

Swine placenta and placentation

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Abstract. During pregnancy the viviparous vertebrates develop a complex system of nutritional membranes surrounding the fetus. In place of the union or apposition of the fetal membranes with the uterine lining is formed the placenta. The placental types may be categorized into several complementary levels that reflect placental characteristics, being the swine placenta classified as chorioallantoic, diffuse, pleated, epitheliochorial and cross to counter-current. Structures, as the yolk sac, have function even before the appearance of the chorioallantoic placenta. The areola is also an accessory structure of the placenta, which may be found in ungulates. The extraembryonic membranes are linked intimately in the placentation, and these are important in swine early pregnancy, since the definitive placenta starts developing by the 18th day of gestation. Modifications in the swine placenta, like the presence of areolas, might have arisen as domestic species adaptations in order to supply nourishing needs during the development of concept.

Keywords: Extraembryonic membranes, Gestation, Placenta, Placentation, Swine pregnancy, Swine placenta.

Introduction

In literature, Mossman (1987) described that functions of extraembryonic membranes is allow the growth and development of the embryo. Somehow, the fetal membranes undergo changes to meet the needs of the embryo during development. These membranes can provide a favorable environment for the embryo as the amniotic membrane and amniotic liquid, or serve as an organ of maternal-fetal physiological exchange like the placenta.

Amoroso (1952) describes that function of the placenta is the nutrients

exchange maternal-fetal. These nutrients can be of two embryothrophic types: histothrophic and hemothrophic. Mossman (1987) describes that histothrophic nutrients are derived from secretions from the uterine glands, resulting from the decomposition of maternal tissues and maternal blood overflow. The hemothrophic nutrients are of origin of the maternal blood stream through the placenta. But there are some accessory structures that transfer nutrients, helping in the physiological exchange by the maternal blood through the chorioallantoic placenta. Structures, as the yolk sac, have function even before the appearance of the chorioallantoic placenta. The areola is also

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anaccessory structure of the placenta, which may be found in ungulates. It has a dome-shaped, coated with trophoblast cells absorbing situated opposite the openings of the uterine glands (Mossman, 1987).

All the placenta of mammals increases the contact area between the maternal and fetal surfaces by intense interdigitation of tissue. When this distribution extends in the major surface chorionic (Leiser and Kaufmann, 1994), or when the villi are distributed regularly by chorion, there are then the diffuse placenta (pigs and horses).

The placenta is a structurally complex organ. This complexity is promoted in part by the interaction of origin maternal and fetal tissues, and the presence of a variety of intermediate layers that are interposed between the maternal and fetal vascular space (Schwarze, 1970).

Therefore, we aimed to conduct a literature review in order to describe the porcine placenta and its extraembryonic annexes, providing detailed data for future research in this area.

Extraembryonic structures: chorion, amnion, allantois and yolk sac

The extraembryonic structures are the chorion, the amnion, the allantois and the yolk sac (Figure 1). These embryonic adnexa are different membranous structures and are deeply involved in placental development (Bertassoli et al., 2012; Bertassoli et al., 2015). These membranes, however, undergo morphological changes, interacting, forming connections and functional complexes or even involution in the course of pregnancy.

The amnion is a thin membrane that delimits a bag fulfilled with fluid - the amniotic fluid, which protects the embryo against mechanical shocks. This cavity derives from the division (rodents and primates) or the folding (mammals in general) of the embryonic ectoderm (Leiser and Kaufmann, 1994).

The allantois arises from the invagination of the posterior part of the embryo's gut. It acts with a respiratory surface in bird and reptile embryos, while,

in mammals, the blood vessels within it carry blood between the embryo and the placenta. The chorion is the outermost extraembryonic membrane in birds, reptiles and mammals and is involved in respiratory gas exchange. Exceptionally in mammals, it is part of the placenta and is additionally involved with nutrition and waste disposal, once it is a thin film that surrounds the embryo and other extraembryonic membranes (Wolpert et al., 2000).

The yolk sac develops as an attached structure of the embryonic midgut and consists of a layer of endodermal epithelium followed by a vascularized fetal mesenchyme (Leiser and Kaufmann, 1994).

The chorionic epithelium is the decisive barrier to maternal-fetal exchanges (Leiser and Kaufmann, 1994). During deployment, the internal layer of mesenchymal tissue derived from embryos able to fulfill the chorion, soon after the mesenchyme develops its own vascularization system. The cavity enwrapped by the chorion is denominated exocoeloma and contains the embryo, the amnion, the allantois and the yolk sac (Assis-Neto et al., 2012; Mançaneres et al., 2013). In order to be responsible for maternal-fetal exchange, the chorion must present a functional circulation. However, it is an avascular tissue and vascularization is provided by allantois vessels exclusively (Kaufmann and Burton, 1994).

The allantois corresponds to the extraembryonic urinary bladder developed from the embryonic intestine and formed with simple layer of squamous cells. These cells are sustained by a thin basement membrane and extraembryonic mesenchyme (Bjorkman, 1986; Assis-Neto et al., 2012).

The amniotic membrane is responsible for fetus hydration and nutrition, lubrication of the birth canal and mechanical protection (Leiser and Kaufmann, 1994). The amnion is composed by epithelial cells that show uniform morphology and did not differ among mammals (Steven, 1982). It is squamous, continuous and organized, forming a membrane similar to the allantoic epithelium, being also supported by a layer

of embryonic, connective tissue, which is the mesenchyme (Assis-Neto et al., 2012; Bertassoli et al., 2015).

The importance of the yolk sac as hematopoietic and placental organ is well known in rodents (Haar and Ackermann, 1971); however, the same is not true in the case of other domestic and wild mammals, in which the information is rather scarce. Its structure, degree of differentiation, time of appearance and disappearance, and physical distinction vary greatly between species and are poorly described in the literature (Mossman, 1987; Tommasi-Jr et al., 2012).

In humans, swine and guinea pigs, the yolk sac is a rudimentary structure, which generally does not participate in maternal-fetal exchanges (Santos et al., 2012). In equine and felines, the yolk sac merges locally with the chorion, forming a choriovitelline placenta (Leiser and Kaufmann, 1994). In domestic animals, the yolk sac starts to regress by the second and third week of pregnancy, as the allantois expands to fuse with the chorion (Hafez and Hafez, 2004). In most mammalian species, the yolk sac is therefore only active during the embryonic period and the membrane involutes by the fetal period.

Placenta

During pregnancy, the viviparous vertebrates develop a complex system of nutritional membranes surrounding the fetus. In place of union or apposition of the fetal membranes with the uterine lining is formed the placenta, a transitional organ composed by maternal and fetal tissues. It is responsible for transporting nutrients from the mother's body to the fetus, as well as promoting metabolic exchanges and performing endocrine functions for the production of hormones that maintain pregnancy (Leiser and Kaufmann, 1994). In this sense, Mossman (1937) provides a more complete definition of the placenta, meaning thus "the position of fetal and parental (maternal) tissue with purpose to physiological exchanges".

The placental types can be further classified into levels that reflect various placental characteristics, such as origin and

types of membranes, form, maternal-fetal interdigitation, interrelation of maternal and fetal blood flow, tissue layers of the maternal-fetal barrier, trophoblast invasion, cell decidualization, sinciotrophoblast formation and separation of placenta at birth. Thus, according to the fetal membranes, the placentas are classified into: chorionic, choriovitelline, vitelline and chorioallantoic. According to a maternal fetal relationship, they are classified as: diffuse, cotyledonary, zonary, bidiscoidal and discoidal. In addition, based on the number of cell layers separating maternal and fetal blood flows, the possible categorizations can be: epitheliochorial, sinoepitheliochorial, sindesmochorial, endotheliochorial and hemochorial (Leiser and Kaufmann, 1994).

Swine placenta

According to Leiser and Kaufmann (1994), the swine placenta is classified as chorioallantoic (due to apposition of the chorion and allantois), regarding origin of the fetal membranes; as diffuse (Figure 2A) regarding its form; as pleated (Figure 2B) regarding interdigitation model; as cross flow to counter-current (Figure 2C) regarding the maternal-fetal blood flow; and as epitheliochorial (Figure 2D) regarding the layers of inter-hematic membrane.

In swine, the trophoblast is in contact with the uterine epithelium and the fetal and maternal microvilli interdigitate; therefore, the placental development comprises, essentially, a wide area, with some layers between fetal and maternal microvasculature. The cell layers are attenuated during pregnancy, reducing the diffusion distance of gestational products, but all the layers remain until the end of pregnancy (Mossman, 1937; Amoroso, 1952).

The fetal membranes determine the formation of the amniotic and allantoic cavities, which are filled with liquid (Toniollo and Vicente, 1993). The amniotic fluid in swine is viscous and yellowish-transparent, while the allantoic fluid has amber-transparent appearance and watery

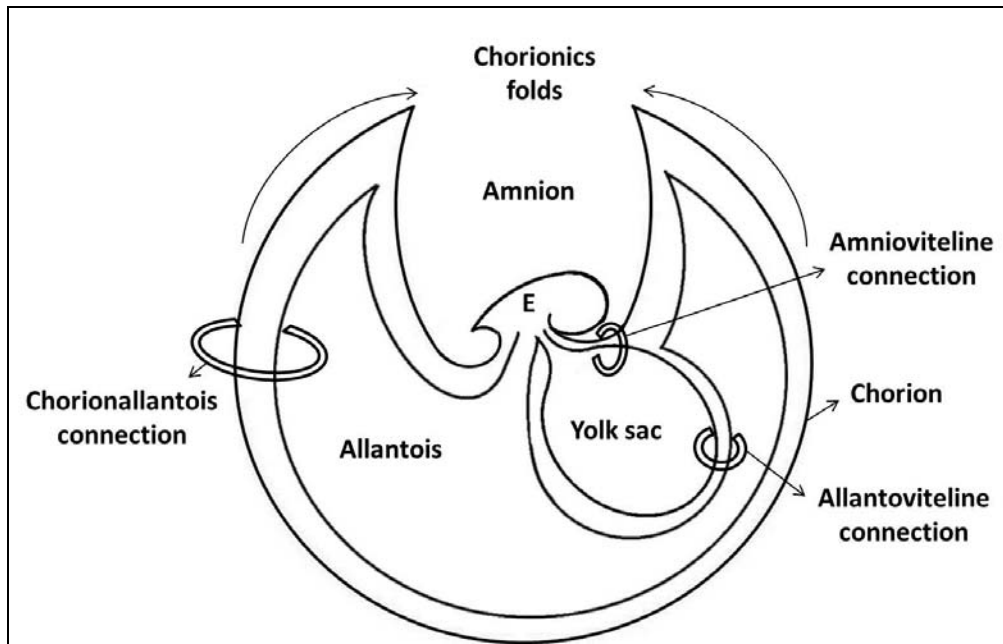


Figure 1. Extraembryonic membranes in development as described by Bertasoli et al. (2012).

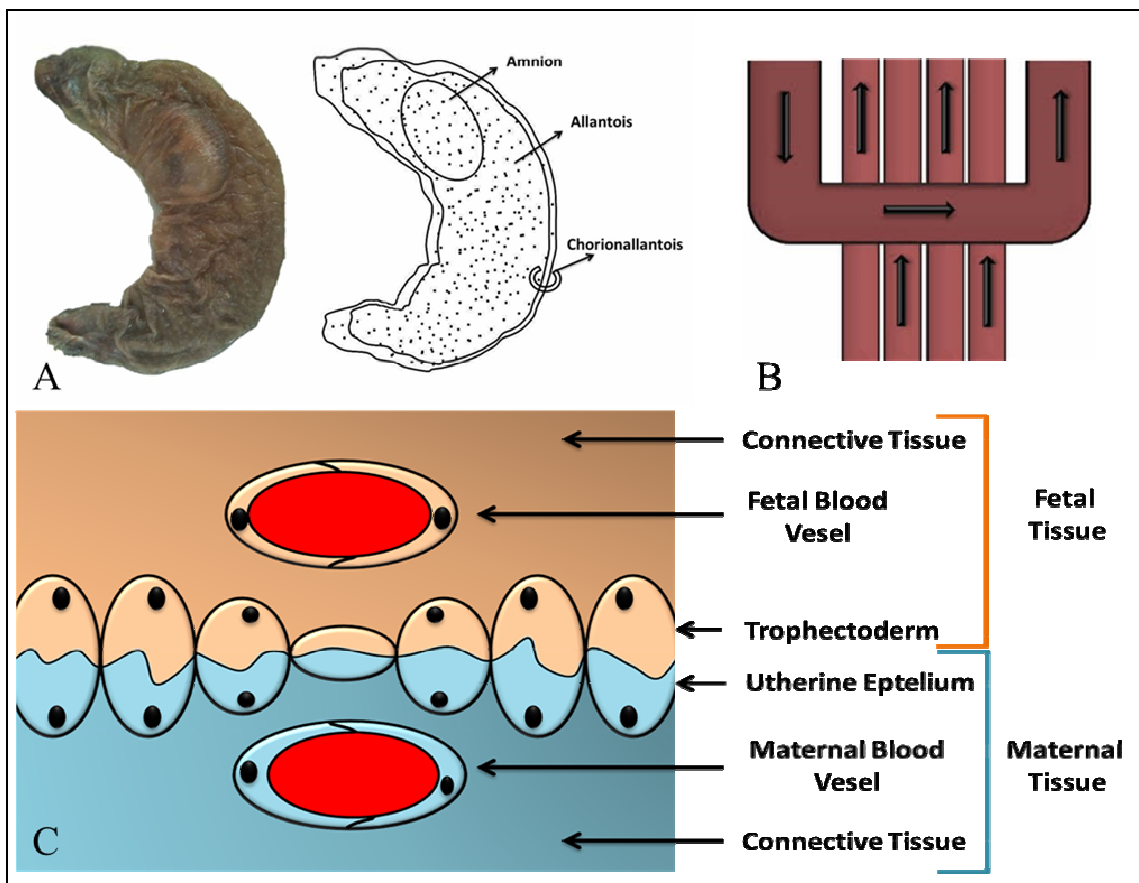


Figure 2. Swine placenta. (A) Embryonic attachment in swine; (B) Blood flow: cross current; (C) Membrane inter-hematic: epitheliochorial type. As described by Roa et al. (2012) and Montiel et al. (2013).

consistency. The swine placenta is composed by the juxtaposition of maternal and fetal parts separated by a thin layer of mucus. The uterine glands open into depressions and outline the depressions corresponding to the contour of the rosettes (areolas) (Abromavich, 1926).

Perry (1981), on his study, points that swine have a simple eutherian placenta, which is diffuse due to the union that extends by all yolk sac surface, except on uterine glands' ends and apertures. Still according to him, the chorion bows on glands' apertures, forming the areolas, which seem like circular marks on chorion surface. This is a remarkable characteristic of the swine placenta.

How the swine placenta is epitheliochorial, there are a maximum number of barriers between fetal and maternal blood. As a result, between maternal and fetal blood, there are the following layers: maternal endothelium, connective tissue, uterine epithelium, uterine lumen, trophoblast, fetal connective tissue and fetal blood vessel endothelium (Beaudoin et al., 1998).

Thus, implantation in swine is superficial and amniogenesis is pleated. The allantoic vesicle is large, occupies the exocoelomic cavity and is permanent. The yolk sac and choriovitelline region disappear in the early stages of gestation and the contact area displays small-unbranched villi, with ancillary structures represented by areolas and chorionic vesicles (Mossman, 1937).

Cummins et al. (2008) assert the swine placenta is similar to that of horses, still regarding the interposition between the maternal and fetal blood by five key obstacles (two endothelia, two epithelia perfectly continuous and uterine light). Nonetheless, the swine placenta is incompletely diffused and presents two territories: chorioallantoic and amniochorionic. Furthermore, the swine placenta has exceptionally three distinct regions, with particular characteristics: the region of chorionic villi or wrinkles, the region of chorionic cavities and the chorionic areolas (Wislocki and Dempsey, 1946).

Except on areolar areas, there is a close contact between the maternal epithelium and protoplasmic processes from fetal chorion during gestation. Since the seventh week of gestation, capillaries from wall and top of villi invade epithelium, becoming a very thin layer. The prismatic (cylindrical) cells from the bottom of villi set characteristic arches, which represent essential elements for placental architecture (Drieux and Thiery, 1949; Hitzig, 1949).

During swine birth, when placental separation happens, there is no loss of uterine or other maternal tissues, and the placenta is therefore decidua. Yet, during pregnancy, the swine uterine mucosa presents abundant tubular glands, which produce a great amount of "uterine milk", absorbed by areolar trophoblast (Beaudoin et al., 1998).

Placental areolas

Friess et al. (1981) and Olio et al. (2014), describe that swine placental areolas present a dome-shape, where uterine glands open. The epithelium arranges on high columns, with long microvilli, tubular systems and vesicles, indicating a high absorptive capacity of the epithelium (Figure 3).

Dantzer and Leiser (1993) cite that the placental areolas form both from fetal and maternal tissue, this last enveloping the areolar cavity. These areolas accumulate histotrophic secretions from an only uterine gland or from several of them, being accordingly classified on regular or irregular areolas respectively. The regular areolas, when they are observed through the fetal membranes (chorioallantoic/chorioamniotic), seem like generally opaque, yet variably translucent, circular spots, which measure a few millimeters and form bigger structures.

According to Miglino et al. (2001), until 7,000 regular areolas may concentrate in each conceptus, while the irregular ones present a variable frequency around 1,500 areolas per placenta. Beyond the areolas, different structures may be found on the fetal placenta, like cists, hipponames and petrifications.

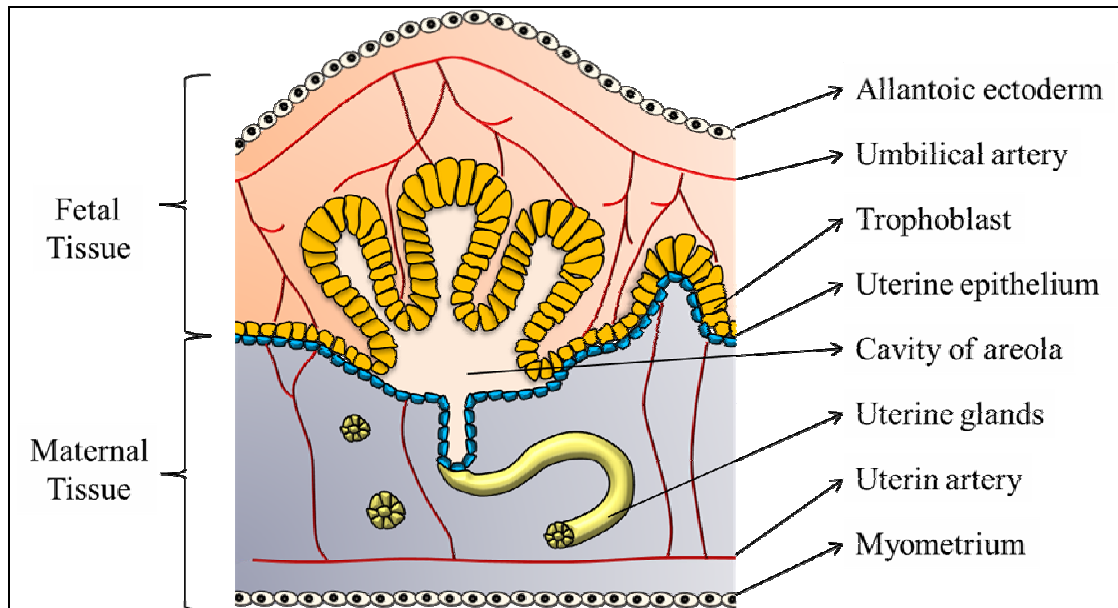


Figure 3. Schema of swine placenta and uterine wall section showing areola as described by Olio et al. (2014).

The swine placenta fetal side presents a capillary network forming papilla, which have protrusions and areolar cavity, or converging to arrange in a circle, directed to the areola margin. The irregular areola show indistinct boundaries, characterized by the aperture of one or more uterine glands. Both the vascular arrangement of irregular and regular areolas implicate on blood influx through capillaries and arterioles, while the efflux from areolar capillaries culminate on venules' convergence toward one or two areolar veins, conducting venous blood on a fashion distinct from that occurring at the areolar area. Therefore, it suggests this architecture favors the control mechanism in the uterus, the placenta and the fetus (Miglino et al., 2001).

Abd-Elnaeim (2003) cites that, in swine, there are interruptions in the inter-microvillus annex from areolar regions. The substance interchange between mother and fetus happen trough the areolar cavity. Yet, in the swine areola, histotrophic secretions or discriminated products from endometrium are absorbed by trophoblast to developing the embryo during pregnancy.

As stated by Wooding et al. (2000), both calcium and iron ions cross the same areolar cell and trophoblast, although via

different pathways. Calcium crosses through cytoplasm, while iron and its transporter protein (uteroferrin) bind the cell membrane during incorporation of a vesicle or lysosome. Uteroferrin is one of the most important molecules for ion transportation by the areolar cavity from mother to fetus in horses (Wooding et al., 2000), as well as in other species, like pigs (Friess et al., 1981; Bazer et al., 1986). On the other hand, opposite to this capitation method, glucose is transported uniquely trough maternal and fetal epithelial micro cotyledonary cells (Wooding et al., 2000; Oliveira et al., 2015).

Areolar glands are subunits specialized on the maternal-fetal substance transference (Friess et al., 1981). As shown in the studies from Bazer (1975), Chen et al. (1975) and Raub et al. (1985), the columnar to cuboidal epithelium composing the uterine glands is related to other functions in the Uteroferrin synthesis. On this way, the secretion released inside the areolar cavity presents metabolic enzymatic activity (Schlosnagle et al., 1974; Friess et al., 1981).

Data from Miglino et al. (2001) have shown only one uterine gland can open interiorly to the areolar cavity, which is different from the equine one, which

often has more than one aperture at this place.

Final considerations

The study of the placenta and the extraembryonic tissues in swine is of utmost importance once pigs are relevant animals for livestock. Based on the literature, as referred by many authors here cited, the placenta is vitally important according as one of its functions is nutrient exchange. The swine placenta is therefore classified as chorioallantoic, diffuse, pleated, epitheliochorial and cross to counter-current. Amnion, chorion, allantois and yolk sac are intimately related to fetal development and embryonic losses, since the placental development in pigs starts around the 18th day of gestation. Modifications in the swine placenta, like the presence of areolas, might have arisen as domestic species adaptations in order to supply nourishing needs during the development of concept.

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Conflict of interest statement

Authors declare that they have no conflict of interests.

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