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Review

A review of uterine structural modifications that influence conceptus implantation and development in sheep and goats

U.M. Igwebuike [a,b,*]

[a] Department of Veterinary Anatomy, University of Nigeria, Nsukka, Nigeria
[b] Abdus Salam International Centre for Theoretical Physics, Trieste, Italy

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ABSTRACT

Evolution of the placenta and viviparity in eutherian animals underscores the need for an intimate relationship between the developing conceptus (embryo/foetus and associated extra-embryonic membranes) and the dam throughout the period of pregnancy. Thus, maternal support is unequivocally important for conceptus survival and development in utero. Under the influence of several pregnancy-associated hormones, the maternal uterine architecture undergoes rapid growth and substantial remodeling early in gestation. These changes are necessary preparations to accommodate and support rapid conceptus development and growth in the later two-thirds of pregnancy. There are species variations in the nature and extent of uterine remodeling during pregnancy. The regulatory influence of these uterine wall modifications on conceptus survival, implantation and placentation in sheep and goats are discussed in this review.

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* Correspondence address: Department of Veterinary Anatomy, University of Nigeria, Nsukka, Nigeria. Tel.: +234 8038726150.
E-mail address: abuchi2002@yahoo.com.

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1. Introduction

The conceptus (embryo/foetus and associated extra-embryonic membranes) of all eutherian species must establish intimate contact with the dam, because maintenance of pregnancy and by inference, conceptus survival and growth requires reciprocal communication between the conceptus and the endometrium during implantation and placentation. Maternal factors are important regulators of conceptus growth and development in utero. Although ruminant animals are characterized by delayed on-set of implantation and superficial placentation, the uterine wall of this species of animals is known to undergo rapid growth and substantial remodeling during pregnancy, in order to accommodate and support conceptus growth and development. The implications of this uterine structural remodeling and its regulatory role in conceptus nutrition, implantation and placentation are the subjects of this review.

2. Histology of the pre-implantation uterine wall

The mature uterine wall is made up of two functional components, the myometrium and the endometrium. The myometrium is the smooth muscle component of the uterine wall. The endometrium is the inner mucosal lining of the uterus and it constitutes the maternal component of the placenta. The endometrium of adult sheep and goats consists of large numbers of raised aglandular areas called caruncles, and intensely glandular intercaruncular areas (Wimsatt, 1950). The caruncles are dense stromal protuberances covered by a simple luminal epithelium. Intercaruncular areas of the endometrium contain large numbers of branched, coiled uterine glands (Amoroso, 1952; Bazer, 1975; Gray et al., 2001a). During early pregnancy, the entire uterine luminal epithelium is characterized by tall columnar cells that rest on a thin basement membrane (Dent, 1973). These epithelial cells are mononucleated, and extend many microvilli from their luminal surfaces. Neighbouring cells are bound together by tight junctions (Dent, 1973; Guillomot and Guay, 1982).

3. The implantation process

The survival, growth and subsequent development of the conceptus depend largely on its successful attachment to the maternal endometrium. Implantation is the process that results in attachment of the conceptus to the maternal endometrium, leading to the establishment of the placental structures. In sheep, superficial implantation and placentation begins on Day 15 to 16 of gestation, but is not completed until Day 50 to 60 of pregnancy (Wimsatt, 1950; Guillomot, 1995). Three stages of the implantation process in ruminants were described by Guillomot et al. (1981) namely: (i) a long pre-attachment period during which the conceptus elongates considerably, (ii) an apposition stage when cellular contacts are established between foetal trophoblast layer and maternal uterine epithelium, and (iii) an adhesion stage that gives rise to the cellular structures of an epitheliochorial placenta.

4. Changes in the uterine wall

During the period of implantation, the uterus grows and remodels substantially in order to accommodate rapid conceptus development and growth in the later two-thirds of pregnancy. Important