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The Patagonian Mara *Dolichotis patagonum* (Zimmermann, 1780) (Rodentia, Caviomorpha, Caviidae) in the Late Pleistocene of Northern Uruguay: Body Mass, Paleoenvironmental and Biogeographical Connotations

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Abstract: The extant Patagonian mara *Dolichotis patagonum* (Zimmermann, 1780) is a cursorial herbivorous rodent that is hare-like in appearance. Nowadays, it occurs in some ecoregions of Argentina (28 °S–50 °S) in lowland habitats, in semi-arid thorn-scrub, in open grasslands and in shrub–land steppe. In this research, we have studied a partially preserved skull (FCDPV-2758), referred to *D. patagonum*, from the Late Pleistocene (Sopas Formation) in northern Uruguay (Arapey Grande River, Salto Department). Body mass estimates and morphological analyses were performed including contemporary specimens of *D. patagonum*, the Chaco mara *Dolichotis salinicola*, and extinct dolichotine species. The body mass estimate using the regression method and geometric similarity suggested a 6–8 kg range for the studied specimen, which is consistent with *D. patagonum* (7–8 kg) and notably greater than *D. salinicola* (1–2.3 kg). A comparative analysis, including the extinct *D. platycephala* and material previously referred to *D. major* from southwestern Uruguay, suggests that the studied specimen falls within the variation of *D. patagonum*, differing in part from *D. chapalmalense* and more clearly from *D. salinicola*, the extinct *D. minor* and *Prodolichotis prisca*. The implications of the wider geographic distributions of the living Patagonian mara at these latitudes in the Late Pleistocene in South America, and the paleoenvironmental significance are discussed.

Keywords: *Dolichotis patagonum*; Patagonian mara; Late Pleistocene Uruguay; body mass

Academic Editor: Dimitris S. Kostopoulos

Received: 3 April 2025
Revised: 6 May 2025
Accepted: 11 May 2025
Published: 24 May 2025

Citation: Ubilla, M.; Ghizzoni, M.; Rinderknecht, A. The Patagonian Mara *Dolichotis patagonum* (Zimmermann, 1780) (Rodentia, Caviomorpha, Caviidae) in the Late Pleistocene of Northern Uruguay: Body Mass, Paleoenvironmental and Biogeographical Connotations. *Foss. Stud.* **2025**, *3*, 7. https://doi.org/10.3390/fossils3020007

1. Introduction

The extant Patagonian mara *Dolichotis patagonum* (Zimmermann, 1780) is the second largest caviomorph caviid after capybara *Hydrochoerus hydrochaeris* Linnaeus, 1766, which is hare-like in appearance and a cursorial herbivorous rodent that feeds mostly on fruits and grasses [1]; at present, it is found only in Argentina, and is usually reported at 28 °S to 50 °S in lowland habitats, semiarid thorn-scrub, open grasslands and shrub-land [1,2]. However, the distribution of the Patagonian mara is currently diminished and fragmented as a result of anthropogenic factors, and it is considered threatened and vulnerable [3,4] (Figure 1).

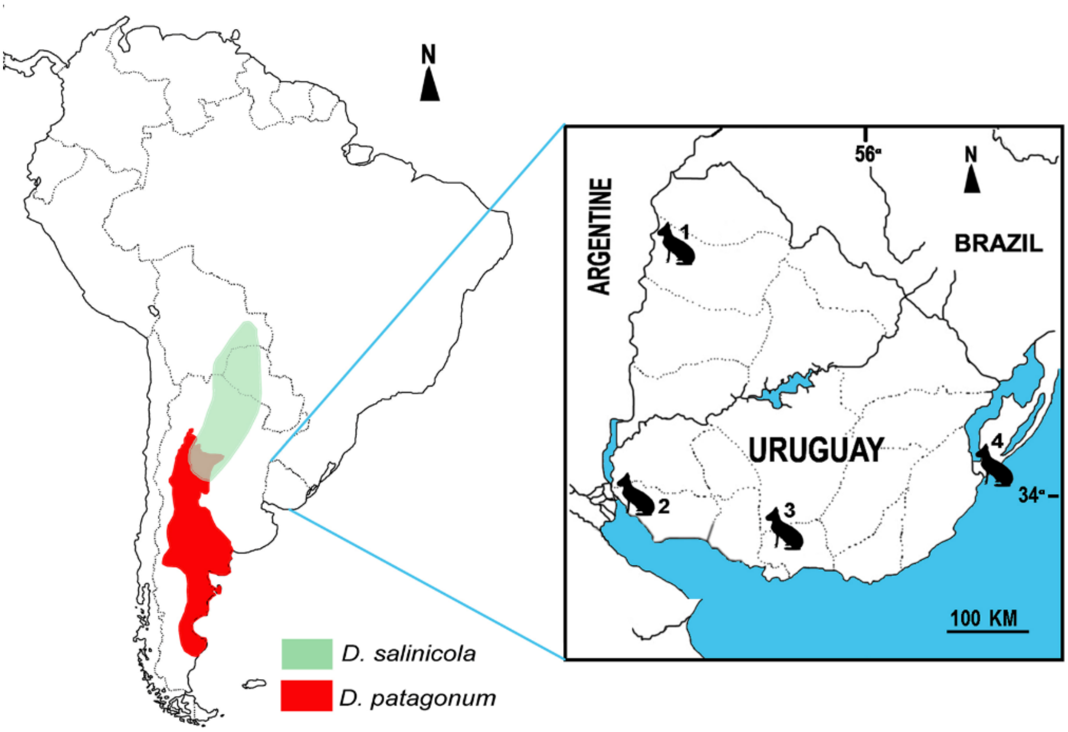

Figure 1. Left: Current distribution of extant dolichotine species *D. patagonum* and *D. salinicola* based on [2–5]. **Right**: geographic locations of Quaternary dolichotines in Uruguay and southern Brazil—(1) *D. patagonum* (FCDPV-2758), Río Arapey Grande, Salto; (2) *D. patagonum* (considered by Calcaterra [6] as *D. major*), Colonia; (3) *D.* cf. *patagonum*, Pilatos creek, Canelones. Based on Calcaterra [6] and Ubilla et al. [7]; (4) Dolichotinae indet. Based on Kerber et al. [8].

In the northernmost part of its distribution, the Patagonian mara population is partially superposed with the extant Chacoan mara *Dolichotis salinicola* Burmeister, 1876 [2,5] (Figure 1). Both species form part of the monophyletic Dolichotinae clade, which includes several extinct species [9] (and references therein). There is controversy regarding the generic assignment of the two extant species, which are considered to belong to different genera, *Dolichotis patagonum* and *Pediolagus salinicola*, or to only one genus, *Dolichotis* [2,9,10] (and references therein). In this study, we apply the second option, including both species under the genus *Dolichotis*, but assume that the argument is not fully resolved. The Dolichotinae clade showed greater diversity in the Neogene–Pleistocene than at present, and several taxa have been described and referred to in this group, some of which are based on fragmentary and taxonomically controversial material [11] (and references therein).

The Patagonian mara *D. patagonum* is recorded as having been present in the Pleistocene and Holocene in Argentina, including at sites east of the current distribution [1,11] (and references therein). Outside Argentina, records of dolichotines in the Pleistocene are very scarce, and some records are based on fragmentary material. In Uruguay, Calcaterra [6] referred to *Dolichotis major* [12] an incomplete skull and mandible from the "Formación Pampeana Superior" (probably the current Dolores Formation of the Late Pleistocene–Early Holocene), Colonia Department, southwestern Uruguay (Figure 1). Later, Ubilla et al. [13] included *Dolichotis*? sp. in a taxonomic list for the Sopas Formation of northern Uruguay, and Ubilla et al. [7] described fragmentary material as *D.* cf. *patagonum* for the Dolores Formation, Canelones, southern Uruguay (Figure 1). Kerber et al. [8] referred isolated teeth to Dolichotinae indet. from the Late Pleistocene in southern Brazil (Figure 1).

In this study, a partially preserved skull (FCDPV-2758), mentioned in Ubilla et al. [14] as *Dolichotis* sp., is studied and referred to here as *D. patagonum*, unearthed from Late

Pleistocene beds (Sopas Formation) in northern Uruguay. Anatomical comparisons and quantitative analyses, including body mass estimation, were performed, considering extant and extinct taxa of the subfamily Dolichotinae. In addition to taxonomic comments, the implications of the geographic distribution of the living Patagonian mara outside Argentina, in the Late Pleistocene of Uruguay, and the paleoenvironmental significance thereof are discussed.

2. Geographic and Geological Setting

The material under study was collected from outcrops of the Sopas Formation [15] in the Arapey Grande River (Salto Department), northern Uruguay (Figure 1). This unit has a patchy expression at the surface, mostly on the sides of rivers and creeks in northern Uruguay (Tacuarembó, Río Negro, Salto and Artigas departments); it includes conglomerates, conglomeratic sandstones, siltstones, sandy siltstones, and carbonates (concretions and duricrusts), and is predominantly brown in color. Fluvial facies are predominant, including paleosols in some places.

This fossiliferous continental unit yields trace fossils, woods, fresh-water mollusks (bivalves and gastropods) and vertebrates dominated by mammals (more than 50 species) [13,14,16–23]. The mammalian assemblage combines extinct plus extant taxa, but many live in other areas of South America and depict shifting range processes and local extinctions. The Sopas Formation is correlated with the Lujanian Stage/Age of the Pampean Region (Argentina) [13], which is considered by Cione et al. [24] to be Late Pleistocene/Early Holocene in age. This unit corresponds to the Upper Pleistocene–Greenlandian Stages/Ages of the International Chronostratigraphic Chart [25]. Ages based on accelerator mass spectrometry (AMS) and Optically Stimulated Luminescence (OSL) from several outcrops range from 60 to 25 ka (MIS-3), and a few are, at the latest Pleistocene [18,26].

Mammalian assemblages include taxa living today under temperate to tropical climates, such as the ocelot *Leopardus pardalis* (Linnaeus, 1758), the river otter *Lontra longicaudis* (Olfers, 1818), the tapir *Tapirus* and the capybara *Hydrochoerus*, among others, indicating the presence of riparian forests and freshwater bodies [13,22,23]. In addition, arid to semiarid environments are suggested by some mammals, such as the wild cavy *Microcavia*, the Chaco peccary *Parachoerus wagneri* (Rusconi, 1930), and extinct camelids [16]. Isotopic and microwear studies performed on the extinct native ungulate *Neolicaphrium recens* Frenguelli 1921, and isotopic analyses on the horses *Equus neogeus* Lund, 1840 and *Hippidion principale* (Lund, 1845), the deer *Morenelaphus* sp. and the peccaries *Brasiliochoerus stenocephalus* (Lund in Reinhardt, 1880) and *Tayassu peccary* (Link, 1795), suggest browser to mixed feeding strategies associated with an open canopy to open grasslands [16,27,28]. The record of the Patagonian mara in the Sopas Formation deserves to be discussed to consider the environmental signal provided by this taxon.

3. Materials and Methods

The institutional abbreviations are listed here. FCDPV: Colección Paleontológica de la Facultad de Ciencias, Vertebrados, Montevideo, Uruguay. 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. MLP-DZV: Mastozoología, Museo de Ciencias Naturales y Facultad de La Plata, Argentina. MNHN-P-PAM: Muséum National d'Histoire Naturelle, Paleontologie, Paris, France. MPC: Museo Municipal Paleontológico Armando Calcaterra, Colonia. IAVA: Museo de Ciencias Naturales Alfredo Vázquez Acevedo, Montevideo, Uruguay. ROMM: Royal Ontario Museum Mammalogy, Toronto, Canada.

The measurements are listed here. APB: maximum length of the bulla. AR: occlusal area of upper cheek toothrow (sum of P4-M3 areas). BZW: zygomatic width (e). D: diastema length. CBL (skull): condylobasal length. COL-COW: occipital condyle length–width. FMH-FMW: foramen magnum high-width. IF: length of the incisive foramen. LT (SL): total length (e). LVS: basal length. M1L: M1 length. M1W: M1 width. M2L: M2 length. M2W: M2 width. M3L: M3 length. M3W: M3 width. OCW: occipital bi-condyle width. PL: palatal length. Pal-I: palatal length without incisor to posterior margin of M3. PW: palatal width at M3. P4-M3L (CTL, LR, UTRW): length of P4-M3. P4L: P4 length. P4W (WR): P4 width. P: palatal length from P4 to anterior margin of the mesopterygoid fossa. upper T: upper incisor transverse diameter. The abbreviations in brackets correspond to the same measure nominated differently by the authors consulted. e means that an estimated value of this measurement is provided due to the fragmentary condition of the studied material.

Statistics abbreviations—CV: coefficient of variation. SD: standard deviation. x: arithmetic mean.

The measurements followed those of Ubilla and Rinderknecht [29,30], except for APB, P and IF following Madozzo-Jaén et al. [9]; OCW following Engelman [31]; SL, CTL, CTW, COL, COW, FMH, FMW, and PAL-I following Bertrand et al. [32]; skull, UTRW, and upper T following Millien [33]; and LVS, AR, LR, and WR following Boivin et al. [34]. The CTW from Bertrand et al. [32] was calculated as the average width of P4-M3. The WR from Boivin et al. [34] corresponds in this case to P4W because it is the maximum mediolateral width of the upper cheek toothrow. The skull and teeth nomenclature follows Ubilla and Rinderknecht [35] and Madozzo-Jaén et al. [9] (Figure S1: Principal anatomical features used in comparative analysis).

Material: The extinct dolichotines *Dolichotis chapalmalense* (Ameghino, 1908), *D. platycephala* Ameghino, 1889, *D. minor* (Gervais & Ameghino, 1880), *D. major* (Gervais & Ameghino, 1880) and *Prodolichotis prisca* (Rovereto, 1914), along with a comparative sample of extant *D. patagonum* and *D. salinicola* (List S1: list of comparative material; Table S1: comparative measurements of fossil material), were used to perform the anatomical and quantitative analyses. Rovereto [36] (p. 202) refers *Orthomyctera chapalmalense* Ameghino, 1908, to the genus *Dolichotis*. Kraglievich [37] subsequently reported that it belongs to a different genus. Ubilla and Rinderknecht [35] suggested identity with *Dolichotis*, and finally, Madozzo-Jaén et al. [9] corroborated this proposal in a detailed analysis of the material. *Orthomyctera rigens* (Ameghino, 1889) and *Orocavia andina* (Rovereto, 1914) were not considered here because both taxa were finally relocated to the Caviinae clade [9,38].

Body mass estimate, scatter plot and multivariate (principal component analysis, PCA) analyses were performed via Past software version 4.11 [39]. The PCA eigenvalues and eigenvectors were calculated via a variance-covariance matrix, and within-group analysis was performed on the specified groups. Factor loadings for the first two components are provided here. In the scatter plots and the PCA, a set of selected comparative skull and teeth variables in fossil samples was used to handle matrices as completely as possible. The selected variables used in the scatter plots are those that incorporate the largest number of fossil taxa used in the comparison (Table S1: comparative measurements of fossil material).

Body mass estimation: The estimation of body mass for the specimen under study (FCDPV-2758) was carried out with the allometric regression method through the application of predictive equations that relate cranio-dental morphological variables with mass in extant rodents. The predictive models used in this study come from Millien [33], Bertrand et al. [32], Engelman [31] and Boivin et al. [34]. Millien [33] developed regression equations via the least squares method, which is based on extant species of rodents. The prediction variables used in this study and applied to the FCDPV-2758 specimen are the upper tooth row length (UTRW), the upper incisor transverse diameter (upper T) and the condyle–basal length of the skull (skull). Bertrand et al. [32] performed predictive equations on extant species of rodents via the reduced major axis method. According to these authors, this considers the existence of error in both variables (dependent and independent), unlike the least squares method, and it has greater suitability for the analysis of interspecific data. The variables used by these authors and analyzed in our study are skull length (SL), cheek–tooth length (CTL), cheek–tooth width (CTW), cheek–tooth area (CTL × CTW), occipital condyle length (COL), occipital condyle width (COW), foramen magnum height (FMH), foramen magnum width (FMW) and palate length without incisors (PAL-I). Engelman [31] reported a strong correlation between occipital condylar width (OCW) and body mass in terrestrial mammals, and constructed predictive models with relatively low prediction errors. Boivin et al. [34] developed predictive body mass equations by analyzing a broad set of cranio-dental variables via the taxonomically weighted ordinary least squares method. To estimate the body mass of the fossil sample, the basal length of the cranium (LVS), the occlusal area of the upper cheek toothrow (AR), the maximum anteroposterior length of the upper cheek toothrow (LR) and the maximum linguolabial width of the upper cheek toothrow (WR), which are specific for caviomorph rodents, were used.

Concomitantly, we performed an estimation by geometric similarity with a specimen of known mass of *Dolichotis patagonum* (ROMM 90847), reported in the Supplementary Materials of Bertrand et al. [32]. This estimation assumes that both individuals, extant and fossil, share similar body proportions overall. The linear dimensions considered are SL, CTL, CTW, COL, COW, FMH, FMW and PAL-I, and the area dimension are CTL × CTW. In terms of geometric similarity, the scaling relationship between mass and length is $M \propto L^3$. Using this relation, mass values for the fossil were determined from the linear measurements and body mass of the living individual. On the other hand, the scaling relationship between the mass and the area is $M \propto A^{3/2}$, and using this relationship, the estimate for the fossil was obtained based on the area and mass of the living one.

4. Results

4.1. Systematic Paleontology

Mammalia Linnaeus, 1758
Rodentia Bowdich, 1821
Hystricognathi Tullberg, 1899
Caviidae Fischer von Waldheim, 1817
Dolichotinae Pocock, 1922
Dolichotis Desmarest, 1819

Dolichotis patagonum (Zimmermann, 1780) (Figures 2, 3A and S2: Additional views of the skull of FCDPV-2758)

Referred material: FCDPV-2758—skull partially preserved with both I, diastemas, both P4-M3 series, right zygomatic arch, right bulla and basisphenoides–basioccipital, both condyles and part of the right paraoccipital apophysis.

Geographic and stratigraphic provenance: Arapey Grande River, Salto Department, Uruguay. Sopas Formation (Late Pleistocene) (Figure 1).

Measurements (mm): APB, 22.3; AR, 158.1; BZW, 70 (e); D, 42; CBL (skull), 119.8; COL, 12.5; COW, 5.1; CTW, 5.6; FMH, 16.6; FMW, 11.8; IF, 22.4; LT (SL), 136.6 (e); LVS, 109.2; M1L, 6.2; M1W, 5.5; M2L, 6.2; M2W, 5.6; M3L, 8.8; M3W, 5.3; OCW, 20.9; PL, 60.7; Pal-I, 69.4; PW, 29.4; P4-M3L (CTL, LR, UTRW), 27.4; P4L, 7.1; P4W (WR), 6; P, 17.9; upper T, 5.4.

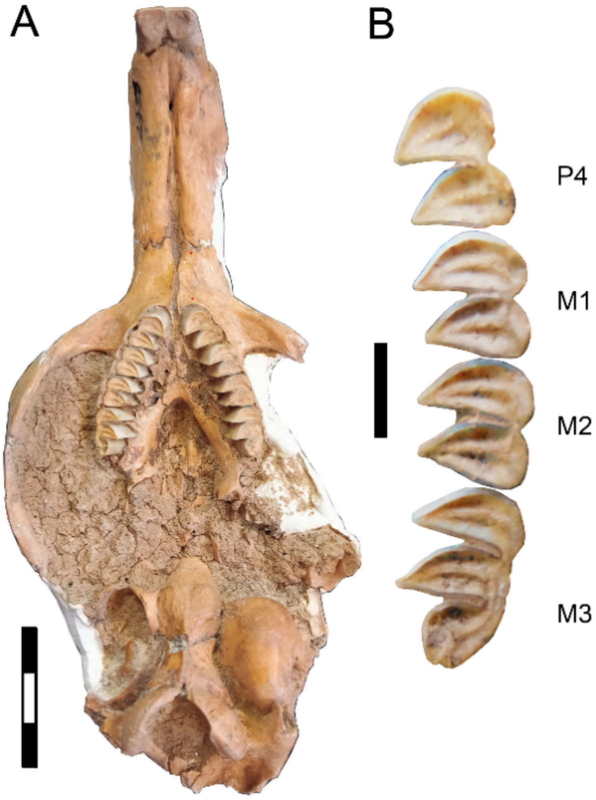

Figure 2. FCDPV-2758 specimen from northern Uruguay (Sopas Formation, Salto Department, Uruguay). (**A**) Palatal view. (**B**) Occlusal view of the left P4-M3 teeth. Scale: 3 cm and 5 mm, respectively.

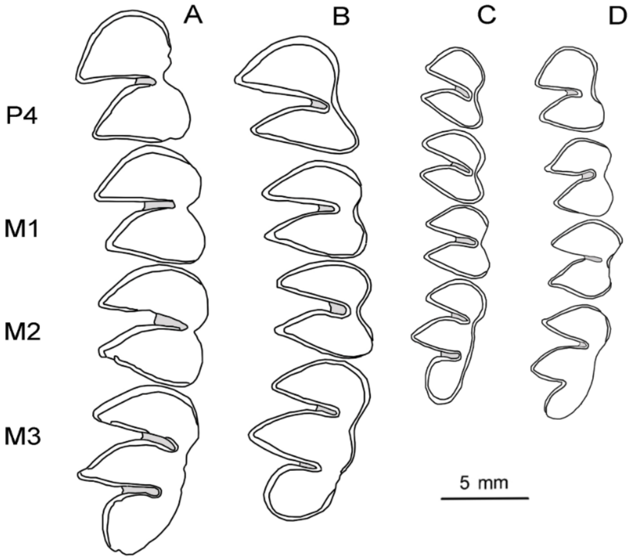

Figure 3. Occlusal surface of left P4-M3 teeth of (**A**) FCDPV-2758, (**B**) *Dolichotis patagonum*, MLP-DZV-1783, (**C**) *D. salinicola* MLP-DZV-673, (**D**) "*Prodolichotis*" sp. MNHN-1633. (**B**–**D**) Modified from Ubilla & Rinderknecht [35]).

Description: The skull is partially preserved and lacks the entire dorsal region, with the rostral region yielding both incisors, a diastema with the incisive foramen mostly extending in the premaxilla, and with the posterior portion obliquely oriented. A small Hill foramen is observed. The maxillary ramus of the zygomatic arch starts at P4. The mesopterygoid fossa extends mesially to M2 and has a relatively rounded shape. Both P4 -M3 series are preserved and mesially convergent, with P4-M2 bilobulate and M1-M2 roughly similar in length, heart-shaped, and have a furrow opposite the hypoflexus. M3, the longest tooth of the cheek-teeth series, has a posterior projection similar to an incipient prism, including cement in the flexus between the second and third prisms, and it displays parallel borders with respect to the second prism. The layer of enamel covering the cheek teeth is interrupted in most parts of the labial face. Auditory bulla with a predominant anteromedial-posterolateral length, with the external auditory meatus at the level of the occlusal surface of the teeth. The basisphenoid-presphenoid is ossified. Although the basioccipital is broken, a slight crest seems to have developed. Occipital condyles in the posterior view are dorsoventrally elongated. The paraoccipital apophysis is broken at the ventral surface of the auditory bulla.

Remarks: Considering the material is incomplete, the total length of the skull is estimated to be approximately 137 mm, which is within the range of *D. patagonum* (126–142 mm) [1,37]. It is larger than *D. chapalmalense* (124 mm fide Madozzo-Jaén et al. [9]) and *D. salinicola* (89–93 mm *fide* Kraglievich [37]). The zygomatic width is estimated to be ca. 70 mm, similar to that of *D. patagonum* and smaller than that of *D. platycephala*, which is estimated to be 82 mm (fide Ameghino [40]).

4.2. Body Mass Estimates

Table 1 shows the body mass estimates obtained for the FCDPV-2758 specimen. The application of the predictive models of Bertrand et al. [32] produces a minimum value of 2620 g (g) and a maximum of 45,249 g. The arithmetic mean of this dataset is 11,286 g (SD = 13,552 g, CV = 120%), and the median is 6445 g. When the models of Millien [33] are applied, a minimum estimate of 6981 g and a maximum of 8352 g are obtained. The arithmetic mean is 7607 g (SD = 693 g, CV = 9%) and the median of distribution is 7488 g. The estimates obtained with the predictive models of Boivin et al. [34] are approximately between 3000 and 6000 g, with an average of 5212 g (SD = 1755, CV = 34%) and a median of 5241 g.

Table 1. Morphological variables analyzed, predictive equations, and body mass estimates (in grams) for specimen FCDPV-2758. Equations (1)–(9) according to Bertrand et al. [32], (10)–(12) according to Millien [33], (13) according to Engelman [31] and (14)–(17) following Boivin et al. [34]. M—body mass, X—morphological variable.

	Variable	**Measurements**	**Predictive Equation**	**Body Mass Estimation (g)**
1	SL	136.6 mm	$\log M = 3.9519 \log X - 4.2316$	16,125
2	CTL	27.4 mm	$\log M = 3.1047 \log X - 0.5796$	7659
3	CTW	5.6 mm	$\log M = 3.3134 \log X + 0.98322$	2899
4	COL	12.5 mm	$\log M = 4.1781 \log X - 0.77376$	6445
5	COW	5.1 mm	$\log M = 3.6294 \log X + 0.92033$	3079
6	FMH	16.6 mm	$\log M = 5.1475 \log X - 1.6249$	45,249
7	FMW	11.8 mm	$\log M = 4.6018 \log X - 1.5143$	2620
8	PAL-I	69.4 mm	$\log M = 3.3273 \log X - 2.0254$	12,629
9	CTL × CTW	153.4 mm^2	$\log M = 1.6137 \log X + 0.1606$	4874
10	skull	119.8 mm	$\log M = 3.49 \log X - 3.332$	8532
11	UTRW	27.4 mm	$\log M = 2.70 \log X - 0.038$	6981
12	upper T	5.4 mm	$\log M = 2.45 \log X + 2.080$	7488
13	OCW	20.9 mm	$\ln M = 7.8157 (\ln X)^{2/3} - 8.2573$	3440
14	LVS	109.2 mm	$\log M = 3.225 \log X - 2.797$	5974
15	AR	158.1 mm^2	$\log M = 1.493 \log X + 0.371$	4508
16	LR	27.4 mm	$\log M = 2.916 \log X - 0.335$	7202
17	WR	6.0 mm	$\log M = 3.029 \log X + 1.143$	3162

The estimates for geometric similarity are in the range of 1535–13,576 g (Table 2). The arithmetic mean is 7959 g (SD = 3429 g, CV = 43%), and the median is 7802 g. There are no outliers in the value set.

Table 2. Body mass estimates (in grams) for the fossil specimen by geometric similarity with a living individual. * from Bertrand et al. [32].

Variable	Measurements *Dolichotis patagonum* (ROMM 90847) *	Body Mass Estimation of FCDPV-2758 (g)
SL	127.69 mm	10,957
CTL	26.73 mm	9640
CTW	6.29 mm	6316
COL	14.73 mm	5469
COW	9.18 mm	1535
FMH	17.45 mm	7705
FMW	10.27 mm	13,576
PAL-I	70.24 mm	8633
CTL × CTW	168.10 mm^2	7802
Body mass	8950 g	

The ratio between the measurements of the fossil sample and those of the living sample is generally close to 1 (x = 0.93, SD = 0.17, CV = 18%) (Figure 4). These results suggest similarities among the measures of both specimens and, consequently, among the skull proportions. The measure with the greatest deviation from ratio 1 is COW, followed by COL and FMW (0.56, 0.85 and 1.15, respectively).

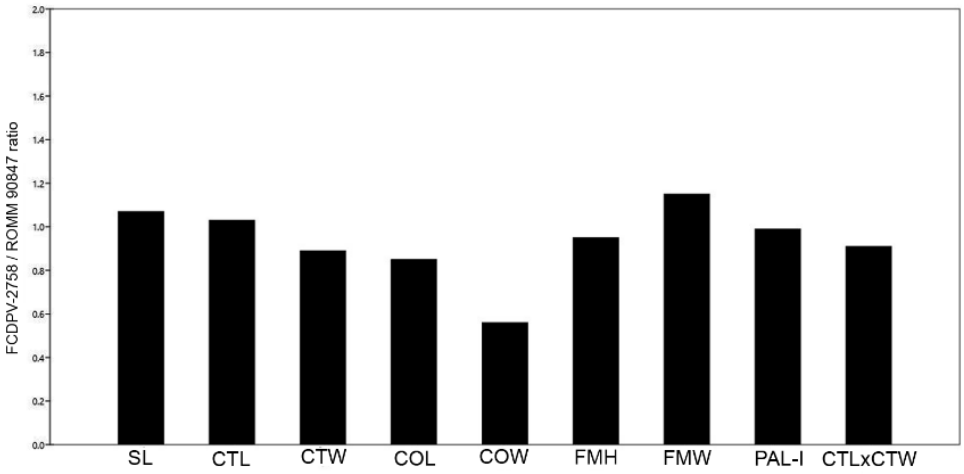

Figure 4. Ratio (quotient) between measurements of the fossil specimen FCDPV-2758 and of an extant specimen of *D. patagonum* (ROMM 90847, Bertrand et al. [32]).

According to the average and median values of estimates obtained through regression equations, the similarity between body proportions and the fact that both would belong to the same taxon make reasonable the hypothesis of an approximate geometric similarity, and therefore a body mass of the fossil that is not very different from that of living Patagonian maras. The minimum value obtained by this method (1535 g) is a clear underestimation, produced by the COW variable that notably differs between the fossil and the living individual. The cranial dimensions allow us to infer that it is an animal larger in length than, for example, the Chacoan mara *Dolichotis salinicola*, with a mass ranging from 1.8 to 2.3 kg [41]. The highest estimate (13,576 g) is produced by the FMW variable, which is slightly more than 50% greater than the mass of ROMM 90847. However, it is plausible, considering that the range of the living Patagonian mara *D. patagonum* is 8–12 kg [42].

According to the median and average values, these results are consistent with those obtained with the equations of Millien [33] (see Table 1), which predict masses close to 7000 and 8000 g. The estimates performed via the equations of Bertrand et al. [32] exhibit a large dispersion of values, including some underestimates (~3000 g) and an extreme value of ~45,000 g, which seems to be unrealistic owing to the estimated size. This last value is considered an extreme overestimation and was eliminated to recompute the average and median values, which were 7041 g and 5660 g, respectively (SD = 4951 g, CV = 70%). The estimate obtained by the OCW variable of Engelman [31] of 3440 g would represent an underestimation in view of the previous discussion and considering that the fossil sample would have had a body mass close to that of the extant Patagonian mara. The estimates based on the basal length of the skull and the upper teeth series length obtained with the equations of Boivin et al. [34] also agree with a body mass close to that of the extant *D. patagonum,* but not the estimates obtained from the area and maximum width of the dental series. According to these authors, the basal length tends to be a better predictor than dental measures (except for largest rodents); as such, the LVS results are trustworthy and support the hypothesis of similarity between the body mass of the studied specimen and that of the extant Patagonian mara.

In addition to the arithmetic mean, the median was included in the analysis. Under some circumstances, when extremely high or low values are obtained, it has an advantage over the arithmetic mean because it is not sensitive to extreme values [43]. This is the case for the studied material FCDPV-2758, with extreme values, which are likely to be under- and overestimated values, and the average would not be representative of the set of estimates.

4.3. Scatter Plots and Principal Component Analyses

In the scatter plots, the extant species *Dolichotis patagonum* and *D. salinicola* are very well differentiated in size, and the specimen FCDPV-2758 under study is included in the variability of *Dolichotis patagonum*, which is similar in size (Figure 5; Figure S3: Additional scatter plots). Similarly, the specimens referred as *D.* cf. *patagonum* by Ubilla et al. [7] in southern Uruguay and the material referred as *D. major* by Calcaterra [6] from southwestern Uruguay are similar in size to *D. patagonum* in the compared selected characters. The extinct *D. chapalmalense,* as noted by Madozzo-Jaén et al. [9], shows a large cheek–teeth series differing in this variable from the study material and *D. patagonum* (Figure 5; additional scatter plots in Figure S5). *Dolichotis minor* is similar in size to the smallest specimens of *D. salinicola* in cheek–teeth and M3 length (Figure S3: Additional scatter plots). However, the extinct *D. platycephala* does not differ in the variables considered from the Patagonian mara. The extinct *Prodolichotis prisca* is related to *D. salinicola* instead.

In the PCA, the extant species are differentiated not only by size (PC1), but also by shape (PC2), and the material FCDPV-2758 is included in the morphospace of *D. patagonum* (Figure 6A) (see more details about the relationship between PC1 and size and between other PCs and shape in Rencher [44]). The first two principal components encompass more than 90% of the total variance (PC1, 77.65; PC2, 12.67), and the characters providing major significance in PC1 are D and P4-M3L, and in PC2, PW, D and P4-M3L (see loadings in Figure S6). *Dolichotis chapalmalense* falls within the morphospace of the Patagonian mara, similar to the material from southwestern Uruguay referred as *D. major* by Calcaterra [6]. However, when PC1 vs. PC3 are considered, *D. chapalmalense* is outside of the morphospace of the extant *D. patagonum* and compared taxa (Figure S4: loading values and additional PCA), which is also evident in the 3D projection (Figure 6B). The extinct *P. prisca* is again related to *D. salinicola*. The remaining compared taxa are included or related to the morphospace of *D. patagonum*. In the 3D projection, the distribution of taxa corroborates the inclusion of the studied material in the space of variation of *D. patagonum* and the material referred to as *D. major* by Calcaterra [6] (Figure 6B).

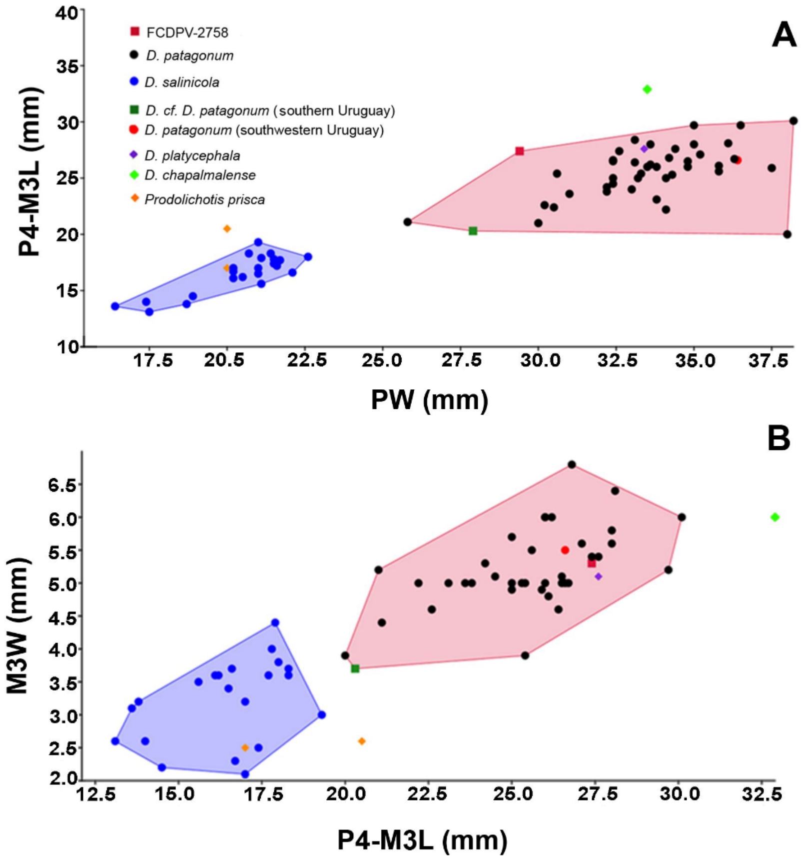

Figure 5. Scatter plots: (**A**) P4-M3L vs. PW; (**B**) M3W vs. P4-M3L.

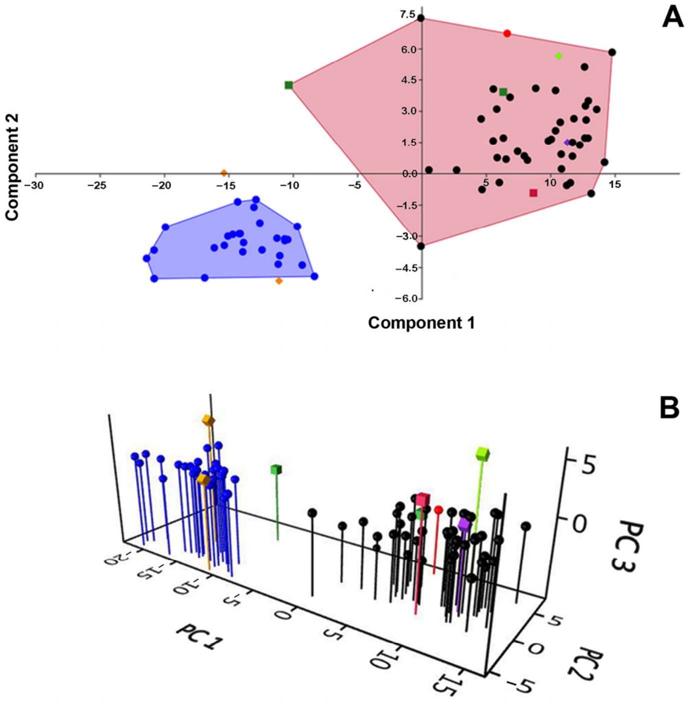

Figure 6. Principal Component Analysis: (**A**) Projection of the first two components based on selected skull and teeth variables (see in Figure S3). (**B**) 3D projection of the first three components. Percentage of variance explained by PC1—77.65, PC2—12.67 and PC3—7.96. Symbols explained in Figure 5.

5. Discussion

5.1. Body Mass

According to the results of central tendency measurements obtained for the distribution of estimates via the aforementioned methods [31–33] and geometric similarity, a body mass of approximately 6–8 kg is proposed for the studied specimen. However, the possibility of reaching or even exceeding 10 kg is not discharged, as shown by some estimates. The comparison of the measurements with those of a living specimen of *D. patagonum* suggests a similar size (in linear dimensions), and consequently, a similar mass. Campos et al. [1] reported for a set of samples collected in Argentina an average of 7.73 kg (SD = 0.62 kg) in males and 8.33 kg (SD = 0.74 kg) in females, which are consistent with the mass range proposed for FCDPV-2758. Concomitantly, the scatter plots and PCA performed on selected teeth and skull variables clearly locate the material in the variation range of the Patagonian mara *D. patagonum*.

We are aware of the potential limitations of using skull and teeth variables to estimate body mass. Nevertheless, when different predictive equations are used, these limitations can be constrained. Brassey [45] noted that estimation via regression has the advantages of simplicity, the possibility of performing predictive equations substantiated by a large dataset based on simple measurements, the lack of a need to rebuild the external form of the animal, as is required in volumetric estimation methods, and its applicability in fragmentary fossil records or isolated skeletal remains. Moreover, some disadvantages, such as erroneous interpretations, subjectivity in the choice of morphological variables, uncertainty in the selection of the current groups of the dataset, mistakes due to taxonomic alterations, ontogenetic stages, and how to manage the results when extrapolations are outside the range of data in extant taxa, should be emphasized. Janis [46] recognized difficulties in obtaining estimates based on skull–dentary variables, indicating that although scaling relationships exist, these relationships are not directly related to those bones supporting the body, such as appendicular bones. These bones may not be good estimators because their morphology is related not only to body mass, but also to other functional or behavioral aspects. In herbivorous mammals, which consume large quantities of food, the skull and dentition patterns are expected to be more closely linked to masticatory mechanics than to body size. Moncunill-Solé et al. [47,48] found similar evidence in small mammals (rodents and lagomorphs among others) and recognized that although craniodental measurements increase with increasing body mass, they are more related to other functional characteristics of the organism and not as closely linked to weight bearing, as are the appendicular elements. Damuth & MacFadden [49] noted that regression equations, even those with low estimate errors, do not guarantee accurate predictions, and that there are many unrecognized error sources; therefore, the statistical errors reported in regressions based on living taxa are underestimates of the inaccuracy of predictions for fossil species.

5.2. Comparative Morphology

The material studied shares morphological characteristics with the Patagonian mara *D. patagonum*, such as a similar design of the occlusal surface of the P4-M3 teeth, with the posterior projection of the M3 separated by a fold including cement and with parallel borders, with the mesopterygoid fossa being U shaped and starting at M2. The body mass is similar to that of extant *D. patagonum*, and all the compared variables are related to the variation in this species. The extant *D. salinicola* is a smaller species, differing not only in size from the studied material and the Patagonian mara but also in several anatomical characteristics, such as a smaller incisive foramina and palate and proportionally larger bullae and a mesopterygoid fossa in V, among others [10].

The extinct dolichotine taxa considered for comparison are mostly described by fragmentary material, except *Prodolichotis prisca* and *D. chapalmalense*. *P. prisca*, a basal dolichotine from the Late Miocene–Early Pliocene in Argentina, is completely discharged not only by its smaller size, similar to *D. salinicola,* but also by several morphological characteristics of its skull and teeth, particularly the mesio-distally oriented posterior projection of its M3 and its lacking cementum between the second prism and this projection.

Dolichotis chapalmalense, an extinct species of the Chapadmalalan Age/Stage of Buenos Aires Province (Early–Late Pliocene) [50], described based on an almost complete skull and mandible, yields differences from the studied material and the Patagonian mara. Although in some comparisons performed here, this extinct species tends to fall into the variation of the extant species *D. patagonum*, it differs in the size of teeth, such as a larger P4-M3 length, and by having an acuminate mesopterygoid fossa with straight divergent margins and a smaller auditory bulla with a shorter anteromedial–posterolateral length, among other things (see [9]).

Dolichotis platycephala was described by Ameghino [40] in the Pleistocene in Argentina based on an incomplete skull severely affected by incrusted sediment, which makes reliable comparisons difficult. It yields similar tooth morphology and shows similar values for the variables compared with the studied material and the extant *D. patagonum*. A difference from the species described by Ameghino [40] seems to be the larger zygomatic width of this species and the rhomboidal shape of the incisive foramen (Figure S5: *Dolichotis platycephala* Ameghino, 1889 (MACN-Pv-556).

Dolichotis major is an extinct species described, at first glance, as part of the genus *Kerodon* by Gervais and Ameghino [12], and is based on a fragment of the skull of the Late Pleistocene–Early Holocene in Argentina. According to these authors, the diagnostic characteristic of this species is a slightly more mesio-distal orientation of the posterior projection of M3. There is cement in the fold, and in addition, its mesopterygoid fossa seems to have started between M2 and M3. In this sense, it seems to differ from the studied material and the current Patagonian mara (Figure S6: *Dolichotis major* (Gervais and Ameghino (1880) (MNHN-P-PAM-267; Figure S8: Lateral and palatal view of *Dolichotis patagonum*), but caution must be taken with respect to the M3 morphology given the variability observed in the extant *D. patagonum*. In fact, in the extant *D. salinicola*, the third lobe extends more posteriorly than they do in the Patagonian mara and Ameghino species (Figure 3C). Notably, Ameghino [40] referred with doubt to this species a mandible—"…it seems likely to me that it comes from the *Dolichotis major*" ("…me parece probable procede del *Dolichotis major*" [40]: p. 222)—which was not found to be associated with the holotype represented by the fragmentary skull. Madozzo-Jaén et al. [9] included this material in this species, and described the horizontal crest extending to the posterior margin of the mandibular condyle as a synapomorphy of a clade integrated by this species and *D. intermedia*. The material from southwestern Uruguay referred as *D. major* by Calcaterra [6] (Figure S9: "*D. major*" (MPC-1035) from Uruguay) can be highlighted, in addition to the corroborated similar size, amongst several characteristics that substantiate its inclusion in *D. patagonum* instead of *D. major*. Notably, there is sediment infilling part of the skull, increasing the distance between both P4s, which can, to some extent, overestimate the palatal width (skull and mandible in Figure S11). According to some characteristics proposed by Campo et al. [10] and Madozzo-Jaén et al. [9], it can be related to the Patagonian mara by the elevated and posterior positions of the orbits, the relative size of the tympanic bulla, and the horizontal crest of the mandible reaching the anteroposterior midpoint of the mandibular condyle, which differs from *D. salinicola*, *D. major* and *D. intermedia*. The most anterior point of the curve between the postcondyloid process and the angular process is above the dorsoventral midpoint of the dentary. The estimated zygomatic width matches that of the Patagonian mara (67.4 mm).

Dolichotis minor, an extinct species described by Gervais and Ameghino [12] from the Pleistocene of Argentina and referred initially to the genus *Kerodon*, based on a partially preserved skull, differs from the Patagonian mara and the material of Uruguay (such as *D. salinicola)* in its minor size. This species has an M3 with its posterior projection parallel to the second prism, with a fold with parallel borders (Figure S7: Occlusal outline of the right P4-M3 of *Dolichotis minor* (Gervais et Ameghino, 1889) (MNHN-P-PAM-265).

According to the available comparative information, including morphology and quantitative comparisons, the identification of the Patagonian mara *D. patagonum* in the studied material from the Late Pleistocene of northern Uruguay seems to be the most parsimonious decision. Two geographic variations at the subspecific level are considered for the extant Patagonian mara [1], which are mostly based on soft characters, but it cannot be discerned that in the Late Pleistocene, other geographic variations developed outside the current geographic area of the species.

5.3. Paleoenvironment and Geographic Distribution

The ecological adaptations of the extant *D. patagonum* are useful for inferring the environment and climatic conditions associated with the Late Pleistocene at these latitudes in South America. The Patagonian mara inhabits some areas in different ecoregions of Argentina [51,52] (Figure S10: Ecoregions in Argentina (from Brown 2018): in the northern steppes of Patagonia, in del Monte, in central western Pampa, in southern Espinal and in southern Dry Chaco, including ecotonal areas between some of these ecoregions [3]. They are mostly characterized by arid to semiarid habitats, including open contexts with bare soils and partially forested areas. The Dry Chaco has a subtropical and warm climate with high temperatures and very scarce precipitation, and with hard wood forests. In the Espinal ecoregion, the climate varies according to its extension, from warm and humid in the north to temperate and dry in the west and south, including the drought season; it is characterized mostly by patches of forests with grasslands and some swamp communities. In the El Monte ecoregion, a temperate dry and warm climate with scarce precipitation predominates, with the drought season resulting in an annual rainfall of approximately 230 to 350 mm. The predominant forest is a high shrub steppe and an open forest of thorny, microphyllous or sharp plants. The Pampa ecoregion, represented by grasslands, in its southern and western central portions is characterized mostly by 400 mm of annual rainfall with a predominantly temperate climate. The Patagonian ecoregion is cold (with an average of 3 °C to 12 °C) and arid, with high fluctuations in rainfall but scarce (200 mm) annual rainfall. It is characterized by semideserts to humid grasslands, with a great variety of shrubby and grassy steppes [51,53–58]. According to Alonso et al. [3], the optimum habitats of *D. patagonum* are steppes and bushes, and the suboptimum habitats are grasslands and forests. This species is characterized as an "edge" species—an inhabitant of open and shrubby areas. These heterogeneous habitats offer food and shelter from predators [3].

The geographic distribution of *D. patagonum* encompasses a dry and cold climate in the Patagonian Province and a temperate and warm climate in the Pampean and southern Chaco Provinces. It is adapted to live under seasonal conditions, including drought periods. In this sense, studies on the feeding behavior of the Patagonian mara in different phytogeographic provinces have revealed an opportunistic strategy of being predominantly grazer, but becoming a mixed feeder during the drought season, and variation of environments [57]. Concomitantly, this species is a long-legged cursorial caviomorph rodent that adapts to living in open areas and specializes in fast locomotion as a mechanism for evading predation [1,10,59,60]. In a broader evolutionary picture, it has been proposed that the acquisition in the lineage of *Dolichotis* of a third incipient lobe, with cement in M3 as a derived condition [35], could be a consequence of abrasive particle feeding due to the installation in the Neogene of more open and arid environments at middle to southern latitudes of South America [9].

The record of *D. patagonum* in the Sopas Formation supports the development of habitats that are suitable for several taxa included in the vertebrate assemblage of this sedimentary unit. As mentioned before, at some outcrops, the Chacoan peccary *Parachoerus wagneri*, an inhabitant of the Dry Chaco, the extinct species of the caviine *Microcavia criolloensis,* the vizcacha *Lagostomus* sp., the flightless avian *Rhea* and the seriema *Cariama* suggest microenvironments agreeing with the presence of the Patagonian mara. In addition, paleoecological studies revealing an open to semi-open canopy are substantiated by the presence of extinct horses, the extinct deer *Morenelaphus*, the extant peccary *Tayassu peccary* and the extinct native ungulate *Neolicaphrium* recens [16,27,28,61]. The seasonality suggested by the record of the Patagonian mara is also substantiated by the presence of migratory avians such as *Cloephaga picta* and earthworm aestivation chambers, which suggest drought periods [19,61]. These scenarios favor the presence of the Patagonian mara in the Late Pleistocene in northern Uruguay, which underwent alterations that were likely associated with climatic changes that caused the extinction of this caviomorph rodent in this area of South America. Concomitantly, other taxa, such as *Microcavia*, *Galea, Lagostomus* and the Chaco peccary *P. wagneri,* are becoming extinct in the area, suggesting that a common cause is likely related to the loss of suitable habitat. Notably, in sediments ranging the last 30 to 8 ka in southern Uruguay (Dolores Formation), some taxa were reported revealing the effect of the Last Glacial Maximum (LGM) (ca. to the last 25 to 18 ka), such as the vizcacha *Lagostomus maximus* and the armadillo *Chaetophractus villosus* [30,62]. Both have become extinct in current times in Uruguay, but are living in the southern-central region of Argentina, and are found in arid to semi-arid conditions. A similar situation, but in southwestern Uruguay, is depicted by the material referred as *D. major* by Calcaterra [6], but considered here as a member of *D. patagonum,* and likely unearthed from the same stratigraphic unit (Dolores Formation). After the LGM and the Antarctic Cold Reversal, increasing climatic amelioration was verified in the latest Pleistocene that, at mid-latitudes of South America, could have been accompanied by a retraction of open areas.

According to the fossil record, *Dolichotis* was a successful inhabitant in the Pleistocene outside the current area of distribution, having been recorded in the northeastern area of Argentina and in the Pampean region of Buenos Aires Province [9,12,40,63,64]; it was also present in Uruguay and probably southern Brazil, severely reducing the area of distribution at the present time, indicating a shifting range and local extinctions.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/fossils3020007/s1, Figure S1: Principal anatomical features used in the comparative analysis; List S1: list of the material used for comparisons; Table S1: Comparative measurements of fossil material; Figure S2: Lateral and Occipital view of the skull and close up view of the auditory bulla of FCDPV-2758; Figure S3: additional scatter plots; Figure S4: loading values and additional PCA; Figure S5: Palatal view of *Dolichotis platycephala;* Figure S6: Palatal view of *Dolichotis major;* Figure S7: Occlusal view of the right P4-M3 of *Dolichotis minor*; Figure S8: Lateral and palatal view of *Dolichotis patagonum*; Figure S9: Palatal and lateral views of skull and lateral view of mandible of "*D. major*" (MPC-1035) from Uruguay; Figure S10: Ecoregions in Argentina.

Author Contributions: Conceptualization (M.U. and M.G.); methodology (M.U., M.G. and A.R.); software (M.U. and M.G.); Investigation (M.U., M.G. and A.R.); data curation (M.U. and A.R.); writing—reviewing and editing (M.U. and M.G.). All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: The raw data supporting the conclusions of this article will be made available by the authors on request.

Acknowledgments: S. Bermúdez (Sistema Museos Colonia), A. Couto (MPC-Colonia), A. Rojas (Facultad de Ciencias), C. de Muizon (MNHN-P), D. Verzi and I. Olivares (MLPV), A. Kramarz (MACN-P), O. Vaccaro (MACN-M), A. Martinelli (MACN-P) for allowing access to collections. C. de Muizon, D. Verzi, and I. Olivares provided photos of *D. major* and *D. patagonum*. A. Corona provided photographic information on *D. platycephala*. M. Boivin (IdGyM, INECOA, CONICET; Argentina) contributed by providing information about her work. J. Ghizzoni, A. Zapata and V. Ghizzoni contributed to the fieldwork. Two anonymous reviewers and editors helped us to improve the manuscript with useful comments and suggestions. Contribution to the Project "Paleontología de Vertebrados" CSIC I+D C302-347.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Campos, C.M.; Tognelli, M.F.; Ojeda, R.A. *Dolichotis patagonum*. *Mamm. Species* **2001**, *652*, 1–5. [CrossRef]
2. Dunnum, J. Family Caviidae G. Fischer, 1817. In *Mammals of South America. Rodent*, 1st ed.; Patton, J., Pardiñas, U., D'Elía, G., Eds.; University of Chicago Press: Chicago, IL, USA, 2015; Volume 2, pp. 690–726.
3. Alonso, V.; Udrizar, D.; Giannoni, S.M.; Campos, C. *Dolichotis patagonum*. In *Categorización 2019 de los Mamíferos de Argentina Según su Riesgo de Extinción*; Lista Roja de los Mamíferos de Argentina, SAyDS-Sarem, Eds.; 2019; p. 337. Available online: https://cma.sarem.org.ar/es/especie-nativa/dolichotis-patagonum (accessed on 20 November 2023). [CrossRef]
4. Roach, N. *Dolichotis patagonum*. IUCN Red List Threat. Species 2016. Available online: https://www.iucnredlist.org/species/6785/22190337 (accessed on 20 November 2023).
5. Bernal, N. *Dolichotis salinicola*. IUCN Red List Threat. Species 2016. Available online: https://www.iucnredlist.org/species/6786/22190451 (accessed on 20 November 2023).
6. Calcaterra, A. Dos roedores fósiles nuevos para Uruguay y confirmación de otro. *Com. Paleont. Mus. Hist. Nat. Montev.* **1972**, *1*, 11–20.
7. Ubilla, M.; Perea, D.; Rinderknecht, A.; Corona, A. Pleistocene mammals from Uruguay: Biostratigraphic, biogeographic and environmental connotations. In *Quaternario de Rio Grande do Sul. Integrando Conhecimentos*, 1st ed.; Ribeiro, A., Girardi, S., Saldanha, C., Eds.; Monografías Sociedade Brasileira de Paleontología: Porto Alegre, Brazil, 2009; pp. 217–230.
8. Kerber, L.; Pereira, R.; Vucetich, M.; Ribeiro, A.; Pereira, J. Chinchillidae and Dolichotinae rodents (Rodentia: Hystricognathi, Caviomorpha) from the late Pleistocene of southern Brazil. *Rev. Bras. Paleontol.* **2011**, *14*, 229–238. [CrossRef]
9. Madozzo-Jaén, M.; Pérez, M.; Deschamps, C. The oldest species of *Dolichotis* (Rodentia, Hystricognathi) from the Pliocene of Argentina: Redescription and taxonomic status of "*Orthomyctera*" *chapalmalense*. *J. Mamm. Evol.* **2021**, *28*, 995–1013. [CrossRef]
10. Campo, D.; Caraballo, D.; Cassini, G.; Lucero, S.; Teta, P. Integrative taxonomy of extant maras supports the recognition of the genera *Pediolagus* and *Dolichotis* within the Dolichotinae (Rodentia, Caviidae). *J. Mamm.* **2020**, *101*, 817–834. [CrossRef]
11. Madozzo-Jaén, M. Systematic and phylogeny of *Prodolichotis prisca* (Caviidae, Dolichotinae) from the northwest of Argentina (late Miocene-early Pliocene): Advances in the knowledge of evolutionary history of maras. *Comptes Rendus Palevol.* **2019**, *18*, 33–50. [CrossRef]
12. Gervais, H.; Ameghino, F. *Les Mammiferes Fossiles de la América Meridional*; Savy e Igon: Paris, France, 1880; pp. 1–225.
13. Ubilla, M.; Perea, D.; Goso, C.; Lorenzo, N. Late Pleistocene vertebrates from northern Uruguay: Tools for biostratigraphic, climatic and environmental reconstruction. *Quat. Internat.* **2004**, *114*, 129–142. [CrossRef]
14. Ubilla, M.; Corona, A.; Rinderknecht, A.; Perea, D.; Verde, M. Marine isotope Stage 3 (MIS 3) and continental beds of northern Uruguay (Sopas Formation): Paleontology, chronology and climate. In *Marine Isotope Stage 3 in Southern South America, 60 ka B.P.-30 ka B.P.*, 1st ed.; Gasparini, G., Rabassa, J., Deschamps, C., Tonni, E., Eds.; Springer: Berlin/Heidelberg, Germany, 2016; pp. 183–205.
15. Antón, D. *Evolución Geomorfológica del Norte del Uruguay*; Dirección de Suelos y Fertilizantes, Ministerio de Agricultura y Pesca: Montevideo, República Oriental del Uruguay, 1975; Unpublished Work.
16. Ubilla, M.; Morosi, E.; Gasparini, G.; Rinderknecht, A. *Brasiliochoerus stenocephalus* (Lund in Reinhardt, 1880), a large extinct peccary in late Pleistocene beds of Uruguay: Comparative, isotopic and paleoecological studies. *J. S. Am. Earth Sci.* **2023**, *129*, 104531. [CrossRef]
17. Martínez, S.; Rojas, A. Quaternary continental mollusks from northern Uruguay: Distribution and paleoecology. *Quat. Internat.* **2004**, *114*, 123–128. [CrossRef]

18. Cabrera, F.; Montenegro, F.; Badín, A.; Ubilla, M.; Martínez, S. Continental mollusk assemblages from the Quaternary of Uruguay. *J. S. Am. Earth Sci.* **2023**, *130*, 104575. [CrossRef]
19. Verde, M.; Ubilla, M.; Jiménez, J.; Genisse, J. A new earthworm trace fossil from palaeosols: Aestivation chambers from the late Pleistocene Sopas Formation of Uruguay. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2007**, *243*, 339–347. [CrossRef]
20. Gasparini, G.; Ubilla, M.; Tonni, E.P. The Chacoan peccary, *Catagonus wagneri* (Mammalia, Tayassuidae) in the late Pleistocene (northern Uruguay, South America): Palaeoecological and palaeobiogeographic considerations. *Hist. Biol.* **2013**, *25*, 679–690. [CrossRef]
21. Jones, W.; Rinderknecht, A.; Montenegro, F.; Vezzosi, R.; Ubilla, M. First report of large cathartids (Aves, Cathartidae) from the late Pleistocene of Uruguay. *J. S. Am. Earth Sci.* **2020**, *107*, 102946. [CrossRef]
22. Manzuetti, A.; Ubilla, M.; Jones, W.; Perea, D.; Prevosti, F. The ocelot *Leopardus pardalis* (Linnaeus, 1758) (Carnivora, Felidae) in the late Pleistocene of Uruguay. *Hist. Biol.* **2022**, *35*, 108–115. [CrossRef]
23. Manzuetti, A.; Ubilla, M.; Jones, W.; Montenegro, F.; Perea, D. The otter *Lontra* Gray, 1843 (Mustelidae, Lutrinae) in the late Pleistocene-early Holocene of Uruguay. *Ann. Paléontol.* **2023**, *109*, 102633. [CrossRef]
24. Cione, A.L.; Gasparini, G.M.; Soibelzon, E.; Soibelzon, L.; Tonni, E.P. *The Great American Biotic Interchange. A South American Perspective*, 1st ed.; Springer: Berlin/Heidelberg, Germany, 2015; pp. 1–97.
25. Cohen, K.M.; Finney, S.C.; Gibbard, P.L.; Fan, J.-X. The ICS international chronostratigraphic Chart. *Episodes* **2013**, *36*, 199–204, Updated 2022. [CrossRef]
26. Ubilla, M.; Perea, D. Vertebrados del Cuaternario continental de Uruguay: Cronología y ambientes. *Paleontol. Electr. APA* **2023**, *23*, 231–240. [CrossRef]
27. Morosi, E.; Ubilla, M. Feeding and environmental studies on late Pleistocene horses in mid-latitudes of South America (northern Uruguay). *Quat. Sci. Rev.* **2019**, *225*, 106025. [CrossRef]
28. Corona, A.; Ubilla, M.; Perea, D. New records and diet reconstruction using dental microwear analysis for *Neolicaphrium recens* Frenguelli, 1921 (Litopterna, Proterotheriidae). *Andean Geol.* **2019**, *46*, 153–167. [CrossRef]
29. Ubilla, M.; Rinderknecht, A. Comparative analysis of *Galea* (Rodentia, Caviidae) and expanded diagnosis of *Galea ortodonta* Ubilla & Rinderknecht, 2001 (Late Pleistocene, Uruguay). *Geobios* **2014**, *47*, 255–269.
30. Ubilla, M.; Rinderknecht, A. *Lagostomus maximus* (Desmarest) (Rodentia, Chinchillidae), the extant plains vizcacha in the late Pleistocene of Uruguay. *Alcheringa* **2016**, *40*, 354–365. [CrossRef]
31. Engelman, R.K. Occipital condyle width (OCW) is a highly accurate predictor of body mass in therian mammals. *BMC Biol.* **2022**, *20*, 37. [CrossRef]
32. Bertrand, O.C.; Schillaci, M.A.; Silcox, M.T. Cranial dimensions as estimators of body mass and locomotor habits in extant and fossil rodents. *J. Vertebr. Paleontol.* **2015**, *36*, e1014905. [CrossRef]
33. Millien, V. The largest among the smallest: The body mass of the giant rodent *Josephoartigasia monesi*. *Proc. R. Soc. B.* **2008**, *275*, 1953–1955. [CrossRef]
34. Boivin, M.; Álvarez, A.; Ercoli, M.D.; Moyano, S.R.; Salgado-Ahumada, J.S.; Ortiz, A.M.; Cassini, G.H. Body mass estimation from cheek tooth measurements in extinct caviomorphs (Ctenohystrica, Hystricognathi): The importance of predictor, reference sample and method. *J. Mamm. Evol.* **2024**, *31*, 43. [CrossRef]
35. Ubilla, M.; Rinderknecht, A. A late Miocene Dolichotinae (Mammalia, Rodentia, Caviidae) from Uruguay, with comments about the relationships of some related fossil species. *Mastozool. Neotrop.* **2003**, *10*, 293–302.
36. Rovereto, C. Los estratos araucanos y sus fósiles. *An. Mus. Hist. Nat. Buenos Aires* **1914**, *25*, 1–249.
37. Kraglievich, L. Diagnosis osteológico dental de los géneros vivientes de la subfamilia Caviinae. *An. Mus. Hist. Nat. Buenos Aires* **1930**, *36*, 59–96.
38. Madozzo-Jaén, M.; Pérez, M. Redescription of a small Caviidae (Rodentia: Hystricognathi) from the Neogene of northwestern Argentina and its systematic implications. *C. R. Palevol.* **2024**, *23*, 269–292. [CrossRef]
39. Hammer, Ø.; Harper, D.A.T.; Ryan, P.D. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontol. Electron.* **2001**, *4*, 1.
40. Ameghino, F. Los mamíferos fósiles de la República Argentina. *Acta Acad. Nac. Cienc. Córdoba* **1889**, *6*, XXXII+1–1026.
41. Gorchow, J. *Dolichotis salinicola*. Animal Diversity Web, University of Michigan (On-Line). 2011. Available online: https://animaldiversity.org/accounts/Dolichotis_salinicola/#BC9848C1-10AC-45DB-B2AA-6CBAD0A5C85F (accessed on 14 December 2023).
42. Baldi, R. Breeding success of the endemic mara *Dolichotis patagonum* in relation to habitat selection: Conservation implications. *J. Arid Environ.* **2007**, *68*, 9–19. [CrossRef]
43. Zar, J. *Biostatistical Analysis*, 5th ed.; Prentice Hall: Upper Saddle River, NJ, USA, 2010; pp. 1–944. Available online: https://bayesmath.com/wp-content/uploads/2021/05/Jerrold-H.-Zar-Biostatistical-Analysis-5th-Edition-Prentice-Hall-2009.pdf (accessed on 15 February 2023).
44. Rencher, A. *Methods of Multivariate Analysis*, 2nd ed.; John Wiley & Sons: New York, NY, USA, 2002; pp. 1–708.

45. Brassey, C.A. Body-mass estimation in Paleontology: A review of volumetric techniques. *Paleontol. Soc. Papers* **2017**, *22*, 133–156. Available online: https://www.cambridge.org/core/journals/the-paleontological-society-papers/article/abs/bodymass-estimation-in-paleontology-a-review-of-volumetric-techniques/16BA5B00CB196283C6D07A24AABAABBA (accessed on 10 February 2023). [CrossRef]
46. Janis, C.M. Correlation of cranial and dental variables with body size in ungulates and macropodoids. In *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*, 1st ed.; Damuth, J., MacFadden, B.J., Eds.; Cambridge University Press: Cambridge, UK, 1990; pp. 255–299.
47. Moncunill-Solé, B.; Jordana, X.; Marín-Moratalla, N.; Moyá-Solá, S.; Köhler, M. How large are the extinct giant insular rodents? New body mass estimations from teeth and bones. *Integrat. Zool.* **2014**, *9*, 197–219. [CrossRef]
48. Moncunill-Solé, B.; Quintana, J.; Jordana, X.; Engelbrektsson, P.; Köhler, M. The weight of fossil leporids and ochotonids: Body mass estimation model for the Order Lagomorpha. *J. Zool.* **2015**, *295*, 269–278. [CrossRef]
49. Damuth, J.; MacFadden, B.J. Introduction: Body size and its estimation. In *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*, 1st ed.; Damuth, J., MacFadden, B., Eds.; Cambridge University Press: Cambridge, UK, 1990; pp. 1–10.
50. Prevosti, F.; Romano, C.; Pardiñas, U.; Forasiepi, A.M.; Hemming, S.; Bonini, R.; Candela, A.M.; Cerdeño, E.; Madozzo Jaén, M.C.; Ortiz, P.E.; et al. New radiometric 40Ar-39Ar dates and faunistic analyses refine evolutionary dinamics of Neogene vertebrates assemblages in Southern South America. *Sci. Rep.* **2021**, *11*, 9830. [CrossRef]
51. Brown, A.; Martínez Ortiz, M.; Acerbi, J.; Corcuera, J. *La Situación Ambiental Argentina 2005*; Fundación Vida Silvestre: Buenos Aires, Argentina, 2006; pp. 1–587.
52. Brown, A. Ecoregiones. 2018. Available online: https://www.arcgis.com/apps/mapviewer/index.html?layers=eb24b243af3c47ab950c558f1e45d91c (accessed on 1 July 2024).
53. Kufner, M.B.; Sbriller, A.P. Composición botánica de la dieta del mara (*Dolichotis patagonum*) y del ganado bovino en el Monte mendocino. *Rev. Arg. Prod. An.* **1987**, *7*, 255–264.
54. Rosati, V.; Bucher, E. Seasonal diet of the Chacoan Cavy (*Pediolagus salinicola*) in the western Chaco, Argentina. *Mammalia* **1992**, *56*, 567–574. [CrossRef]
55. Sombra, M.; Mangione, A. Obsessed with grasses? The case or mara *Dolichotis patagonum* (Caviidae, Rodentia). *Rev. Chilena Hist. Nat.* **2005**, *78*, 401–408. [CrossRef]
56. Rodríguez, D.; Dacar, M. Composición de la dieta de la mara (Dolichotis patagonum) en el sudeste del Monte Pampeano (La Pampa, Argentina). *Mastozool. Neotrop.* **2008**, *15*, 215–220.
57. Puig, S.; Cona, M.; Videla, F.; Méndez, E. Diet of the Mara (*Dolichotis patagonum*), food availability and effects of an extended drought in northern Patagonia (Mendoza, Argentina). *Mamm. Biol.* **2010**, *75*, 389–398. [CrossRef]
58. APN. *Fichas Ecorregiones*; Administración de Parques Nacionales: Buenos Aires, Argentina, 2024. Available online: https://www.google.com/url?sa=t&source=web&rct=j&opi=89978449&url=https://www.sib.gob.ar/portal/wp-content/uploads/2021/10/fichas_ecorregiones.pdf&ved=2ahUKEwjHk_K58aeNAxU7GLkGHZx3AHwQFnoECBkQAQ&usg=AOvVaw3Pu5zJyQnJTUgH_QT8WQ_j (accessed on 20 November 2023).
59. Elissamburu, A.; Vizcaíno, S. Limb proportions and adaptations in caviomorph rodents (Rodentia, Caviomorpha). *J. Zool. Lond.* **2004**, *262*, 145–159. [CrossRef]
60. Vasallo, A.; Rocha-Barboza, O. Limb bone stress in the mara *Dolichotis patagonum* (Caviomorpha, Caviidae, Dolichotinae). *Hystrix* **2020**, *31*, 35–39.
61. Tambussi, C.; Ubilla, M.; Acosta, C.; Perea, D. Fossil records and palaeoenvironmental implications of *Chloephaga picta* (Gmelin, 1789) (Magellan Goose) and *Cariama cristata* (Linnaeus, 1766) (Seriema) from the Late Pleistocene of Uruguay. *N. Jarb. Geol. Palaeontol. Mh.* **2005**, *5*, 257–268. [CrossRef]
62. Perea, D.; Toriño, P.; Rego, N.; Vezzosi, R.; Montenegro, F. *Chaetophractus villosus* (Desmarest, 1804) (Xenarthra: Euphractinae) in Uruguay (Upper Pleistocene): Taxon age, biogeography, and paleoclimatic implications. *J. Mamm. Evol.* **2022**, *29*, 773–782. [CrossRef]
63. Álvarez, B. Los mamíferos fósiles del Cuaternario de Arroyo Toropí, Corrientes (Argentina). *Ameghiniana* **1974**, *11*, 295–311.
64. Francia, A.; Zurita, A.; Orfeo, O.; Miño-Boilini, A.R.; Erra, G.; Zacarías, S.; Rodríguez-Bualó, M.; Alcaraz, M.A.; Lutz, A.I. Paleontología y geología del Pleistoceno de la provincia de Corrientes, Argentina. *Acta Geol. Lill.* **2019**, *26*, 165–192.