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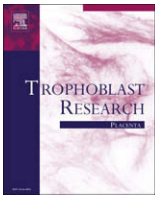

Reasons for Diversity of Placental Structure

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A B S T R A C T

Many early embryonic stages are nearly indistinguishable in different Eutheria. However, implantation stages and placental morphological types vary tremendously. A number of factors favor this conflicting diversity. 1. Whereas embryo development takes place in the isolation of the amniotic cavity, the extraembryonic membranes of the conceptus develop in close association with the uterus of a genetically different organism. 2. Early conditions for the developing conceptus are anaerobic whereas later in development efficient aerobic conditions are essential for continued growth of the fetus. 3. Developing extraembryonic membranes have the potential to form two partially sequential placentas. The yolk sac can participate in forming a choriovitelline placenta, including an interhemal region, and can be adapted to various non-respiratory functions as gestation proceeds. Development of the chorioallantoic placenta begins later than the choriovitelline placenta but can overlap with this before supplanting it. The original development of the extraembryonic membranes occurs when the conceptus is sufficiently small that neither its nutritional requirements nor its respiratory needs are the burden to the maternal organism that they are later in gestation. Despite these developmental factors promoting different methods of forming the definitive placenta, the placental type is consistent within most families indicating that the divergence in placental structure accompanied evolution of differences between groups.

1. INTRODUCTION

Development of the embryo appears to be similar in different species, and is tightly controlled. Neural fold stages, somite stages, and other early embryonic stages are nearly indistinguishable in different Eutheria. However, placental types vary as do the implantation stages leading to these types. Therefore there must be factors favoring placental diversity and mechanisms by which this diversity can be achieved.

There are also non-variable features of placental development, including formation of viable young, decrease in size of the placenta relative to the fetus as gestation proceeds, early anaerobic conditions but later increasing aerobic needs, and first erythrocyte formation in the extraembryonic membranes. While it might be thought that the definitive placental type should always be one in which efficiency is greatest, i.e. least amount of increased energy expenditure by the maternal organism per increment of fetal weight gain, this is not necessarily the case. Taking just the condition of young at birth, altricial (immature) vs. precocial (highly developed): when the later involves large animals with the necessity to run or swim soon after birth, there is a relatively long gestation period. Extending the period of growth to limit the drain on the maternal system, i.e. decreasing the conflict between maternal well-being and fetal growth [1], may be more important than absolute efficiency. Similarly it may be particularly important to diminish the possibility of excessive exchanges of fetal and maternal cells when there is a longer gestation period, which could increase the possibility of various immunological and other problems [2].

No matter what the possible advantages and disadvantages of different placental types are, there is no question that there is a great deal of placental diversity among mammals.

2. PLACENTAL DIVERSITY AS ILLUSTRATED BY HEMOMONOCHORIAL PLACENTAS

Recently Wildman [3] listed 41 eutherian species in which some of the genomics was known to compare with their placental type. Of those, more than 60% were listed as having hemochorial placentas. Many years ago I suggested that hemochorial placentas could be divided roughly into three types: hemomonochorial, hemodichorial and hemotrichorial, depending on the number of trophoblast layers in the interhemal region [4]. However, even taking just the hemomonochorial type, there is a great deal of structural difference (Figs. 1–3). For example, the villous hemomonochorial placenta with syncytial trophoblast may have

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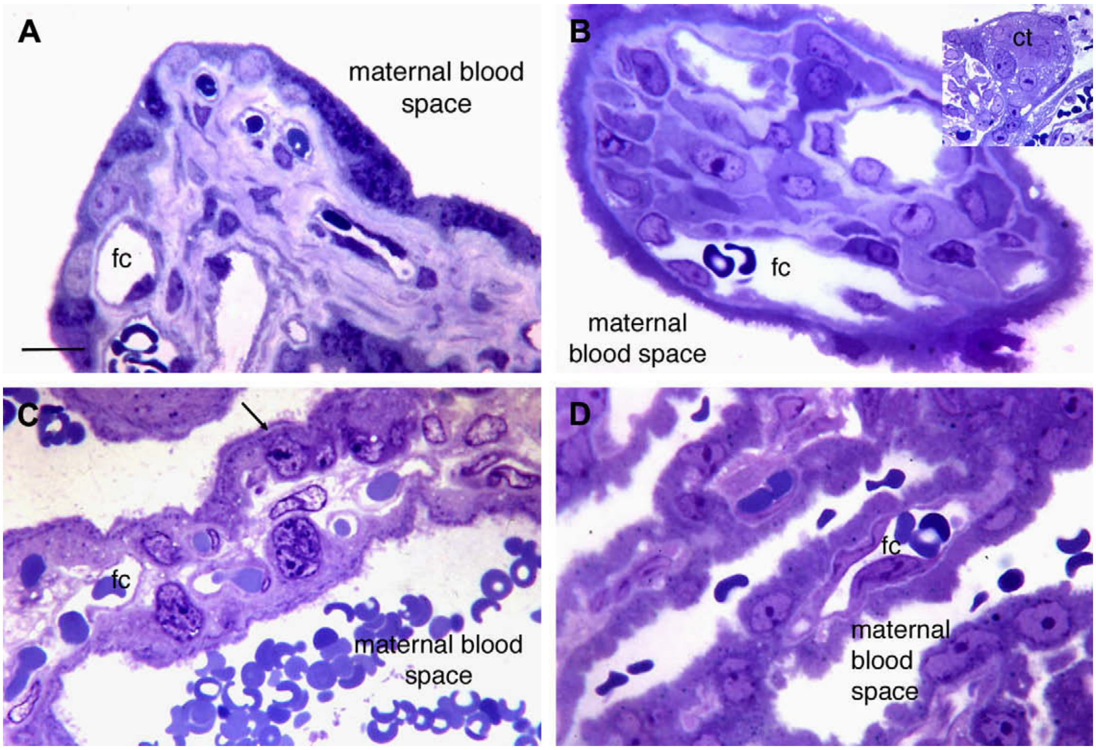

Fig. 1. Hemomonochorial placentas. A. Note the cytotrophoblast (Langhans) cells underlying the syncytial trophoblast in this villous hemomonochorial placenta of the human. B. Mature villus in the hemomonochorial placenta of the armadillo. Note the epithelioid mesenchymal cells. Inset: Growing villi in a mid-term placenta. Note that the cytotrophoblast cells (ct) are only at the tip of the villus. C. Midgestation labyrinthine placenta of the marmot, a sciuromorph rodent. Note the intrasyncytial bays (arrow). D. Labyrinth of the guinea pig, a hystricognath rodent. Syncytial trophoblast lines the maternal blood space but there are no intrasyncytial bays. (Transmission electron microscopy is definitive in determining the syncytial or cellular nature of trophoblast lining maternal blood spaces and in confirming the presence or absence of intrasyncytial bays.) fc = fetal capillaries. All micrographs except the inset are at the same magnification. Scale bar = 12 μm. Inset: 31 μm.

persistent cellular trophoblast along the villi as in the human (Fig. 1A) [5], or may lack cellular trophoblast in this position with cytotrophoblast only at the villus tips as in the armadillo (Fig. 1B) [6]. In labyrinthine placental types with syncytial trophoblast, the trophoblast may have intrasyncytial bays and laminae as in sciuromorph rodents such as the marmot (Figs. 1C and 3A) [7] and elephant shrews [8], or may not have bays such as various of the hystricognath rodents illustrated here in the guinea pig (Fig. 1D) [9]. The hyena, in addition to being a labyrinthine placental type with syncytial trophoblast and intrasyncytial bays, has hemophagous regions (Fig. 2A) [10]. In species with a labyrinthine placenta but cellular trophoblast, some have intratrophoblast bays and laminae, such as molossid bats (Figs. 2B and 3B) [11], while others such as the jumping mouse (Fig. 2C) and jerboa do not [12], nor do hyraxes [13]. Some of the Tenrecidae such as the hedgehog tenrec *Echinops* (Fig. 2D) and the shrew tenrec *Microgale* not only have cellular trophoblast in the placental labyrinth, but in addition have hemophagous regions [14]. It should be noted that, despite the widespread distribution of intrasyncytial and intratrophoblast bays and laminae, their function is almost totally unknown and under-investigated [15].

Thus, without considering the presence or absence of spongy zones or the persistence of inverted or non-inverted yolk sacs, there are eight different types of placenta within the hemomonochorial group.

3. MAJOR FACTORS TENDING TO INCREASE DIVERSITY OF PLACENTAL STRUCTURE

Several factors in development of extraembryonic membranes tend to increase the diversity in placental structure: the fact the early stages are anaerobic; that there are two organisms interacting; and that there are potentially two placental systems, the yolk sac and the chorioallantoic placenta.

3.1. *Anaerobic early stages*

Since the early stages of development are clearly anaerobic [16], there is no necessity for immediate development of a good system of oxygen transfer. Furthermore the amount of tissue involved and therefore the drain on the maternal organism is very small at this early stage. Therefore some of the areas of potential conflict between needs of the maternal organism and the developing conceptus are minimal, and there is no need for development at this stage to be particularly efficient. Neither do variations in extraembryonic membrane formation necessarily affect embryo formation. An example of this is mutations in the T locus or brachyury in mice, in which the allantois does not form properly but the embryos proceed well until the time of formation of the chorioallantoic placenta [17].

3.2. *Conceptus–uterine interaction*

The interaction of the uterus and conceptus can be highlighted by two very different examples of developmental cooperation. In myomorph rodents such as rats and mice, multiple blastocysts implant in a bicornuate uterus. The decidual response of the endometrium is responsible for an extensive series of events aiding implantation and placentation. These include orienting the conceptus and the initial deterioration of the uterine epithelium, especially mesometrial to the implantation site [18], as well as eventual inversion of the yolk sac. In the nine-banded armadillo on