

Morphological characteristics of the uterus and uterine cervix of the plains viscacha (*Lagostomus maximus*)

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Abstract

The plains viscacha is a hystricognathi rodent with special reproductive characteristics. Despite poly-ovulation of 800 oocytes, it generates a high embryonic mortality since from 10 to 12 implantations only one or two offspring are born. The present work analyses the morphological, morphometrical, histochemical and lectin histochemical characteristics of the uterus and uterine cervix of pregnant and non-pregnant viscacha. Anatomically, the uterus has two horns each one continued with a short cervix devoid of glands. The structure of the uterus is like that of other species; however, the proportion and size of its glands varies according to the physiological state. In viscacha, there is no uterine body and cervixes cannot be differentiated externally. The formation of two sack bottoms is determined by the presence of a middle raphe in the cranial portion of the vagina. The so-described anatomy is different from that described in other hystricognathi such as guinea pig and coypu. The cervix presents two microscopically differentiable regions: the endocervix and the ectocervix lined by epithelia with different characteristics. The general characteristics of the uterus of *L. maximus* do not show specific differences with those of other mammals that might explain its peculiar gestation.

KEYWORDS

Hystricognathi, lectin histochemistry, uterine horn

1 | INTRODUCTION

The plain viscacha (*Lagostomus maximus*) is a South American hystricomorpha rodent that has unique reproductive characteristics such as a poly-ovulation of around 800 oocytes and poly-implantation of 10–12 embryos of which, usually, only the two closest to the vagina are born (Weir, 1971a). To interpret the phenomenon of poly-ovulation, several studies were carried out on the ovary of this species. These studies demonstrated the presence of numerous cordons of cortical and medullary tissue that fold and invaginate to increase the contact surface with the outer part of the organ (Flamini, Barbeito, Gimeno, & Portiansky, 2009), the

low levels of oocytes apoptosis (Jensen, Willis, Leopardo, Espinosa, & Vitullo, 2008) and the great development of the interstitial glands (Flamini et al., 2009; Gil et al., 2007).

In this species, the morphological and histochemical features of the vagina (Flamini, Díaz, Barbeito, & Portiansky, 2012), the uterine tubes (Flamini, Barbeito, & Portiansky, 2012) and the placenta (Flamini et al., 2011) were also described. Compared with other hystricomorpha and unlike what happens with the ovary, no substantial differences were found in the morphology of these organs. However, within this sub-order, viscacha is the only species in which the presence of a well-developed and constant female prostate was demonstrated (Flamini, Barbeito, Gimeno, & Portiansky, 2002).

Considering the poly-implantation characteristics and the high embryonic death, it is surprising the scant references related to the uterus and, particularly, the cervix of this species. Some works date back more than 40 years and bring few data. Thus, Giusti and Hug (1922) just reported the weight of two complete uteri but did not describe them neither macroscopically nor microscopically. The more general aspects of the anatomy and physiology of the reproductive tract of the female plains viscacha were described by Weir (Weir, 1971a). It was established that the uterus is double and consists of two horns and two cervixes, without the presence of a uterine body. Histologically, they are formed by mucosa, muscular and serous layers. As for the physiological changes during pregnancy, implantation ends on day 24, but only on days 26–28, the decidua is prominent (Roberts & Weir, 1973).

Here, we describe macro- and microscopically the uterus and cervix of *L. maximus*. Also, we characterise the uterine saccharide pattern using lectin histochemistry, as a necessary step in the designing of studies to understand the possible origin of poly-implantation and embryonic resorption processes described in this species.

2 | MATERIALS AND METHODS

2.1 | Sample collection

Thirty adult plains viscacha females were used. Their weight ranged between 4 and 5.5 kg. Animals were captured in different fields of ECAS (Estación de Cría de Animales Salvajes), Ministry of Agribusiness, Buenos Aires province, Argentina. The traps were placed at noon and withdrew the next day in the morning. With this method, it was possible to catch more than one animal per trap. All procedures performed on viscacha were approved by the Institutional Committee for

the Care and Use of Laboratory Animals (CICUAL) at the School of Veterinary Sciences, National University of La Plata, Argentina (protocol #52-4-15T).

The periods in which the traps were placed were as follows: (a) March–April, which coincides with the onset of oestrus; (b) July–August, where most births occur; and (c) December–January, where most females are in anoestrus (Flamini et al., 2009).

Captured animals were anaesthetised by administration of an intramuscular dose of ketamine hydrochloride (Ketanest, Scott Cassara Laboratory) (50 mg/kg BW). Subsequently, they were perfused with a 4% paraformaldehyde solution (Gage, Kipke, & Shain, 2012). Necropsy of the females was performed immediately after slaughter, isolating the entire reproductive tract and removing the uterus and cervix for study. Based on the anatomical characteristics of the female genital system, females were divided into the following categories: anoestrus ($n = 4$), follicular phase ($n = 5$), early pregnancy (with multiple implantations) ($n = 12$) and late pregnancy (with two implantations) ($n = 9$) (Flamini et al., 2009).

2.2 | Histological techniques

Samples obtained were processed for their inclusion in paraffin. The following histological techniques were performed on 5- μ m-thick serial cuts: haematoxylin and eosin for general tissue description, Masson trichrome to differentiate connective tissue and Gomori reticulin to evidence reticular fibres. The following histochemical techniques were also applied: PAS (periodic acid–Schiff) to evidence glycoconjugates (GCs) with oxidizable vicinal diols and glycogen (Mc Manus, 1948) and Alcian blue to demonstrate acid glycoconjugates. A colouring solution (pH 2.5) was used to evidence glycoconjugates with carboxylic groups and O-sulphated esters;

Lectin	Acronym	Specificity ^{a,b}	Hapten
Group I		Glc/Man	
<i>Canavalia ensiformis</i>	CON-A	α -D-Man; α -D-Glc	α -D-Methyl-Man
Group II		GlcNAc	
<i>Triticum vulgare</i>	WGA	β -D-GlcNAc; NeuNAc	NeuNAc
Group III		GalNAc/Gal	
<i>Dolichos biflorus</i>	DBA	α -D-GalNAc	D-GalNAc
<i>Glycine maximus</i>	SBA	α -D-GalNAc; β -D-GalNAc	D-GalNAc
<i>Recinus communis</i>	RCA-1	β -Gal	Lactosa
<i>Arachis hypogaea</i>	PNA	β -D-Gal (β 1–3)> D-GalNAc	Lactosa
Group IV		L-Fuc	
<i>Ulex europaeus</i>	UEA-1	α -L-Fuc	L-Fuc

TABLE 1 Lectins used and their carbohydrate specificities

^aGoldstein and Hayes (1978).

^bGal, galactose; GalNAc, *N*-acetylglucosamine; Glc, glucose; GlcNAc, *N*-acetylglucosamine; L-Fuc, L-fucose; Man, mannose; α -D-Methyl-Man, α -D-Methyl-mannose; NeuNAc, acetyl-neuraminic acid (sialic acid).

sulphated glycoconjugates were identified with a pH 1.0 solution, while for highly sulphated glycoconjugates, a pH 0.5 solution was used (Lev & Spicer, 1964; Suvarna, Lyton, & Bancroft, 2013).

2.3 | Lectin histochemistry

Labelling with biotinylated lectins was used to identify specific sugar residues of GCs. Seven different specific lectins (Vector Laboratories, Inc.) were used (Table 1). Paraffin-embedded sections mounted on slides coated with HistoGrip (Zymed Laboratories) were deparaffinised with xylene, incubated in 0.3% H₂O₂ (100 volumes) in methanol for 30 min at room temperature to block endogenous peroxidase activity. Samples were then hydrated, washed in

0.01 M phosphate-buffered saline (PBS), pH 7.2, and treated with 0.1% bovine serum albumin in PBS for 15 min to inhibit the non-specific binding. Sections were incubated with biotinylated lectins for 30 min at room temperature and rinsed in PBS for 15 min. Samples were then treated with the avidin–biotin–peroxidase complex (ABC) for 45 min (Vector Laboratories, Inc). The horseradish peroxidase was activated by incubation with a buffered 0.05 M Tris-HCl solution, pH 7.6, containing 0.02% diaminobenzidine (DAB—BioGenex) and 0.05% hydrogen peroxide (H₂O₂) for 4–10 min.

Three sections per sample of each animal were analysed. Classification of staining was as follows: no labelling (0), weak labelling (1), moderate labelling (2) and strong labelling (3) (Flamini, Díaz, et al., 2012; Tano de la Hoz, Eyheramendy, Felipe, & Díaz, 2016).

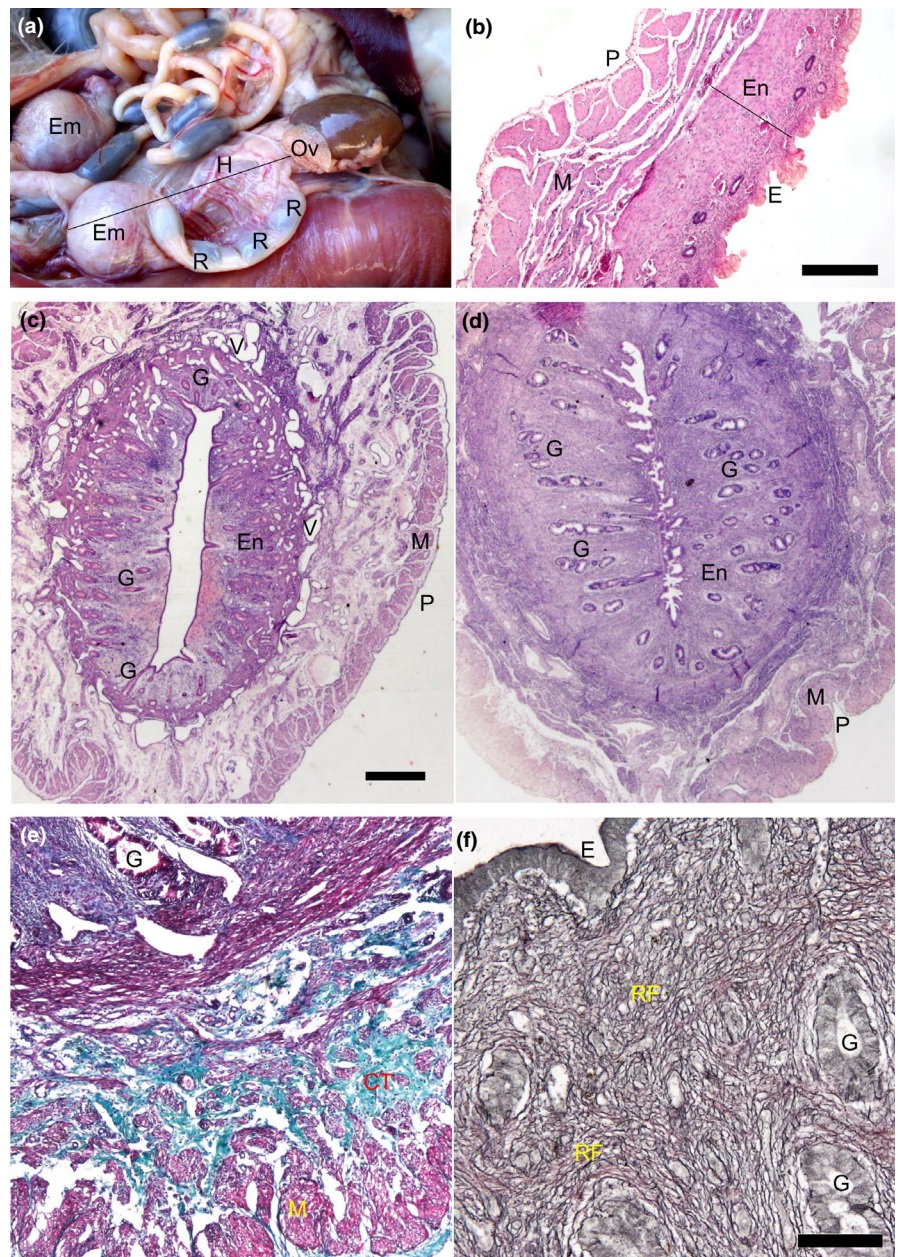


FIGURE 1 Macro- and microscopical appearance of the uterus of *Lagostomus maximus*. (a) Macroscopic appearance of the uterus of *L. maximus*. Ov: ovary. H: uterine horn. R: resorption. Em: viable embryo. (b) Microphotography of the uterine horn at late pregnancy. En: endometrium. E: epithelium. M: myometrium. P: perimetrium. Haematoxylin and eosin. Bar for B and E: 300 μ m. (c) Microphotography of the uterus in female in anoestrus. En: endometrium. G: uterine glands. M: myometrium. P: perimetrium. Haematoxylin and eosin. Bar for (C and D): 500 μ m. (d) Microphotography of the uterine horn in a female at follicular phase. En: endometrium. G: uterine glands. M: myometrium. P: perimetrium. Haematoxylin and eosin. (e) Microphotography showing a sector of the endometrium and myometrium. G: gland. M: myometrium smooth muscle. CT: connective tissue. Masson's trichrome. (f) Uterine endometrium of a female at follicular phase. E: luminal epithelium. G: endometrial glands. RF: reticular fibres. Gomori. Bar: 100 μ m

TABLE 2 Length of uterine horns of non-pregnant females

Physiological state	Right horn	Left horn
Anoestrus	6.45 ± 2.05	6.40 ± 2.26
Follicular face	4.12 ± 0.63	3.85 ± 0.60

Note: All values are expressed as mean cm ± SE

2.4 | Morphometry

Macroscopic morphometry was performed using a calliper. Histological morphometric studies were performed on the haematoxylin and eosin-stained sections. For this purpose, histological images were captured from a microscope (Olympus BX53) using a mounted digital video camera (Olympus DP73). Digitised images were analysed using an image analyser (Image-Pro Plus v6.3, Media Cybernetics). The major axis of the cells of the uterine epithelium and uterine glands, and the thickness of the endometrium were the analysed parameter.

2.5 | Statistical analysis

The macro- and micromorphometric data were expressed as mean ± SEM and analysed by ANOVA. The Bonferroni test was used to establish the significance of the differences. Significant differences were considered those with a value of $p < 0.05$.

3 | RESULTS

3.1 | Macroscopic findings

3.1.1 | Uterus and cervix

The uterus was attached to the abdominal cavity through the mesometrium, a peritoneal fold which covered the total

length of the organ (Figure 1a). This fold was extensive, which would allow easy movement of the organ inside the cavity.

Anatomically, the organ is formed by two uterine horns which, macroscopically, cannot be distinguished from the cervixes that enter the cranial portion of the vagina. All sectors of the horns had the same morphological characteristics and identical colour.

A longitudinal sectioning of the uterus showed that each uterine horn had an irregular central light due to the presence of folds. Each horn continued with its cervix that independently enters the cranial portion of the vagina. This particularity classifies the uterus of this species as double type. At the vagina, numerous longitudinal folds of the cervix were observed. Analysing the organ, it can be affirmed that there is no uterine body, so that on each side of the vaginal side of the cervixes, bottom pouches are formed. These bottom pouches were present at each lateral side of the beginning of a middle septum, which can be seen in the cranial portion of the vagina.

The horns presented different morphological characteristics and size in relation to the physiological state of the female. Non-pregnant female's horns maintained a relatively uniform diameter for most of its length, although a thinning towards the uterine tubes and a caudal dilatation at the level of the union with the vagina were observed. Data corresponding to the length of the uterine horns of non-pregnant females are presented in Table 2. Differences between females in anoestrus and females at the follicular phase and between both uterine horns were not significant.

Females with multiple implantations showed greater variations in uterine morphology. Uterine horns with gestation of few days presented a cluster appearance, due to the presence of several (3–6) implants of different sizes (Figure 1a). Those that were closer to the uterine tube were always smaller than those located closer to the vagina. In a longitudinal section

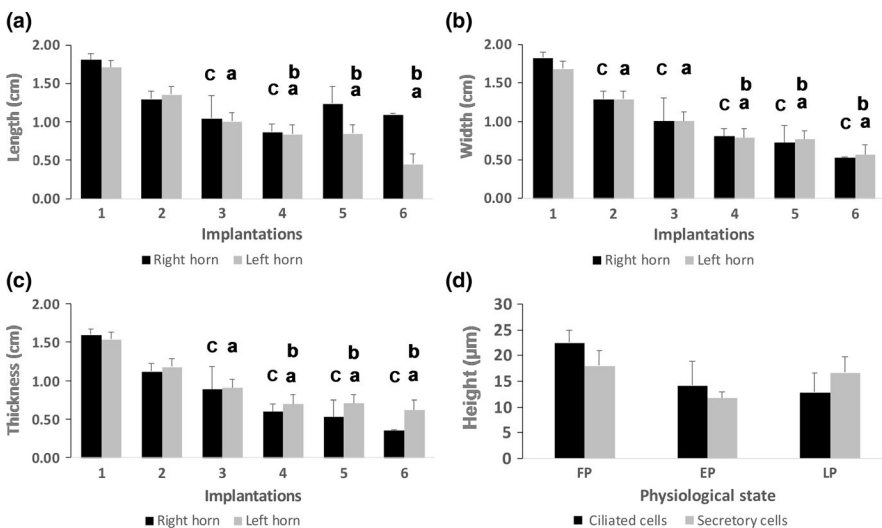


FIGURE 2 Morphometric analysis of the implantations and epithelial cells of the uterine mucosa. (a) Length of the implantations. (b) Width of the implantations. (c) Thickness of the implantation. All values are expressed in cm (d). Height of the ciliated and secretory cells in different physiological states. All values are expressed in µm. Fp: Follicular phase. Ep: Early pregnancy. Lp: Late pregnancy. ^a $p < 0.01$ vs. implant 1. ^b $p < 0.01$ vs. implant 2. ^c $p < 0.05$ vs. implant 1

of the uterine horn, it was observed that the smaller implants were brown or black and amorphous. The major implantations, however, were white-yellowish with some greyish sites and had zones of different texture. The largest implantations had an eccentric cavity in the shape of a crescent. The rest of the implantations were variable in both colour and consistency. Morphometric data of the implantations are presented in Figure 2a-c.

Females with more advanced pregnancy (three or more months of gestation) usually showed a foetus per uterine horn. Of a total of nine females caught in this physiological state, five showed some particularities: a female had a developed foetus in the right horn, sharing it with a reabsorpted implant, while in the left horn it had only one foetus; another animal presented a developed foetus in the left horn while in the right one three united implants were seen, without presenting a recognizable internal structure (homogeneous aspect), dark grey to black colour. This image is compatible with an embryonic reabsorption pattern. Three females had two foetuses developed in the right horn and one in the left horn, which would give rise to a delivery of three offspring. All at-term foetuses had their body covered with adult characteristic hair, had teeth and nails and could be sexed. The uterus of the pregnant females presented a very thin wall, allowing the observation of the foetus through it, as well as the placement of the placenta. The morphometric data corresponding to the uterine horns of the at-term pregnant females can be observed in Table 3. In no case, differences between both horns were significant.

Most of the mature foetuses present in a horn had different sex than those in the opposite horn. In four cases, the foetuses were two males and in two cases were two females. In the three cases where the pregnant females had three offspring, the following particularities were found: two male foetuses were located in the right horn and a female in the left one; two females in the right horn and one female in the left; and, in the third case, one male and one female in the right uterine horn and one male in the left one.

3.2 | Microscopic findings

3.2.1 | Uterus

General structure

Microscopic observation of the uterus revealed three well-defined tunics. The innermost tunic was the mucosa or endometrium, formed by the superficial epithelium that continues with the chorion or lamina propria of connective tissue with glands. The middle one was the muscular tunic tissue or myometrium, formed by smooth muscle fibres, while the outermost layer was formed by the serosa or perimetrium (Figure

TABLE 3 Morphometry of the uterine horns in pregnant females with at-term foetuses

Morphometric analysis	Right horn	Left horn
Length	10.17 ± 0.73	9.79 ± 0.60
Width	5.38 ± 0.28	5.34 ± 0.25
Thickness	3.79 ± 0.33	3.89 ± 0.27

Note: Values are expressed as mean cm ± SE.

1b-d). No differences were found in the structure of these tunics along the cervix.

Endometrium

The superficial epithelium was formed by a single layer of cylindrical cells. Two different types of cells were recognised: ciliated and secretory. Ciliated cells had a central nucleus, with the chromatin arranged in the form of fine granules, oval or round in accordance with the height of the cell. The cytoplasm was acidophilus in its entirety. During anoestrus, no ciliated cells were observed.

When stained with haematoxylin and eosin, secretory cells were found between the ciliated cells, although they were difficult to distinguish. They were characterised by presenting an oval nucleus, located in the central region or slightly displaced towards the inferior third of the cytoplasm. Nuclear chromatin was arranged in fine granules, and the nucleolus was evident. The cytoplasm appeared pale in some regions, which gave it a vacuolated appearance.

Using techniques for the identification of carbohydrates, the presence of PAS-positive and Alcian blue-positive material was demonstrated in the glycocalyx region of the secretory cells (Figure 3a). PAS- and AB-positive staining could also be recognised inside granules in the apical area of the cells. Staining with AB blue was intense when used at pH 2.5, while at pH 1, the labelling was weak and at pH 0.5 was negative (Figure 3b).

The lamina propria was formed by connective tissue invaded by glands. Using Masson's trichrome technique, fine collagen fibres arranged in irregular beams were observed (Figure 1e). These fibres were less abundant in the subepithelial region where the cellular nuclei predominate. Although cells were observed in the deepest area of the mucosa, the connective tissue had abundant collagen fibres. Reticular fibres were distributed throughout the thickness of the chorion where they formed a network outside the superficial epithelium and condense at the periphery of the glands (Figure 1f). They also formed a mesh around the muscle fibres and blood vessels. The thin elastic fibres were evenly distributed in the thickness of the mucosa and were more conspicuous around the muscle fibres and blood vessels.

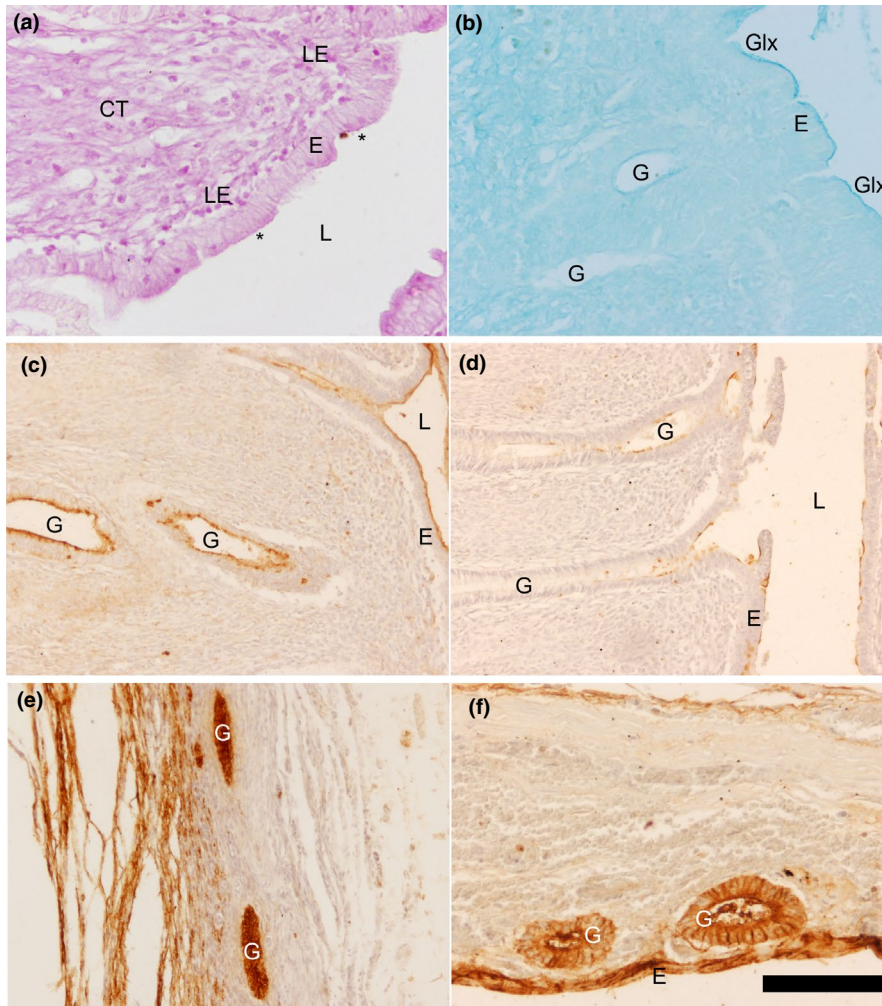


FIGURE 3 Histochemical and lectin histochemical aspect of *Lagostomus maximus* uterus. (a) Uterine horn of a female at follicular phase. L: lumen of the uterine horn, E: positive PAS epithelial surface, LE: leucocytes. *PAS cells positive. Bar: 100 μm . (b) Detail of the endometrium in a female at follicular phase. E: superficial epithelium, G: gland, Glx: glycocalyx. Alcian blue pH 2.5. Bar: 100 μm . (c) Detail of the endometrium in a female at follicular phase. RCA-1 lectin. L: lumen, E: superficial epithelium, G: glands. The glycocalyx of the luminal and the glandular epithelium are observed. Bar: 200 μm . (d) Detail of the endometrium in a female at follicular phase. Lectin UEA-1. L: lumen, E: superficial epithelium, G: glands. The glycocalyx of the luminal and the glandular epithelium are observed. Bar: 200 μm . (e) Endometrium of a female at early pregnancy. DBA lectin. G: endometrial glands present in the resorption zone. Bar: 200 μm . (f) Detail of the endometrium in a female at late pregnancy. SBA Lectin. E: superficial epithelium, G: endometrial glands. Bar: 100 μm

The tubular uterine glands showed special characteristics depending on the female different physiological states. During anoestrus, glands were scarce, shallow and had a narrow light. During the follicular phase, glands were deep, reaching the muscular tunic, and had a tortuous route. Branches of the adenomeres were observed in some glands. The light of the glands was wide.

In the pregnant females with multiple implants, the uterine glands were also deep and tortuous, but their light was narrow, in a similar fashion as was observed during anoestrus. At term pregnancy, glands were sparse and similar in structure to those found in anoestrous females.

Connective tissue also exhibited features that varied with the physiological states. During anoestrus, many fibroblasts with large nuclei with very fine chromatin granules were observed. Infiltrative cells, mainly lymphocytes, were also identified. The collagen fibres were thin and sparse. Regular amount of amorphous intercellular substance and small-calibre blood vessels was observed. In pregnant females, the connective tissue was lax, but had fewer cells. The blood vessels were small, congestive and were located very close to the superficial epithelium.

At the implantation sites, superficial epithelium disappeared in areas of intimate contact with the embryo or reabsorbed embryonic mass, leaving the embryo in direct contact with the chorion of the uterus. In very advanced pregnancy, the thickness of the uterine mucosa was greatly reduced.

Morphometry. The height of the cells lining the organ lumen varied according to the physiological state of the female. Morphometric data are shown in Figure 2d. Their average height during oestrus was $9.35 \pm 1.89 \mu\text{m}$.

Thickness of the endometrium and diameter of the uterine glands' measurements are presented in Table 4.

Bars corresponding to females in anoestrus were not represented since, at this physiological state and due to the absence of cilia, both cell types cannot be distinguished. Even so, the height of the epithelium was measured, taking cells at random.

In the uteri of the non-pregnant females, no differences were found between the different regions of the uterine horns.

Lectin histochemistry. The use of different biotinylated lectins to demonstrate the presence of GCs on the superficial

TABLE 4 Morphometric analysis of the uterine mucosa in different physiological states

Physiological state	Thickness	Glandular diameter
Anoestrus	436.88 ± 67.10 ^a	58.2 ± 4.00 ^c
Follicular phase	1,052.71 ± 1.97	107.93 ± 1.33 ^d
Early pregnancy	895.53 ± 34.95	56.42 ± 0.39
Late pregnancy	70.22 ± 27.18 ^b	37.91 ± 5.66

Note: All values are expressed in $\mu\text{m} \pm \text{ES}$ and represent the mean $\pm \text{ES}$.

Significance:

^aVs. the remaining groups;

^bVs. follicular phase and early pregnancy;

^cVs. follicular phase and late pregnancy;

^dVs. early pregnancy and late pregnancy.

epithelium and cells of the glands showed a pattern of variable distribution in females according to their physiological condition. Table 5 shows the reactivity of the different lectins on the superficial and glandular epithelium of the uterus.

The WGA, SBA and RCA-1 lectins showed an intense reaction (Figure 3c-f), mainly in the glycocalyx region of the superficial epithelial cells, in all the analysed groups. On the other hand, the UEA-1 labelling was very intense

in the glycocalyx of the uterine epithelium of females in anoestrus and moderate, in the same region, in females in follicular phase (Figure 3d), whereas it was negative in pregnant females. The reactivity with the WGA, SBA and UEA lectins in the apical surface of superficial secretory cells and uterine glands was moderate in females in anoestrus. In the same animals, the reactivity with RCA-1 was negative. CON-A and PNA lectins reacted moderately in the glycocalyx of the uterine epithelium of females in anoestrus, while reactivity was negative for pregnant viscacha. The affinity for the lectins CON-A, PNA and DBA showed variations (Figure 3e), mainly in females in follicular phase: negative reactivity in some cases, whereas in others, the reaction was moderate or weak. The labelling pattern for the different lectins in the glands showed similarities with that observed in the superficial epithelium of the organ.

Myometrium

This tunic is formed by two strata of smooth muscle: one internal circularly arranged and one external showing longitudinal fibres. Between both strata, a vascular stratum formed

TABLE 5 Lectin histochemical reaction of the superficial epithelium of the uterus and the glandular epithelium in its basal and apical zones

Lectin	Zone	Anoestrus		Follicular phase		Early pregnancy		Late pregnancy	
		Epithelium	Gland	Epithelium	Gland	Epithelium	Gland	Epithelium	Gland
WGA	Glycocalyx	3	3	3	2	3	2	3	2
	Apical	2	2	2	1	0	0	1	2
	Basal	0	0	0	0	0	0	0	0
CON-A	Glycocalyx	2	2	1/0	1/0	1	0	0	0
	Apical	2	2	1/0	1/0	2	0	2	2
	Basal	0	0	0	0	0	0	0	0
DBA	Glycocalyx	0	0	2/0	2/0	3	3	1	0
	Apical	0	0	2/0	2/0	3	3	2	1
	Basal	0	0	0	0	2	2	2	0
SBA	Glycocalyx	3	3	3	2	3	3	3	3
	Apical	2	1	2	1	2	1	3	3
	Basal	0	0	0	0	+	0	3	0
PNA	Glycocalyx	2	2	2/0	2/0	0	0	0	0
	Apical	0	0	0	0	0	0	2	0
	Basal	0	0	0	0	0	0	0	0
RCA-1	Glycocalyx	3	3	3	3	2	0	3	3
	Apical	0	0	2	2	2	0	2	2
	Basal	0	0	0	0	0	0	0	0
UEA-1	Glycocalyx	3	3	2	1	0	0	0	0
	Apical	2	2	2	1	0	0	0	0
	Basal	0	0	0	0	0	0	0	0

Note: (0) no labelling; (1) weak labelling; (2) moderate labelling and (3) strong labelling.

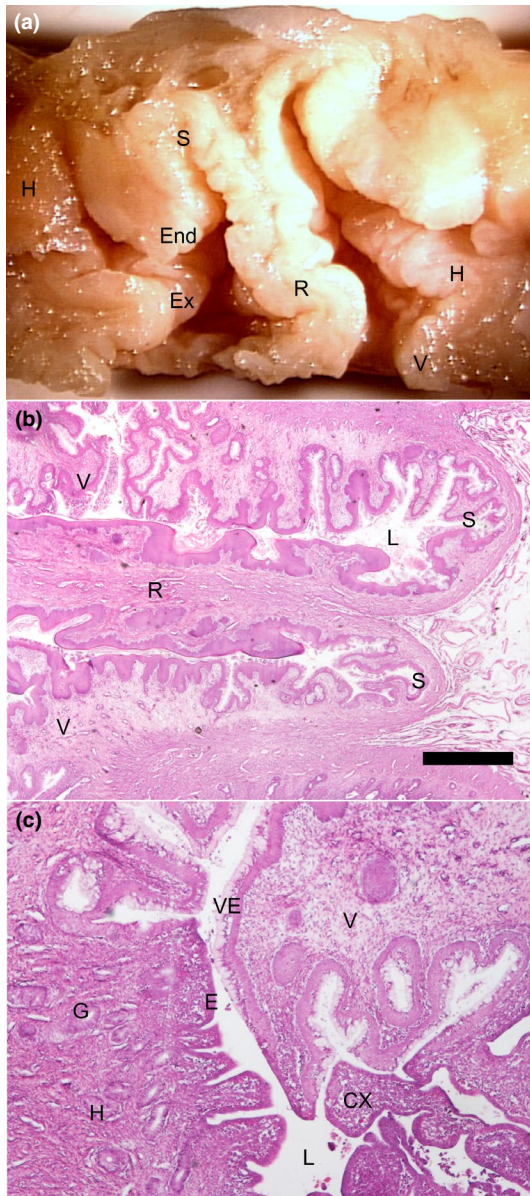


FIGURE 4 Macro- and microscopical aspect of the uterus of *Lagostomus maximus*. (a) Longitudinal section of the uterine cervix. H: uterine horn. R: medium raphe. V: vagina. End: endocervix. Ex: exocervix. S: bottom of sac. (b) Microphotography of the bottoms of sack. L: lumen. V: vagina. R: middle raphe of the cranial sector of the vagina. S: bottom of sack. Haematoxylin and eosin. Bar for B and C: 300 μ m. (c) Detail of the uterine cervix. L: lumen. H: uterine horn. E: uterine epithelium. VE: epithelium of the vagina. CX: cervix. G: gland. Haematoxylin and eosin

by connective tissue with little amount of collagen fibres and abundant arteries and veins of different calibre is located.

Thickness of the myometrium was greater in non-pregnant females than in those with an advanced gestation. In the latter case, the muscle fibres formed a thin tunic as a consequence of the dilation that the uterus underwent during gestation.

Perimetrium

It consists of lax connective tissue and mesothelium. This structure was maintained in all the physiological states analysed. No histological and histochemical differences were found between the different sectors of the uterine horn of not pregnant or with multiple implantations animals.

3.2.2 | Cervix

In viscacha, there is no uterine body and the cervix cannot be externally differentiated. At low magnification, it can be observed that the light narrowing at the end of the uterine horn corresponds to the cervix, which continues with the vagina (Figure 4a). The presence of an intermediate septum starting at the bifurcation of the uterine horns and projecting by few centimetres into the vagina was confirmed. The presence of this septum determined the formation of two deep bottoms of sack, one at each side of it (Figure 4b).

The onset of the cervix was microscopically recognised by the absence of uterine glands. In addition, its lumen was very irregular due to the presence of mucosal evaginations that were higher and more frequent than those observed in the uterine horns. Each cervix presented two morphologically differentiable regions: the endocervix and the ectocervix (Figure 4c). The endocervix mucosa was lined with cylindrical epithelium. The ectocervix possessed stratified epithelium with two to three cellular layers of which the outermost presented mucin-producing cells in most females either in anoestrus or in pregnant. During the follicular phase, this cellular layer detached and the epithelium became stratified squamous and cornified. Detachment of the superficial mucosal cells was also observed in the bottom pouches. The epithelium of the ectocervix was like that of the vaginal epithelium with which it is continued.

In both portions of the cervix, the elastic fibres were distributed parallel to the superficial epithelium, all along the structure. The muscular tunic was arranged in two layers separated by abundant connective tissue.

4 | DISCUSSION

Within eutherian, there are numerous reproductive peculiarities. Probably, one of the most divergent reproductive characteristics is observed in the plains viscacha (*L. maximus*). This species ovulates between 200 and 800 oocytes (Weir, 1971b), for which it requires a large exposed ovarian surface, which in turn is achieved through the presence of cordonal projections. Also, the size of the mature follicles is reduced, which allows many of them to reach ovulation (Flamini et al., 2009). There is no record of another mammal with such a high ovulation rate. Most of these oocytes do not form

implantations. However, between 8 and 12 embryos manage to implant, but usually only two survive. Knowing the characteristics of the uterus may allow to find the morphological basis of this strange event.

Within hystricomorpha, poly-ovulation has been described in *Atherurus africanus*, a species that delivers a single offspring. However, the number of oocytes produced in each cycle is lower than that of *L. maximus* and no multiple implantations were found in this animal (Mayor et al., 2002). In a study analysing numerous species of multiparous North American rodents, members of the Geomyidae and Heteromyidae families, as well as some members of the Cricetidae family, were found to have a balance in the numbers of offspring that breed in each uterine horn (Baird, Elmer, & Birney, 1985). This finding coincides with that found in viscacha, both when it has multiple implantations and at-term pregnancies.

The uterus of viscacha is double, formed by two horns and two cervixes, without the presence of a body. This is common to many hystricognathi (Weir, 1971c, 1971d, 1974). Although guinea pig (*Cavia porcellus*) has no body, it has a unique cervix (Breazile & Brown, 1976), as was described for the agouti (*Dasyprocta aguti*) (Weir, 1971d). However, more recent studies indicate that the black agouti (*Dasyprocta fuliginosa*) has a double uterus (Mayor, Bodmer, & Lopez-Bejar, 2011), so that different types of uterus may be found even within the same genus. In some hystricomorpha, such as the African porcupine (*Atherurus africanus*) there is a small uterine body, so considering the uterus as double-horned (Mayor, López-Bejar, Jori, Fenech, & López, 2003; Mayor et al., 2002). In viscacha, the length of both horns proved to be similar, unlike in *Atherurus africanus*, which has a longer left horn. Unlike *L. maximus*, this species is mono-embryonic. However, no data were found on differences in implantations between horns (Mayor et al., 2003).

The effect of sex hormones on the mammalian uterine epithelium has been studied in different species, including hystricomorpha rodents such as the guinea pig (Garris, 1998). During oestrus, *L. maximus* uterine epithelium is significantly higher and presents a large number of PAS-positive granules as compared to anoestrus. Similar changes were found in mice following intraperitoneal injection of 17 β -oestradiol, which results in an increase in height and the appearance of a positive PAS reaction (Nilson & Norberg, 1963; Nilsson & Wirsén, 1963). Also, the type of epithelium varies with the reproductive stage: it is cylindrical in most cases, but during the follicular phase, it may present a pseudostratified appearance like that of sow and cow (Priedkalns, 1993) and even to some hystricomorphic rodents such as *A. africanus* (Mayor et al., 2002). In contrast, in other hystricomorpha such as the black agouti (*D. fuliginosa*) (Mayor et al., 2011) and *Myocastor coypus* (Felipe, Callejas, & Cabodevila, 1998), epithelium is cylindrical simple in all stages.

We analysed the morphometric changes occurring in the uterine endometrium of viscacha and determined that in the follicular phase females, this mucosa presents greater thickness and the glands are of broader light. Mehrotra and Finn (1974) conducted a study on the endometrium of ovariectomised guinea pigs and subsequently treated with 17 β -oestradiol and progesterone. These authors observed that at the beginning of the cycle, when the oestrogenic stimulus was high, there was an increase in luminal mitotic activity followed by an increase in the number of mitosis in the glands Mehrotra and Finn (1974). In our study, we did not analyse mitotic activity. However, the increase in glandular size is probably due to an increase in the amount of their cells, caused by oestrogenic stimulation during the follicular phase, which coincides with the experimental results obtained in guinea pigs.

The height of the luminal epithelium of the endometrium in viscacha during the follicular phase was higher than in the other states. These observations coincide with the results obtained in mice during oestrus and in experiments performed after intraperitoneal injection of 17 β -oestradiol. In these animals, the epithelium became cylindrical, its surface was covered with a substance that reacted strongly with the PAS technique, and the crypts were deep (Nilsson & Wirsén, 1963), but in the pregnant females, the epithelium was lower. A similar effect was observed when zeranol (oestrogen) was administered to chinchilla, a species more closely related to viscacha, to observe histological and morphometric changes in the endometrium. In this case, animals treated with zeranol showed a greater growth of the endometrial glands accompanied by an increase in mucosal projections (Figueroa, Fernández Román, Anzaldúa Arce, & Martínez-Pérez, 2001).

In mouse (*Mus musculus*), the luminal epithelium of the uterus markedly varies when treated with progesterone. In this species, the administration of three doses of progesterone modifies the epithelial cells in their apical portion which tends to rise in projections, whereas at the last moment of pregnancy, when oestrogens begin to rise, these projections disappear (Martin, Finn, & Carter, 1970). In the viscacha at term of pregnancy, the luminal epithelium presents some cells with projections in triangular form, similar to the elevations observed in the mouse. It can be assumed that at this point in gestation, progesterone levels are higher than those of the more recently pregnant females, in which the aforementioned evaginations are not found.

Variations found in the uterus of viscacha according to the moment of the cycle considered are in contrast with the results of Weir (1971a, 1971b) who affirmed that in hystricognathi rodents, it is not possible to detect variations in the uterus that reflect cyclic modifications of the ovary.

Uterine glands are significantly deeper and have a broader light at the follicular stage. In guinea pigs, an increase in

mitotic activity was demonstrated in the glands during the follicular stage (Mehrotra & Finn, 1974), which could explain this increase. In chinchillas, members of the Chinchillidae family as is *L. maximus*, the injection of zeranol generates similar results. Decreased gland size during the early pregnancy stage may be indicating that in this species, histotrophic nutrition is only important in very early stages.

Few morphometric studies of the uterus of hystricomorpha rodents were performed. Mayor et al. (2002) found in *A. africanus* a greater thickness of the endometrium and myometrium in pregnant females as compared to those at the follicular phase. These data differ from that found in viscacha. In this regard, it should be noted that *A. africanus* deliver a single embryo. Moreover, in that study no differentiation was made between different gestational stages. In other hystricomorpha such as *D. fuliginosa*, the thickness of the endometrium and myometrium was greater at the follicular phase than at pregnancy (Mayor et al., 2011), as was found for viscacha.

In females with pregnancy at term, the presence of projections of the uterine mucosa similar to those found in the mouse after progesterone injection was observed (Martin et al., 1970). Like in the mouse, these projections disappear when the predominant hormones were oestrogens.

Our results show that unlike those obtained by Weir (1971a, 1971c, 1971d), viscacha presents variations in the uterine morphology related to the reproductive stage. However, in the non-pregnant animals, no differences were found along the uterine horn to explain why only the offspring that are implanted in the most caudal part of the organ survive. The morphological characteristics of reabsorption implants resemble those found in other rodents, such as the mouse, when embryonic death occurs in the presence of pathological conditions (Woudwyk, Gimeno, Soto, Barbeito, & Monteavaro, 2013).

In the studied population ($n = 30$), those females that were not pregnant were in follicular phase or in anoestrus. This classification was made based on the observation of the ovary and the vaginal epithelium. Interestingly, we did not find any female viscacha that were in the luteal phase (prior to implantation). This could be due to the number of females captured, the periods in the year selected for the capture or, simply, the social behaviour of these animals, since they live in shared colonies between females and males (Llanos & Crespo, 1952), which could imply that during oestrus almost all females become pregnant.

The lectin-labelling pattern in the uterus of viscacha is similar to that shown in other species for some of the lectins analysed in this work. Thus, SBA and WGA showed an intense labelling of the luminal and glandular epithelium in all the physiological states as was observed in heifers by Cobo, Campero, Gimeno, and Barbeito (2004). This indicates the possible presence of β -D-GalNAc residues

recognised by both lectins. When the hormonal stimulus is low in the anoestrous stage of viscacha, the superficial and glandular epithelial cells of the uterus present a lectin-labelling pattern similar to that found in postmenopausal women (Gheri, Gheri Bryk, Taddei, Moncini, & Noci, 1996).

In cattle, the endometrial labelling pattern was also examined at different stages of gestation. In pregnant cows with more than 80 days of gestation, the labelling with UEA-1 was negative, both in the superficial epithelium and in the glands. In cows with less than 40 days of gestation, the labelling pattern for DBA and SBA lectins varied between strong and moderate, both for the superficial epithelium and for the uterine glands (Munson, Kao, & Schlafer, 1989).

Viscacha and bovines have different types of placentation, being monohemochorial for the former (Flamini, Díaz, et al., 2012) and synepitheliochorial for the latter (Roa, Smok, & Prieto, 2012). However, the lectin-binding pattern of pregnant viscacha is like that observed in pregnant cows. These results indicate that changes in the saccharide pattern during pregnancy are similar in both species.

Bychkov and Toto (1987) investigated the distribution of five lectins in different stages of the oestrous cycle, during gestation and during women's menopause. These authors demonstrated that in pregnant women, the PNA, RCA-1 and UEA-1 lectins intensely marked the apical zone of the cytoplasm. Similarly, the RCA-1 lectin intensely stained the superficial epithelial cells of the uterus of viscacha females with full-term pregnancy, but the reaction was moderate in viscacha with early pregnancy. However, the UEA-1 lectin was negative in the two gestation periods considered, whereas PNA was negative in viscacha with multiple implantations while moderate in at-term pregnancies.

According to Bychkov and Toto (1987), there was a weak reaction in the proliferative phase of the women's cycle when using the WGA lectin. On the contrary, in viscacha this lectin intensely stained the glycocalyx and had a moderate presence in the epithelial apical portion. Although the pattern varies in relation to the species, some carbohydrate residues are always produced in the oviduct, although with different intensity (Bychkov & Toto, 1987).

The cervix of viscacha is double as in other hystricomorpha such as chinchilla, coypu (Hafez, 1970) and black agouti (Mayor et al., 2011), and unlike what happens in myomorphs, such as rat (*Rattus sp*) and mouse (da Costa Ferreira Junior, 1995; Graham, 1966). However, other hystricomorpha such as guinea pig (Breazile & Brown, 1976; dos Santos et al., 2016), *Galea spixii* (dos Santos et al., 2014) and *A. africanus* (Mayor et al., 2003) also present a single cervix, which shows that the characteristics of the uterine cervix diverge within the same group and do not appear to have taxonomic value. Felipe, Callejas, and Cabodevila (2001) described that in coypu, the cervix projects into the cranial

area of the vagina, forming an annular space, the fornix, which subdivides the zone into five bottoms of sack. On the other hand, in *L. maximus* we could only find two deep and folded bottoms of sack, which are the result of the expansion of the septum dividing the cranial portion of the vagina (Flamini, Díaz, et al., 2012).

As occurs in other hystricomorpha (Felipe et al., 1998), the cervix is divided according to the characteristics of its mucosa into an endocervix and an ectocervix. The endocervix continues to the uterine horn, so it has a simple columnar epithelium similar to this one. Its onset is recognised by the lack of glands as occurs in the coypu (Felipe, Cabodevila, & Callejas, 2002) and in the black agouti (Mayor et al., 2011). In some females of viscacha, the endocervix has a bistratified epithelium with superficial mucosal cells. Unfortunately, we have not found references that describe a similar epithelium in the endocervix of other species. The ectocervix is recognised by its stratified epithelium. The transition between both epithelia is like that observed in rat, mouse (da Costa Ferreira Junior, 1995; Graham, 1966) and coypu (Felipe et al., 2002). It is characterised by the absence of glands, unlike that found in the Caviidae rodent *G. spixii*, where glands persist (dos Santos et al., 2014). The presence of a cubic or cylindrical stratified epithelium with superficial mucosal cells is characteristic of some rodents such as the mouse, but not in species such as the Australian plains mouse (*Pseudomys australis*), nor in the hystricomorpha *A. africanus* (Mayor et al., 2002). This type of epithelium appears during pregnancy and anoestrus in a manner like that described in the vagina of *L. maximus* (Flamini, Díaz, et al., 2012).

The connective tissue of the cervix is very cellular, as in Mitchell's hopping mouse (*Notomys mitchellii*) and unlike what happens in the Australian plains mouse (*Pseudomys australis*), in which the collagen fibres are more abundant (Breed, 1985). In all the studied species, there are abundant elastic fibres necessary for the dilatation of the delivery canal. In our work, we also found many these fibres, but we could not find differences in their arrangement between ectocervix and endocervix, as was observed in the rat (Battlehner, Caldini, Pereira, Luque, & Montes, 2003). In viscacha, the elastic fibres of both portions are distributed throughout the cervix, predominantly in a parallel arrangement to the surface. We have not found references in other species that can correlate the elastic fibre arrangement with the size of the offspring and whether these differences can be generalised to other species that deliver large or small offspring. In pregnant or ovariectomised rats treated with progesterone, eosinophils infiltrate into the cervical lamina propria (Luque & Montes, 1989). This infiltration has been related to the remodelling of collagen fibres. The scarcity of this type of fibres in the cervix of viscacha could explain the absence of this cellular type in pregnant females.

In her preliminary description, Weir (1971a) argued that viscacha does not have a muscular cervix. However, our observations show the presence of muscle bundles separated by abundant connective tissue, which do not form a continuous muscular layer as in other hystricognathi species, such as porcupine (Mayor et al., 2002) and black agouti (Mayor et al., 2011).

In previous works, several groups including ours demonstrated morphological and molecular characteristics of the ovary related to ovulation (Flamini et al., 2009; Jensen et al., 2008). So far, there were few studies analysing the uterus and cervix in this species. As it was found in the uterine horn, no differential morphological characteristics were observed in the uterus that could be related to the special reproductive characteristics of this species, nor were anatomical differences observed between the places in the uterine horns in which the embryos survive and those in which resorption occurs. The cervix of viscacha differs in some characteristics from other hystricomorpha. However, it is like that of other members of the group. This may suggest that the cervix does not have a significant taxonomic value.

The morphological similarities between the uterus of viscacha and that of other related species do not explain the high levels of implantation and embryonic death observed in this species. Therefore, deeper studies are needed to analyse these unique characteristics of *L. maximus*.

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