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The Extraembryonic Membranes

"The fetal membranes are extremely variable in shape and size and are probably responsible for confusing more students of embryology than any other tissue!" -M. B. Renfree, 1982

For more Literature Cited and information, see Renfree, 1982 or Mossman, 1987.

The Extraembryonic Membranes of Monotremes

The placenta is an organ that has its origin in the extraembryonic membranes of the amniote egg. While the monotremes are oviparous, the quantity of yolk in the moroblastically cleaving eggs is not sufficient to provide all the nutrients needed for the completion of embryonic development. The small egg (4.4 mm diameter) develops to form a rapidly dividing outer cell layer ("epiblast", "trophoblast") that envelops the egg to form a "bilaminar" blastocyst. The uterus of the monotreme secretes a double-layered shell about the embryo. This shell is porous and allows uterine secretions to enter the region between the outer and inner layers. The uterus then secretes a third layer of shell. The shell is still porous to oxygen and nutrients. Intrauterine growth of the embryo is not seen in reptiles or birds, and the development of the monotreme trophoblast for nutritive exchange may presage its functions in eutherians and marsupials. The egg is laid when the embryo has formed 18 (in the platypus) or 19 (in the echidna) somites. Like the birds, a chorioallantoic membrane will form and become vascularized.

Placental Classification I: Typology by Diffusion Barriers

One way of classifying placentas is by the number of layers separating the fetal and maternal blood supply. This type of categorization was put forth at the beginning of this century by Grosser and simplified by Steven (1975). The main placental types can thus be characterized as epitheliochorial (three maternal layers and three fetal layers), endotheliochorial (one maternal layer, three fetal layers), hemochorial (no maternal layers; three fetal layers). It should be noted that many placentas are mosaics having different regions which may be best characterized by one term, and other regions best characterized by another. The "type" of placenta attributed to any mammal concerns the majority of the absorptive area of the placenta.

Placental Classification II: Gross Structure

In 1604, Fabricius introduced a classification scheme based on the macroscopic structure of the sites where attachment occurs between the embryo and the endometrium of the uterus. He listed four main placental types. These are now referred to as the diffuse, cotyledonary, zonary, and discoidal placentas.

In diffuse placentae, seen in horses, pigs, camels, lemurs, opossums, kangaroos, and whales, the chorionic sac meets the uterine endometrium over its entire surface. The villi of the chorion are distributed evenly throughout the surface of the chorion, and they extend into processes in the uterine endometrium. Cotyledenary placentae, common to ungulates such as cows, deer, goat, and giraffe, have their villi clumped together into circular patches called cotyledons. The fetal cotyledon meets with maternal regions called caruncles to form the placentome where maternal-fetal exchanges take place. In the zonary placenta, which is characteristic of carnivores, the chorionic villi

have aggregated to form a broad band that circles about the center of the chorion. Such zones may be complete circles (such as those in dogs and cats) or incomplete (such as those in bears and seals). It is thought that zonary placentae form from diffuse placentae in which the villi at the ends regress, leaving only those in the center to function. At the edges of the zonary placenta is the hemophagous organ, which is green. The color is due to the degradation of hemoglobin into bilivirdin. This provides iron for the developing fetus. The discoid placenta is seen in numerous groups--humans, mice, insectivores, rabbits, rats, and monkeys. In such placentae, part of the chorion remains smooth, while the other part interacts with the endometrium to form the placenta.

Literature Cited

Mossman, H. W. 1987. *Vertebrate Fetal Membranes.* Rutgers University Press, New Brunswick, NJ

Renfree, M. B. 1982. Implantation and placentation. In Austin, C. R. and Short, R. V. (eds.) *Reproduction in Mammals 2. Embryonic and Fetal Development* (Second edition). Cambridge University Press, Cambridge. Pp. 26-69.

Steven, D. H. (ed.) *Comparative Placentation.* Academic Press, NY.