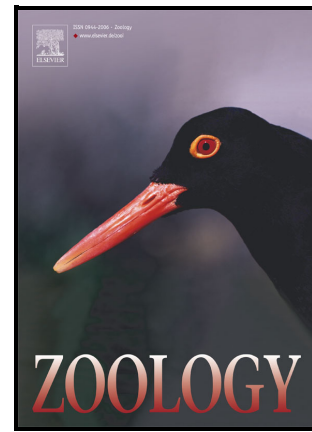# Journal Pre-proof

Embryonic-placental relationship in *Lagostomus maximus* as compared to other hystricognath rodents and eutherian mammals

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Embryonic-placental relationship in Lagostomus maximus as compared to other hystricognath rodents and eutherian mammals

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ABSTRACT

Reproductive specializations in caviomorphs (infraorder Hystricognathi), are very peculiar within the Order Rodentia. These include long gestations, the birth of offspring with an extreme degree of precociality, and short lactation periods. This study describes the embryo-placental relationship of viable implantation sites (IS) of the plains viscacha, Lagostomus maximus, after 46 post-coital days. The observations recorded in this study are comparatively discussed with those of other hystricognaths and eutherians. At this stage, the embryo resembles that of other eutherians. At this time of embryo development, the placenta exhibits a size, shape, and organization similar to that it will have in its mature state. Besides, the subplacenta is already highly folded. These characteristics are adequate to sustain the development of future precocial offspring. The mesoplacenta, a structure present in other hystricognaths and related to uterine regeneration is described for the first time in this species. This detailed description of the placental and embryonic structure contributes to the knowledge of the reproductive and developmental biology of the viscacha, as well as that of hystricognaths. These characteristics will allow testing other hypotheses related to the morphology and physiology of the placenta and subplacenta, and their relationship with the growth and development of precocial offspring in Hystricognathi.

1. INTRODUCTION

Rodentia constitutes the most abundant and diverse order of mammals (Wilson and Reeder, 2005; Wilson et al., 2016). Within this order, the South American representatives of the infraorder Hystricognathi, i.e. caviomorphs, are a highly diverse clade in terms of overall bauplan, body size, and life strategies (e.g. Patton et al., 2015; Wilson et al., 2016). They are recorded as fossils from the late middle Eocene or early Oligocene (Antoine et al., 2012; Campbell et al., 2021). Extant representatives are divided into four superfamilies: Erethizontoidea (New World porcupines), Cavioidea (guinea pigs, maras, mocos and capybaras), Chinchilloidea (chinchillas, pacaranas, and plains viscachas), and Octodontoidea (spiny rats, chinchilla rats, degus, coruros, and tuco-tucos). Most recent phylogenies based on molecular data recovered cavioid-erethizontoid and chinchilloid-octodontoid as sister clades (Upham and Patterson, 2015; Álvarez et al., 2017). The superfamily Chinchilloidea includes the families Chinchillidae, with the subfamilies Chinchillinae and Lagostominae, and Dinomyidae. Lagostominae comprises the single extant genus and species Lagostomus maximus which occurs from the dry lowlands of south-central Bolivia, western Paraguay, south through chaco, pampas, and steppe habitats of central and southern Argentina (Patton et al., 2015). Reproductive specializations in caviomorphs are very peculiar within Rodentia (Roberts and Perry, 1974; Franco de Oliveira et al., 2012; Acuña et al., 2020). These include long gestations (i.e. 154 days in Lagostomus maximus and 213 days in the Caviinae cavioid Galea musteloides), the birth of offspring with an extreme degree of precociality, and short lactations periods (i.e. 42 days in the cavioid Cuniculus paca and 45 days in the cavioid Dasyprocta prymnolopha) (Roberts and Perry, 1974; Zenuto et al., 2002; Luna et al., 2015). Other reproductive characteristics are species-specific like those seen in Lagostomus maximus (plains viscacha). L. maximus has the highest

polyovulation rate (200-800 oocytes/estrus) and poly-implantation rate (10-12 implantation sites (IS)/uterine horn) within eutherian mammals. Despite this large number of IS the female delivers only two precocial pups derived from the caudal IS. The remaining IS (cranial and middle) are resorbed between 26-70 post-coital days (pcd) (Weir, 1971a, 1971b; Roberts and Weir, 1973). The mortality rate of embryos has been related to variations in serum progesterone levels (Dorfman et al., 2013) and regional differences in uterine morphology (Acuña et al., 2020; Flamini et al., 2020; Giacchino et al., 2020). Although the morphological characteristics of embryonic death are similar event among mammals (Drews et al., 2020), in no other species its rate is so high and occurs with such regularity as in the plain viscacha (Acuña et al., 2021, 2022).

Available information on the embryonic/fetal and placental development of Hystricognathi is incomplete (Roberts and Perry, 1974; Rojas et al., 1982). According to the data collected by Roberts and Perry (1974), the post-implantation development of all studied Hystricognathi follows a similar pattern. Referring to late gestation of Hystricognathi, there are no studies related to reproductive specializations of the group, and species-specific particularities. Although there are studies describing the macroscopic exomorphology of embryos/fetuses in Dasyprocta prymnolopha (Fortes et al., 2013), Dasyprocta leporina (de Oliveira et al., 2017) and Cuniculus paca (El Bizri et al., 2017), they do not describe their microscopic appearance. As for placentation, most available information comes from placentas of females with near-term gestations of Cuniculus paca, Cavia porcellus, Dasyprocta aguti, Hydrochoerus hydrochaeris (Miglino et al., 2002; Kanashiro et al., 2009), Galea spixii (Oliveira et al., 2008), Kerodon rupestris (Oliveira et al., 2006), and Lagostomus maximus (Flamini et al., 2011; Barbeito et al., 2021). On the other hand, there are no studies that relate the morphology of the placenta and the embryo with the extensive gestation.

Bearing in mind the reproductive particularities of L. maximus (Flamini et al., 2009, 2019, 2020) it can be considered that this species uses a large energy flow for the production of gametes that would not be fertilized as well as zygotes that would not develop until the end of gestation (Weir, 1971a, 1971b). This is striking for a species with poly-implantation and K-strategy where precocial young are born (Jackson et al., 1996). It is essential to broaden the knowledge of its reproductive biology and establish common and differential patterns with other caviomorphs that have reproductive processes more like most eutherians (Theiler, 1989; Drews et al., 2013; McGeady et al., 2017). This work aimed to describe the embryo morphology, extraembryonic adnexa, and placentation in viable IS (caudal) of L. maximus at 46-53 pcd.

2. MATERIALS AND METHODS

2.1 Animals and euthanasia

The capture of the females of L. maximus was carried out in the ECAS (Estación de Cría de Animales Silvestres; S°34_50.900 W°58_06.900, Ministry of Agrarian Development of the province of Buenos Aires). In this property, animals live freely, in gregarious groups inside caves ("vizcacheras") and without reproductive control. The sampling period was carried out between the months of May and June of the year 2019. This sampling time was based on the results obtained in previous works of our group (Flamini et al., 2009, 2011, 2019), which ensures the capture of females with intermediate gestation. Five females were captured during this period, but only three were in intermediate gestation according to the ultrasonographic study (Acuña et al., 2022). The three pregnant females of L. maximus were anesthetized and euthanized according to the protocol previously approved by the Institutional Committee for the Care and Use of Laboratory Animals of the School of Veterinary Sciences of the

National University of La Plata (CICUAL, FCV-UNLP, code: 68-17T) (Acuña et al., 2018). Briefly, captured viscachas were intramuscularly anesthetized by administering a single dose of xylazine (Anasedan, Laboratorio Vetbrands) (8 mg/Kg of body weight) followed by ketamine (Ketanest, Laboratorio Scott Cassara) (50 mg/Kg body weight) (Acuña et al., 2018).

2.2 Sampling and microscopic morphology

After death, the entire reproductive system was removed through the abdominal cavity (Figure 1). Each IS was numbered following the craniocaudal direction of the uterine horns. Six caudal IS (two per female) were measured to determine gestational time as described by Leopardo and Vitullo (2017). Subsequently, each IS was isolated from the rest, processed for inclusion in paraffin, sectioned at 3 μm-thick sections, and stained with hematoxylin-eosin and PAS (Periodic Acid Schiff), following previous protocols (Acuña et al., 2021) to proceed with its morphological description. After microscopic observation, digital images were captured using a video camera (Olympus DP71, Japan) attached to a research microscope (Olympus BX53, Japan). The morphological descriptions were based on the nomenclature proposed by different authors (Theiler, 1989; Drews et al., 2013; McGeady et al., 2017).

3. RESULTS

Within each IS the embryo, the placenta, the subplacenta, some extraembryonic adnexa, and the decidua were recognized, forming part of an interstitial implantation that occupied a high percentage of the uterine lumen (Figure 2A). In each IS, the implant was attached to the endometrium at the level of the mesometrial pole through the

mesoplacenta. This structure had a simple cylindrical epithelium and loose connective tissue (Figure 2B).

The embryo was located at the mesometrial end of the IS. Sagittal sections along the IS revealed the presence of different structures and developing organs, including thoracic and pelvic limbs, thyroid glands, lungs, stomach, liver, digestive tract, posterior cardinal veins, dorsal aortas, genital ridges, nephrogenic cord, and Wolff's ductus (Figure 3A-C). A discoid-shaped placenta, wider at its upper than the lower end, was located between the embryo and the subplacenta. The placenta had a large interdigitation (Figure 4A). In the placenta, two trophoblast populations were recognized: the cytotrophoblast and the syncytiotrophoblast, whose dispositions showed a tendency towards a lobular organization of the organ (Figure 4B). The syncytiotrophoblast had numerous nuclei and was grouped in a single layer surrounding the maternal blood chambers, generated from blood vessels that had lost their wall (Figure 4C). In addition, embryonic blood vessels containing blood cells were observed in the placenta. Thus, it was possible to recognize the dual vascularization of the organ (Figure 4D), forming a monohemochorial maternal-embryonic interface.

The subplacenta was located between the excavation of the placenta and the decidua. It showed a lamellar organization (Figure 5A). Each lamella was formed by a core of mesenchymal tissue containing maternal and fetal blood vessels, surrounded by more than five cell layers-thick cytotrophoblast (Figure 5B). Tissues surrounding the subplacenta were disorganized (Figure 5C-D). Within them, cells such as lymphocytes and neutrophils were observed.

Among the embryonic adnexa, the amnion and the amniotic cavity containing the embryo, and the yolk sac were recognized. The amnion had a simple cuboidal epithelium and mesenchymal connective tissue. The yolk sac was divided into a parietal

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layer, in apposition with the placenta, and a visceral layer, located outside the amnion (Figure 5E). In the visceral layer, the endoderm was observed, composed of a simple columnar epithelium, mesenchymal connective tissue, and blood vessels containing hemangioblasts (Figure 5F).

The decidua was differentiated into basalis and parietalis, the former being the most extensive. Both were composed of loose connective tissue containing voluminous and polygonal cells, with a central nucleus and PAS+ cytoplasm and surrounded by abundant blood vessels of maternal origin (Figure 5G). In the basal part of both deciduas maternal blood vessels, syncytiotrophoblast, and PAS+ amorphous material were observed (Figure 5H).

4. DISCUSSION

4.1 Placentation, mesoplacenta, and extraembryonic adnexa

In hystricognaths, as in other studied species of the Order Rodentia (Geisert and Spencer, 2021), a chorioallantoic placenta develops associated with an inverted yolk sac (Bonatelli et al., 2005; Kanashiro et al., 2009). The chorioallantoic placenta is formed by the main placenta and the subplacenta (Wooding and Burton, 2008; Barbeito et al., 2021; Geisert and Spencer, 2021).

In a previous study carried out on IS of 26-32 pcd, we observed that the caudal IS had trophoblast extensions towards the decidua, constituting the future site where the placenta would begin to develop (Acuña et al., 2021). It is worth mentioning that placentation of L. maximus begins at 35 pcd, a period that partially coincides with the beginning of embryonic resorption (Weir, 1971a; Roberts and Weir, 1973; Roberts and Perry, 1974). In this work, we describe the anatomical and histological characteristics of

the placenta, subplacenta, decidua, and other extra-embryonic adnexa such as the yolk sac and amnion present in caudal IS observed between 45 and 53 pcd in L. maximus.

Although the main characteristics of these structures were described by Flamini et al. (2011) and Barbeito et al. (2021), among them, labyrinthine organization, cell types (cytotrophoblast, syncytiotrophoblast, giant trophoblast cells, natural killer cells) and vascularization. In the present work we carry out an analysis in which the morphology of the placenta and subplacenta is related to the embryos that are developing in a specific period of gestation. Also, we found a previously undescribed structure: the mesoplacenta.

The developing main placenta showed, at this stage of development, a conic shape, and a tendency towards having a lobulated organization. Also, it shows a dual vascularization provided by fetal blood vessels and maternal blood chambers. The chorioallantoic placenta of hystricognaths (Mess, 2003, 2007a), shows a definitive shape and differentiation when gestation reaches 70-80% of its duration (Roberts & Perry, 1974). However, despite the gestational age of the animals analyzed in this study, the definitive shape and tendency toward organization were already present.

In the present work, we also observed that the placenta, at 46 pcd, has a great interdigitation. Comparative studies revealed that interdigitation, i.e., the degree of contact between maternal and embryonic/fetal tissues in the exchange area, significantly influences the embryonic/fetal growth rate. Thus, species with labyrinthine placentas, such as the viscacha, deliver newborns similar in size to those of species with villous or trabecular placentas, although the latter do so in less than half the time (Leiser and Kaufmann, 1994; Wooding and Burton, 2008). This suggests that there could be trade-offs between embryonic/fetal growth rates (higher with higher interdigitation) and gestation time (shorter with higher interdigitation), in association with the type of

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interdigitation (Capellini et al., 2011). Such trade-offs could be the result of mother-pup conflict over maternal resource allocation, with paternal genes favoring greater interdigitation and thus greater fetal growth, and maternal genes responding by reducing gestation time (Capellini, 2012). These results emphasize the role of interdigitation as a means of increasing surface area for exchange and are consistent with within-species studies showing that greater surface area for exchange is associated with heavier neonates (Capellini, 2012). Regarding what was observed in our study in the IS of 46 pcd of the viscacha and other works (Miglino et al., 2002; Bonatelli et al., 2005; Kanashiro et al., 2009), this group would be an exception, since in relation to the embryo-placental development, is observed a large area of exchange and interdigitation, a low embryonic/fetal growth rate with a long gestation time (Robert and Perry, 1974), and the development of precocial offspring (Mess, 2003).

Regarding subplacenta, it is a structure with a very similar morphology among the studied hystricognaths (Miglino et al., 2002, 2004; Oliveira et al., 2008), although absent in all other eutherians (Miglino et al., 2021). It is located between the placenta and the decidua and is a source of invasive trophoblast (Mossman, 1987; Mess, 2007d). According to the gestational time of the specimens analyzed in this study, the subplacenta had a lamellar arrangement. This characteristic could be related to the increase in the exchange surface, i.e., gases such as oxygen, since the subplacenta responds to the amount of available oxygen: its area increases when its availability is restricted (Thompson et al., 2016; Miglino et al., 2021). In addition, it is known that as gestation progresses, eutherian fetuses demand higher oxygen transfer (Enders, 2009). Particularly in L. maximus, it is known that it has an increase in thickness of the subplacenta as pregnancy progresses (Flamini et al., 2011). This potential morphophysiological relationship in the subplacenta, together with other aspects in the

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placenta such as type of placentation and invasion of the trophoblast, countercurrent arrangement of blood vessels, thinning of the trophoblast lining, constitute relevant characteristics in studied hystricognaths (i.e., Cuniculus paca and Octodon degus) (Miglino et al., 2002) that contribute to their precocial reproductive strategy (Mess, 2007b, 2007c). A recent study on the morphology, vascularization, and secretory activity of steroid hormones during pregnancy of some species of caviomorphs (Hydrochoerus hydrochaeris, Cuniculus paca, Dasyprocta leporina, Kerodon rupestris, and Cavia porcellus) confirm the endocrine role of this structure (Miglino et al., 2021). In the areas surrounding the subplacenta, we observed a remarkable tissue disorganization. This would be related to the invasive capacity of the subplacenta (Mess, 2003), since the enzymes secreted by the trophoblast degrade fibrillar components of the extracellular matrix such as collagens (Chen and Khalil, 2017; Gualdoni et al., 2022).

In this study, we found that the subplacenta was in contact with the decidua. Unlike what was observed in the early gestation of L. maximus (26 pcd) (Acuña et al., 2021), the decidua basalis and parietalis, which contain abundant PAS+ cells, occupied a large part of the IS. Of both deciduas, the basalis was the most extensive, a characteristic that was also observed in another caviomorph, such as Chinchilla lanigera (chinchilla) (Roberts and Perry, 1974). In addition, in proximity to the decidua basalis, amorphous PAS+ material was observed. This was also observed in the subplacenta of Cavia porcellus (guinea pig), Proechimys guairae (casiragua), and Chinchilla lanigera (Roberts, 1973). Presumably, these would be nutrients that are being transferred from the decidua to the fetus (Roberts and Perry, 1974). Considering the similarities in the placental structure, we could assume the same role in L. maximus.

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The microscopic observation allowed us to identify a structure not described so far in L. maximus: the mesoplacenta. This structure is derived from the decidua and continues with the endometrium of the mesometrial pole of the IS. The mesoplacenta is not exclusive to the viscacha, since it was described in other caviomorphs, such as Chinchilla lanigera (Tibbitts and Hillemann, 1959), Dasyprocta aguti (agouti), and Cuniculus paca (paca) (Miglino et al., 2002). According to Becher (1921a, 1921b), the mesoplacenta thins as gestation progresses. Comparative studies carried out in other species have established equivalences between the mesoplacenta and other structures such as the placental stem in Hydrochoerus hydrochaeris and Cavia porcellus (Ibsen, 1928; Uhlendorf and Kaufmann, 1979). It was suggested that the mesoplacenta serves to restrict the damage inflicted on the uterus at the time of delivery, allowing the rapid regeneration of the organ, thus enabling the occurrence of a subsequent pregnancy after a postpartum mating (Uhlendorf and Kaufmann, 1979). This suggestion is related to the observations of Flamini et al. (2009), who studied the ovarian biology of L. maximus in specimens from the Argentine Pampean region, with a humid subtropical climate. These authors observed that around 70.6% of the females became pregnant after postpartum estrus, unlike what was observed in specimens from the Litoral region of Argentina (dry climate) with sporadic and irregular postpartum estrus (Llanos and Crespo, 1952). Possibly, the differences in the occurrence of postpartum estrus in the specimens from both regions are due to environmental conditions, since the species has crepuscular habits and its endocrine activity depends on the seasonal variations of the geographical areas (Flamini et al., 2009).

In L. maximus, a yolk sac was also observed. It was differentiated into a parietal leaf and a visceral leaf. The latter is vascularized, and hemangioblasts were observed inside the vessels. The yolk sac constitutes the first hematopoietic site of the embryo

(Baron et al., 2012). It is the producer of mesenchymal stem cells, as described in the cricetid rodent Necromys lasiurus (Favaron et al., 2014) and the bovid Bos taurus (Oliveira et al., 2017). A previous study carried out during the placentation of L. maximus concluded that the visceral leaf of the yolk sac forms folds whose cells present abundant microvilli in their apical domain (Flamini et al., 2011). In other caviomorphs, such as the paca (Cuniculus paca), the cells of this leaf present a high endocytic activity that is associated with a passive transfer of immunity from the mother to the fetus (Bonatelli et al., 2005). Considering the morphofunctional stability of the placenta and the extra-embryonic adnexa among the caviomorphs, it could be considered that in L. maximus the yolk sac could also perform the same function. The blood vessels of the visceral layer of the yolk sac are part of the fibrovascular ring, a structure that through morphological studies and phylogenetic mapping has been considered a synapomorphy of hystricognaths (Mess, 2005).

4.2 Embryonic morphology

Uterine heterogeneity in L. maximus influences the differential development of IS, favoring caudal ones over the rest (Acuña et al., 2020, 2021; Giacchino et al., 2020). Caudal IS are the only viable sites from which fetuses will develop (Weir, 1971a, 1971b; Roberts and Weir, 1973). The characteristics of the early embryonic development of caviomorphs, including the viscacha, were described by different authors early in the 1970s and compiled by Roberts and Perry (1974). Particularly for L. maximus, many of these characteristics were updated, among them, cavitation, gastrulation, and neurulation (Leopardo and Vitullo, 2017). Other characteristics of early embryonic development were related to embryonic death (Giacchino et al., 2020; Acuña et al., 2021, 2022). Until now, no data was available regarding other gestational periods. In this study, we established that the embryonic development of the viable IS of

L. maximus observed after 46 pcd does not differ from the development pattern of other eutherians such as the Muridae Rattus norvegicus domestica (Marcela et al., 2012), the Bovidae Bos indicus (Alberto et al., 2013), the Felidae Felis silvestris catus, and the Canidae Canis familiaris (Pieri et al., 2015). Even so, this work provides the first contributions to embryonic morphology in caviomorphs, from viscacha embryos of 46 pcd.

5. CONCLUSION

Gestation of hystricognaths is long compared to other rodents. It is hypothesized that this is related to the slow rate of growth of the embryos, particularly in early gestation, where development is more focused on the development of the placenta than on the formation of the embryo. This study described the morphology of the embryo and placenta in L. maximus caudal (viable) IS after 46-53 pcd. In addition, the embryo-placental relationship was inferred since the placenta showed a higher degree of development than the embryo. This could be due to the gestation extension leading to the delivery of precocial offspring. On the other hand, the mesoplacenta was described for the first time in this species. It is a structure linked to uterine regeneration and particularly in L. maximus, would facilitate the occurrence of postpartum estrus in specimens from the Pampean region of Argentina, as compared to those specimens with different geographical locations (Litoral region) (Llanos and Crespo, 1952). The results obtained in this study will contribute to the knowledge of the reproductive biology of caviomorphs. The morphological characteristics observed in the placenta and the embryo will contribute to the design of comparative, phylogenetic, and developmental biology studies with other eutherian species that will allow us to understand the reproductive strategies of the different taxa and their adaptations to different environments.

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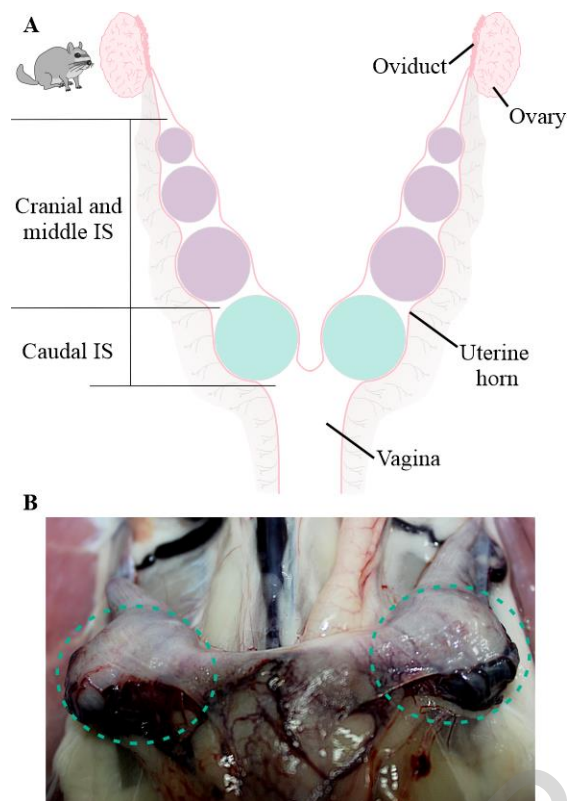
Legends to the figures

Figure 1. Reproductive system of Lagostomus maximus at 46-53 post-coital days. A. Schematic of some reproductive organs and cranial, middle, and caudal implantation sites. B. In situ caudal implantation sites circumscribed by green dotted line ovals.
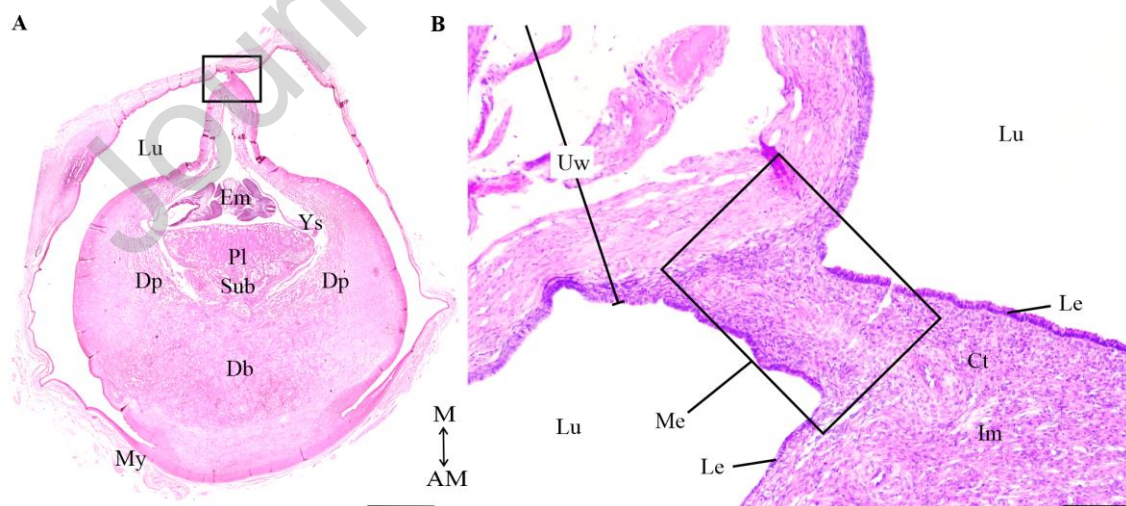

Figure 2. Microscopic morphology of a caudal implantation site of Lagostomus maximus at 46-53 post-coital days. A. Interstitial implantation showing the embryo, placenta, subplacenta, decidua basalis and parietalis, yolk sac, and mesoplacenta

(rectangle). B. Detail of the mesoplacenta. Abbreviations: AM: antimesometrial; Ct: connective tissue; Db: decidua basalis; Dp: decidua parietalis; Em: embryo; Im: implantation; Le: luminal epithelium; Lu: lumen; M: mesometrial; Me: mesoplacenta; My: myometrium; PI: placenta; Sub: subplacenta; Uw: uterine wall; Ys: yolk sac. Hematoxylin-eosin. Scale bar: 500 µm (A), 200 µm (B).
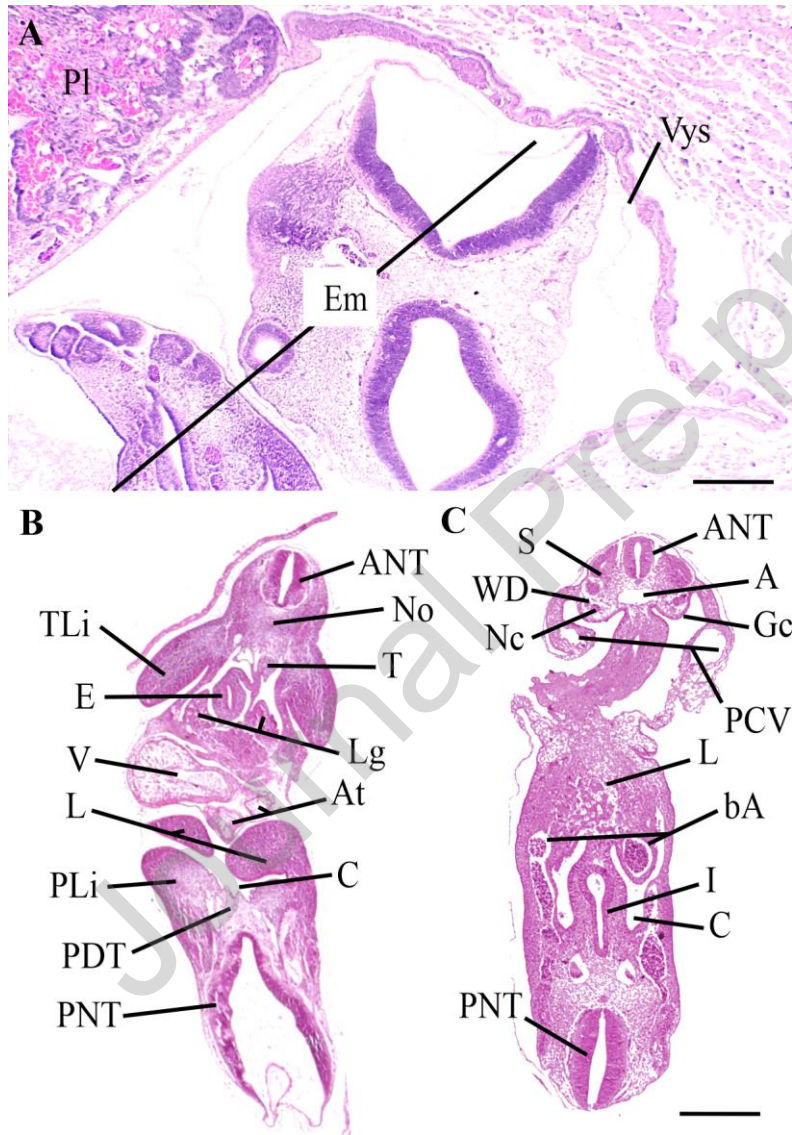

Figure 3. Embryo morphology of a caudal implantation site of Lagostomus maximus at 46-53 post-coital days. A. Embryo. B and C. Anterior and posterior sections, respectively, to the coronal plane of the embryo in which different structures/organs can be recognized. Abbreviations: A: dorsal aorta; ANT: anterior nerve tube; At: atrium; C: coelom; bA: branches of the dorsal aorta; E: esophagus; Em: embryo; Gc: genital crest;

I: gut; L: liver; Lg: lungs; Nc: nephrogenic cord; No: notochord; PCV, posterior cardinal veins; Pl: placenta; PDT: posterior digestive tract; PLi: pelvic limb; PNT: posterior nerve tube; S: somites; T: thyroid gland; TLi: thoracic limb; V: ventricle; Vys: visceral yolk sac; WD, Wolffian duct. Hematoxylin-eosin. Scale bars: 200 µm (A), 40 µm (B-C)

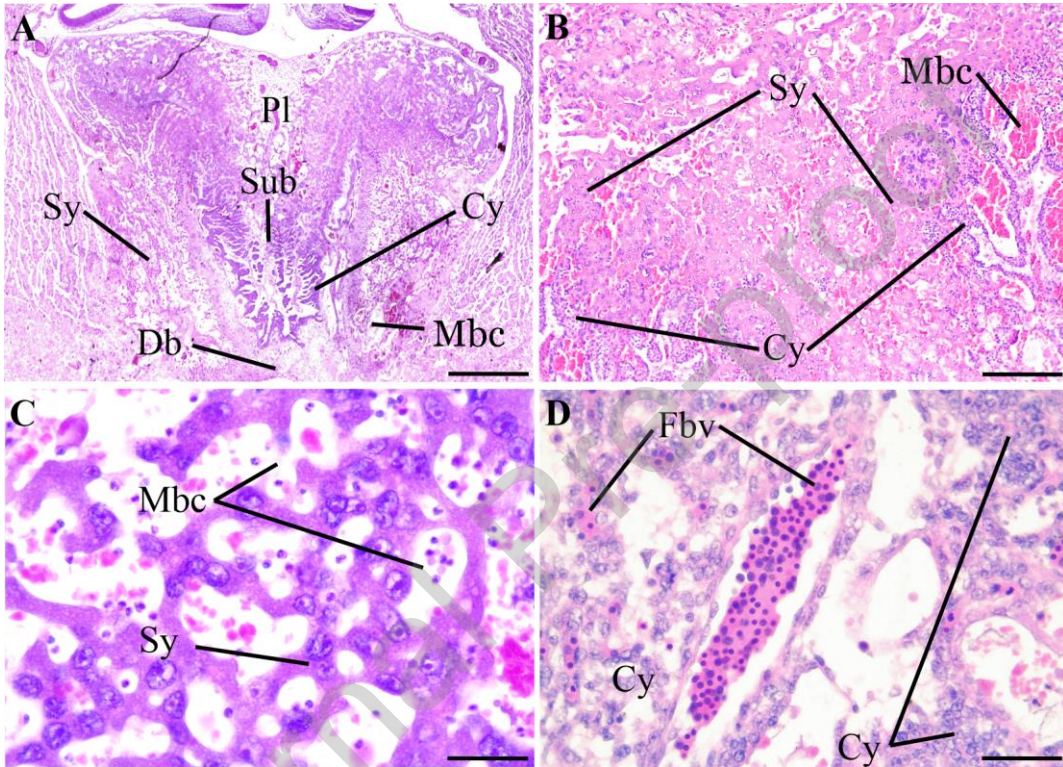

Figure 4. Placentation and placenta of a caudal implantation site of Lagostomus maximus at 46-53 post-coital days. A. Main placenta. B. Trophoblastic populations: Syncytiotrophoblast and cytotrophoblast. C. Maternal syncytiotrophoblast and blood chambers. D. Fetal cytotrophoblast and blood vessels. Abbreviations: Cy: cytotrophoblast; Db: decidua basalis; Fbv: fetal blood vessels; Mbc: maternal blood chambers; Pl: placenta; Sub: subplacenta. Sy: Syncytiotrophoblast. Scale bars: 500 µm (A), 200 µm (B), 40 µm (C-D).
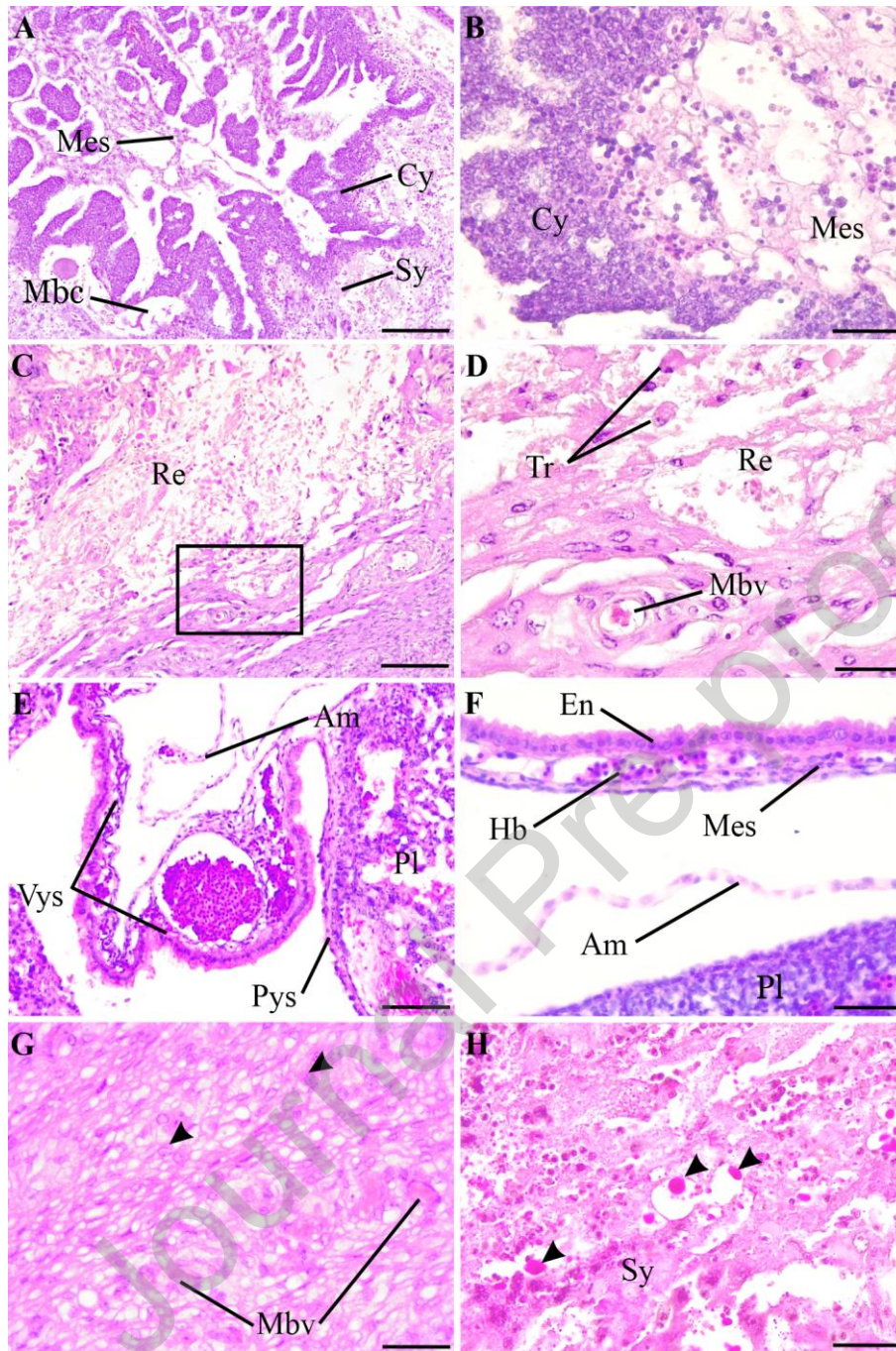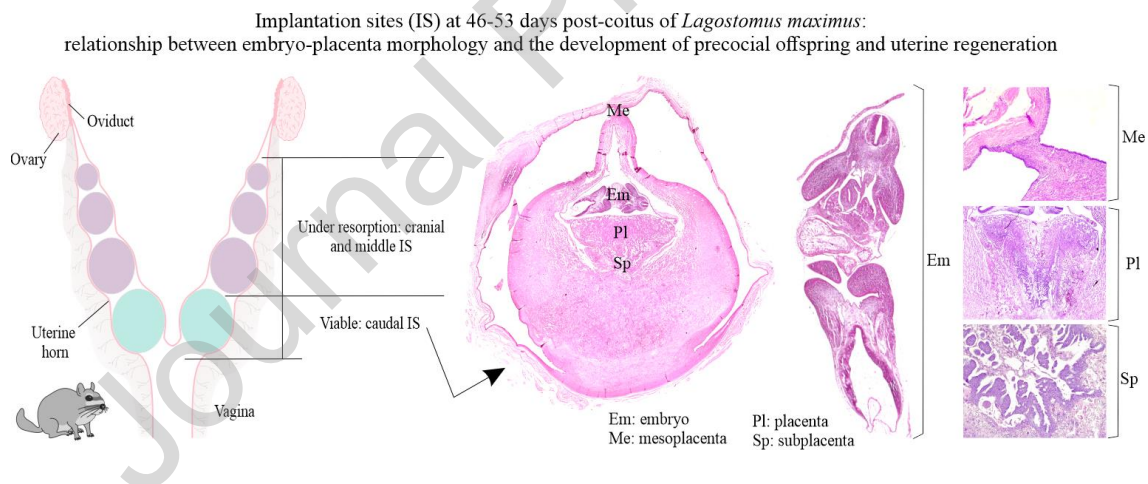
Figure 5. Subplacenta and extraembryonic adnexa of a caudal implantation site of Lagostomus maximus at 46-53 post-coital days. A. Lamellar organization of the subplacenta. B. Lamella with peripheral cytotrophoblast and mesenchyme in the center. C. Remodeling connective tissue. D. Magnification of the box in C, where some trophoblast cells and maternal blood vessels are observed. E. Amnion and parietal and visceral yolk sac. F. Details of the visceral yolk sac with blood vessels containing

hemangioblasts. G. PAS+ decidual cells (arrowheads) and maternal blood vessels. H. Arrowheads point to amorphous PAS+ material. Abbreviations: Am: Amnion; Cy: cytotrophoblast; En: endoderm; Hb: hemangioblasts; Mbc: maternal blood chamber; Mbv: maternal blood vessels; Mes: mesenchyme; Pl: placenta; Pys: parietal yolk sac; Re: remodeling connective tissue; Sy: syncytiotrophoblast; Tr: trophoblast; Vys: visceral yolk sac. Hematoxylin-eosin (A-F) and PAS (G,H). Scale bars: 200 μm (A,C,E,G), 40 μm (B,D,F,H).

Graphical abstract

Implantation sites (IS) at 46-53 days post-coitus of *Lagostomus maximus*: relationship between embryo-placenta morphology and the development of precocial offspring and uterine regeneration

Em: embryo   Pl: placenta
Me: mesoplacenta   Sp: subplacenta

Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Highlights

- Viscacha embryo morphology at 46-53 days post-coitus is similar to other eutherians

- The mesoplacenta, a structure present in other eutherians, is first described

- The placenta exhibited characteristics similar to those of its mature state

- The placenta morphology is related to the precocial offspring

- The maturational development of the placenta precedes that of the embryo

- The results contribute to the prenatal development of hystricognath rodents