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Chorioallantoic and yolk sac placentation in the plains viscacha (*Lagostomus maximus*) – A caviomorph rodent with natural polyovulation

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ABSTRACT

Objectives: Reproduction in the plains viscacha is characterized by the polyovulation of hundreds of oocytes, the loss of implantation and the development of 1–3 offspring. Our goal was to determine whether placental development was affected by these specializations.
Study design: Thirteen placentas from early pregnancy to near-term pregnancy were analyzed using histological, immunohistochemical and transmission electron microscopy.
Results: An inverted, villous yolk sac was present. Placentas were formed by the trophospongium, labyrinth and subplacenta. A lobulated structure with a hemomonochorial barrier was established early in pregnancy. Proliferating trophoblast that was clustered at the outer border and inside the labyrinth was responsible for placental growth. Trophoblast invasion resulted from the cellular trophoblast and syncytial streamers derived from the subplacenta. Different from other caviomorphs, numerous giant cells were observed.
Conclusions: The principle processes of placentation in caviomorphs follow an extraordinarily stable pattern that is independent of specializations, such as polyovulation.

1. Introduction

The plains viscacha, *Lagostomus maximus* Desmarest, 1817, is a guinea pig-related caviomorph rodent with an ample distribution throughout Argentina [1]. It is one of the larger rodents of South America, with females weighing between 2 and 4.5 kg, and males weighing between 5 and 8 kg [1]. This species is characterized by the unique reproductive feature of natural polyovulation. Originating from the suppression of apoptosis, females polyovulate up to 800 oocytes per cycle [1–6] and just 10 to 12 blastocysts are implanted [7,8]. However, usually only two fetuses are maintained to birth after 154 days [1,2]. The surviving fetuses are those implanted near the cervical end of the uterus [4]. With the exception of basic data obtained from delivered tissues [9], placentation in *L. maximus* is unknown. Placentation has been well studied in several caviomorph species [10–25] because they are more attractive animal models for human placentation than other rodents [26,27]. Similarities to humans include the processes of trophoblast invasion and placental growth, a hemomonochorial barrier and a precocial reproductive strategy [13,18,19,21,24–29]. Previous data indicate that placentation in caviomorphs occurs in a stable pattern that is largely independent of body size [17,20,25]. However, no parallel mechanism to the unusual polyovulation in the plains viscacha has been observed in other caviomorphs. Thus, we aimed to substantiate its potential influence on the differentiation of both the chorioallantoic and yolk sac placenta in *L. maximus*.

2. Methods

Samples were obtained from free-living female viscachas from Estación de Cría de Animales Silvestres, Buenos Aires. The procedures followed that of established studies [e.g., [22,25]]. Materials included 15 placentas from early pregnancy to full-term pregnancy (Table 1). They were analyzed using the following techniques: histology (hematoxylin and eosin (HE) and periodic acid-Schiff (PAS) staining), lectinhistochemistry with DBA (*Dolichus biflorus*) lectin for recognize uNK cells, immunohistochemistry for cytokeratin (to mark epithelial/trophoblast cells; mouse monoclonal anti-human primary antibody 1:300; Clone 1A4, DakoCytomation) and vimentin (to identify mesenchymal/endothelial cells; mouse monoclonal anti-human primary antibody 1:200; V9, sc-6260, Santa Cruz Biotechnology), proliferating cell nuclear antigen (mouse monoclonal anti-human primary antibody 1:800; PC10, sc-56, Santa Cruz Biotechnology; negative control using PBS) and transmission electron microscopy (TEM).

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Table 1
Morphometric parameters of fetuses and placentas at different gestation stages.

Pregnancy stage[a]	Age (days)	*N*	CRL (cm)	PD (cm)
Early pregnancy	40–60	6	3.0–5.7	1.1–2.8
Middle-term pregnancy	80–120	5	8.0–10.5	2.2–3.4
Near-term pregnancy	130–150	4	11–13.0	2.5–3.0

N: number of animals studied; CRL: fetal crow-rump length; PD: placental diameter.
[a] Total gestation time = 154 days.

3. Results

3.1. The general structure of chorioallantoic placenta and yolk sac

The chorioallantoic placenta had a discoidal shape with a main placenta and a distinct subplacenta (Fig. 1A) and was attached to the uterus by a peduncle. The umbilical cords included a variable number of vessels; most often, there were two arteries and two veins. From early pregnancy onward, the main placenta was lobulated and was characterized by a labyrinth and a trophospongium around the lobes (Fig. 1B,C). The labyrinth was dually vascularized from the maternal and fetal systems, whereas the trophospongium had no fetal capillaries (Fig. 1B,C). The chorioallantoic placenta was covered by the non-villous parietal yolk sac above a well-developed

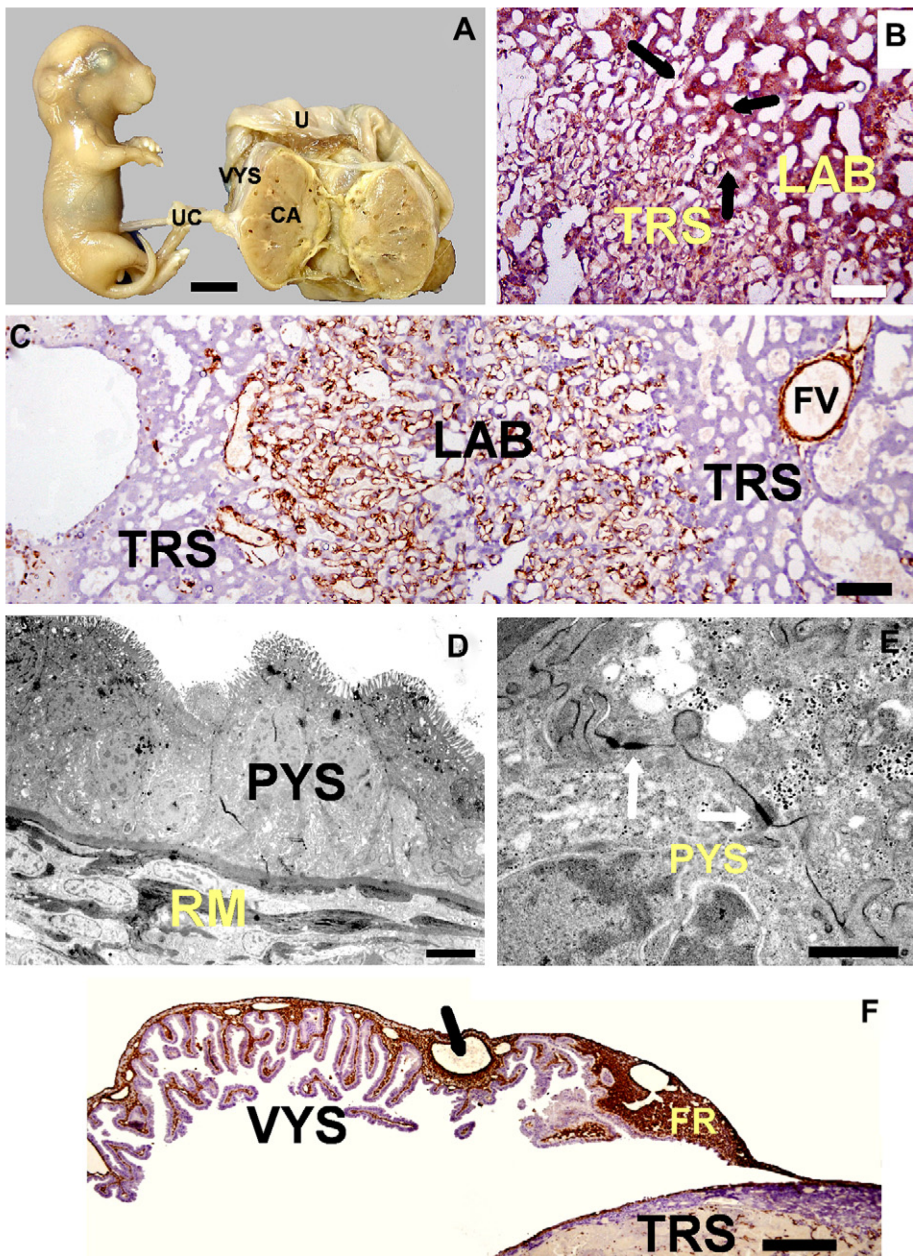

Fig. 1. The general structure of chorioallantoic and yolk sac placenta. (A) Embryo in mid-gestation with umbilical cord (UC), chorioallantoic placenta (CA), visceral yolk sac (VYS) and uterus (U). (B,C) Early pregnancy. (B) Immunostaining for cytokeratin marked trophoblast (arrows) in the trophospongium (TRS) and the labyrinth (LAB). (C) Immunostaining for vimentin. Only the labyrinth showed fetal vessels (FV) with positive endothelial cells. (D,E) Near-term pregnancy. TEM. One-layered parietal yolk sac (PYS) above the Reichert's membrane (RM). The cells had close contact (noted with arrows) at the bottom. (F) Early pregnancy. Vimentin. The visceral yolk sac (VYS) was well vascularized (arrow) and villous. A fibrovascular ring (FR) was present. Bar A: 1 cm. Bars B, C: 100 μm. Bar D: 2 μm. Bar E: 1 μm. Bar F: 500 μm.