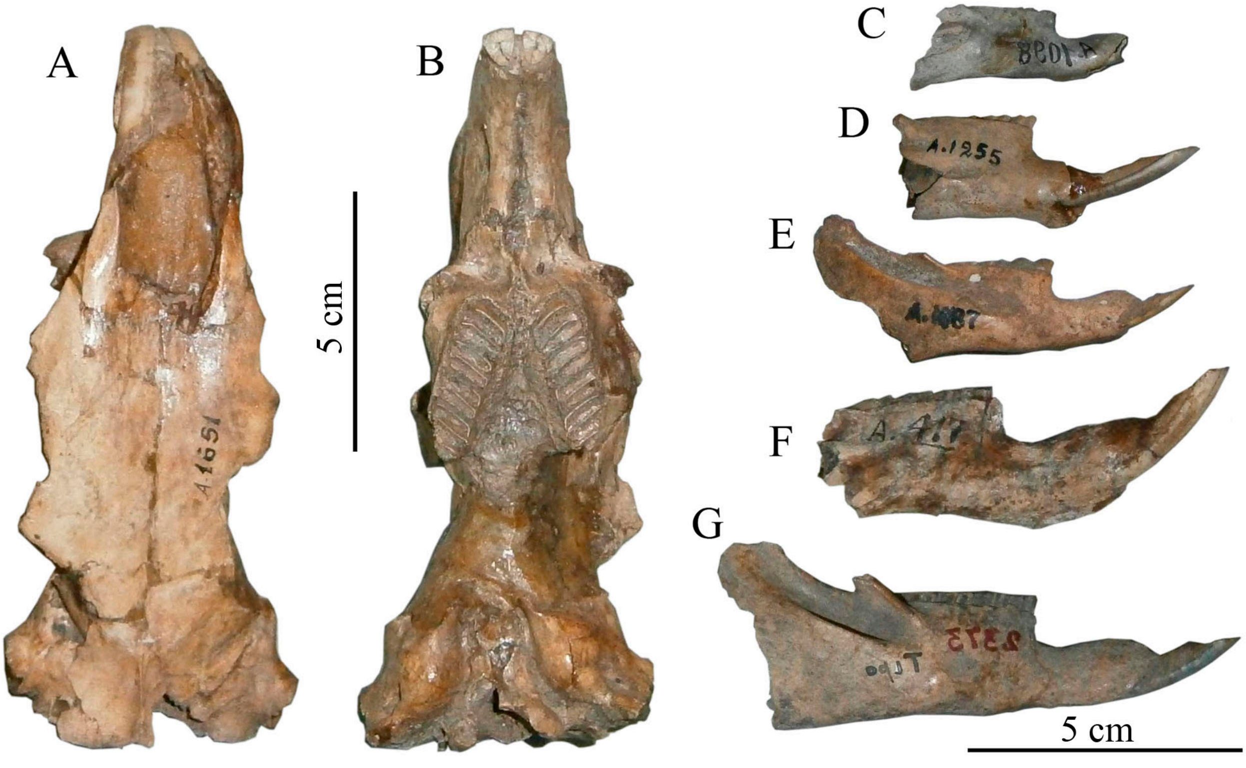

Fig. 7. Pleistocene species of *Lagostomus* from Argentina (holotypes). **A**–**B**, Skull in dorsal and palatal view of *L. cavifrons*; **C**, left mandible of *L. minimus* (reversed side); **D**, right mandible of *L. debilis*; **E**, right mandible of *L. heterogenidens*; **F**, right mandible of *L. hegenus*; **G**, left mandible of *L. angustidens* (reversed side).

Miocene Patagonian setting (including the Monte Desert and Southern Andes). *Lagostomus* seemingly then dispersed into the Pampean and part of the Chaco regions following regression of the ‘Paranean Sea’, which created broad plains throughout this geographical area (Ortiz-Jaureguizar & Cladera 2006 and references therein). Today, *Lagostomus maximus* inhabits predominantly lowland areas ranging from 20 to 600 m elevation, although it is occasionally found up to 2000 m (Llanos & Crespo 1952, Anderson 1997). It tends to occupy open to semi-open Pampean humid grasslands and dry thorn scrub in the Chaco area (Cabrera & Willink 1973), the southern portion of the Chaqueña Subregion (Morrone 2001). Based on these known habitat preferences, we infer a similar openly vegetated semi-arid palaeoenvironment for the latest Pleistocene of southern Uruguay. This interpretation is supported by the associated fauna, which includes *Microcavia criolloensis* (Ubilla 2008), *Dolichotis* sp. cf. *D. patagonum*, *Galea ortodonta* (Ubilla & Rinderknecht 2014), and small camelids resembling extant vicuña and guanaco (Ubilla *et al*. 2009). Age estimates place this setting within the last phases of MIS-3, spanning *ca* 60 to 25 ka and characterized by millennial-scale climatic changes (Van Meerbeeck *et al*. 2011), and in the Last Glacial Maximum when cold and arid conditions were especially pronounced (Tonni *et al*. 1999).

The current distribution of *L. maximus* does not include Uruguay or southern Brazil, but does encompass the Entre Ríos province of Argentina (Fig. 1). The Uruguay River might form a geographical barrier preventing current dispersal. Llanos & Crespo (1952) described an almost complete independence from water for this species. Marine regression (*ca* 120 to 130 m below current sea level) during the LGM (Murray-Wallace & Woodroffe 2014) could, therefore, have facilitated earlier colonization of Uruguay (and probably southern Brazil) by exposing large portions of the continental shelf along the Río de la Plata and Paraná-Uruguay river systems (Violante & Parker 1999, Flegenheimer *et al*. 2003, Ponce *et al*. 2011). Post-LGM sea level fluctuations, including Holocene transgressive episodes (Cavallotto *et al*. 2004, Violante & Parker 2004, Martínez & Rojas 2013, Murray-Wallace & Woodroffe 2014 and references therein) seemingly established the fluvial and estuarine geographical barriers that precluded redistribution of *L. maximus* from the Argentinean Pampean region.

The eventual disappearance of *L. maximus* from Uruguay is coincident with other mammalian taxa, including *Galea*, *Microcavia*, *Chaetophractus* and *Dolichotis*, all of which still exist elsewhere in South America (Ubilla & Rinderknecht 2014). This segregated biodiversity pattern can be attributed to local extinctions and shifting distributional ranges caused by alterations in the environment during the latest Pleistocene or early Holocene.

Conclusions

(1) The occurrence of the plains vizcacha, *Lagostomus maximus*, is demonstrated in Uruguay during the Late Pleistocene based on an articulated skeleton. A taxonage of 11 879 ± 95 years BP (cal. BP 13 898–13 941) is considered the LAD for this species in this country.

(2) Comparisons relative to an ontogenetic and sexually dimorphic sample of modern *Lagostomus maximus* skeletons has determined that the equivalent fossils from Uruguay belong to sub-adult or young adult female individuals. Molars, a structure widely used by mammalian palaeontologists, reach a stable size in the sub-adult stage, precluding their use in body-size estimations, differentiating sub-adults from adults and delimiting taxa.

(3) *Lagostomus cavifrons* from the Pleistocene of Argentina is considered synonymous with *L. maximus*. Its character states concur with the range of intraspecific variability, in particular adult males. Likewise, the other Argentinean Pleistocene species *L. angustidens*, *L. striatus*, *L. heterogenidens*, *L. egenus*, *L. minimus* and *L. debilis* concur with ontogenetic morphs and are here assigned to *Lagostomus* sp.

(4) Today *L. maximus* occupies subtropical humid to semi-arid grasslands and dry thorn to desert scrub. In particular, semi-arid environments are postulated for southern Uruguay during the latest Pleistocene. These conditions correlate with the last phases of MIS-3, and particularly the Last Glacial Maximum.

(5) Our identification of *L. maximus* in the Pleistocene of Uruguay indicates a local extinction or shift in species range. Its disappearance likely occurred during the latest Pleistocene or early Holocene and might have been related to environmental changes.

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