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Placentation in different mammalian species

La placentation dans différentes espèces de mammifères

Pascale Chavatte-Palmer*, Anne Tarrade

UMR BDR, INRA, ENVA, université Paris Saclay, domaine de Vilvert, bâtiment 231, 78350 Jouy-en-Josas, France

Abstract

The placenta is a complex, transient organ associated with viviparity, which is located at the interface of the dam and fetus during pregnancy. It is formed after attachment, or implantation, of the blastocyst on the uterine lining and derives from complex cellular and molecular interactions between uterine and embryonic tissues. In mammals, there are many forms of placentation but this organ has the same function in all species: it is responsible for orchestrating materno-fetal exchanges, together with endocrine and immunological functions.

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Keywords: Placenta; Mammals; Comparative anatomy; Pregnancy

Résumé

Le placenta est un organe transitoire complexe associé à la viviparité, situé à l'interface entre la mère et le fœtus pendant la grossesse. Il est formé après la fixation (ou l'implantation) du blastocyste à la muqueuse utérine et dérive d'interactions cellulaires et moléculaires complexes entre l'utérus et les tissus embryonnaires. Chez les mammifères, il existe différents types de placentation, mais cet organe exerce la même fonction dans toutes les espèces à savoir des échanges materno-fœtaux, mais aussi des fonctions endocrines et immunologiques.

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Mots clés : Placenta ; Mammifères ; Anatomie comparée ; Gestation

1. Introduction

The implantation of the embryo into the uterus is an evolutionary process associated with viviparity and placentation. This reproductive strategy ensures an efficient protection and nutrition of the embryos and thus promotes their survival. In all placental mammals, the establishment of an intimate contact between the embryo and the mother follows a succession of common critical steps whose chronology and timing may considerably vary from species to species. Moreover, these processes present a great diversity based on anatomo-histology of the uterus as well as endocrine and molecular interactions between the uterine and the embryonic tissues.

2. Anatomical and physiological considerations

The structure of the placenta is dependent on the anatomical structure of the uterus. The uterine anatomy differs among mammalian species (Fig. 1) and is adapted to certain characteristics of their reproductive biology, such as trans-uterine migration of blastocysts and litter size. There are three main types of uteri:

- double uterus (rodents, lagomorpha) with 2 uterine cervices and two separate uterine horns;
- bicornuate uterus (ruminants, swine, equidae, carnivores, cetaceans) with 1 cervix, 1 uterine body of variable length and 2 communicating uterine horns;
- simplex uterus (primates, bats) with 1 cervix and 1 large uterine body without uterine horns.

* Corresponding author.

E-mail address: pascale.chavatte@jouy.inra.fr (P. Chavatte-Palmer).

The uterine tissue is composed of an external muscular coat (myometrium) surrounding an inner mucosa (endometrium) to

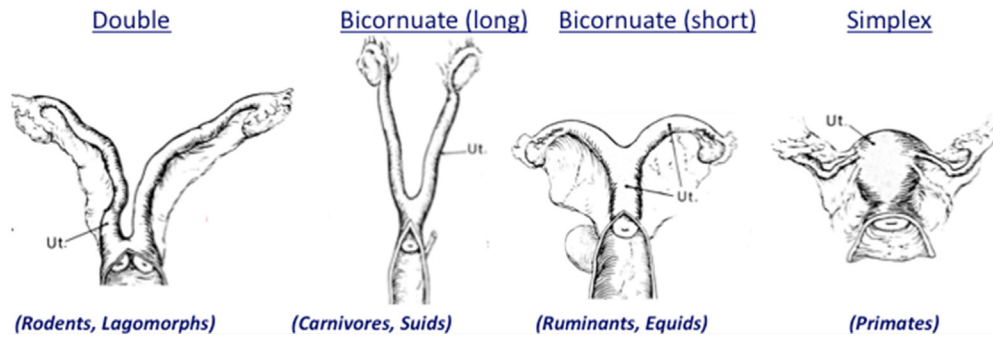


Fig. 1. Comparative anatomy of the uterus.

which the embryo attaches, forming the placenta: this is referred to as the implantation. The endometrium, more or less wrinkled depending on species, consists of a single luminal epithelium resting on a connective tissue (stroma) richly vascularised and interspersed with uterine glands that open into the uterine lumen. This basic structure is common to all mammals and generally all of the endometrial surface is responsible for the establishment and formation of the placenta. There are, however, anatomical peculiarities specific to certain species. Thus in ruminants, areas of endometrial thickening appear during organogenesis where uterine glands are not present. These areas, called caruncles, are lead to the development of distinct placental structures named placentomes. They are aligned along the uterine horns and their number varies according to the species from 5 (deer) to 150 (giraffe).

The timing of the implantation, which corresponds to the beginning of placental development and the length of gestation also varies between species and is described in Table 1.

3. Extra-embryonic membranes

The placenta per se (sometimes referred to as the fetal placenta) is derived from the fertilized egg and therefore contains the same genetic heritage and is of the same sex as the conceptus [1].

Table 1
Comparative chronology of gestation (in days post-conception).

Species	Day of implantation (embryonic stage)	Definitive placentation	Gestational length
Mice	4.5 (blastocyst)	14.5	20
Rat	5.5	–	22
Hamster	4	–	16–19
Guinea pig	6	–	68
Rabbit	6.5 (gastrula)	–	31
Human	6–7 (blastocyst)	90	280
Cat	13	–	63
Swine	13–14 (gastrula)	–	115
Sheep	15 (neurula)	40	145
Cattle	19–20 (neurula)	50–60	280
Horse	30–38 (organogenesis)	60	330

3.1. Trophoblast

The main tissue in direct contact with the uterus is the trophoblast or trophoctoderm. This epithelium results from cell segregation at the blastocyst stage into an embryonic lineage and an extra-embryonic lineage. During development, the extra-embryonic mesoderm from the embryo migrates and merges with the trophoblast to form the chorion that surrounds the embryo and fetus and its annexes (Fig. 2).

The placental trophoblast structure varies according to species and during pregnancy. Only pigs and cetaceans possess a cytotrophoblast, i.e., a mononuclear trophoblast throughout gestation. There are no invasive process in these species. In ruminants and equines, a fraction of the mononuclear trophoblast cells differentiates into binucleated cells with distinct properties in both orders, in connection with an invasive process. In the vast majority of other orders of mammals, the original cytotrophoblastic layer splits into a layer of cytotrophoblast which is retained and another that forms a syncytiotrophoblast by cell fusion and which provides most of placental functions.

3.2. Amnion

The amnion is the membrane delimiting the fluid-filled cavity containing the fetus. Although the amnion partially merges with the chorion, it is not directly involved in the structure of the placenta in most mammals. It nevertheless represents a significant placental annex to fetal development. The amniotic cavity provides mechanical protection of the fetus and its development in liquid medium, freeing external pressures.

3.3. Yolk sack

The yolk sack is a vestige of vertebrate evolution. In many mammals, it is the first vascularised extra-embryonic structure. The yolk sac is formed during the migration of the extra-embryonic mesoderm. Sandwiched between the trophoblast itself and the parietal endoderm, it merges with the latter to define a cavity inside the blastocoele (or exocoelome). A primitive vascular network then differentiates within the yolk sack mesoderm.

The fate of the yolk sack during pregnancy is variable depending on the species. In most rodents, the yolk sack undergoes a

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