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Review

Bovine placenta: A review on morphology, components, and defects from terminology and clinical perspectives

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A R T I C L E I N F O

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A B S T R A C T

The bovine placenta has been the subject of many studies. Concurrently, several specialized terms have been developed to describe its development, morphology, components, function, and pathology. Many of these terms are simple, some are difficult to understand and use, and others are antiquated and may not be scientifically accurate. Defining and adopting terminology for the bovine placenta that is clear, precise and understandable, and available in a single source is expected to facilitate exchange of clinical and research information. This review presents a brief overview of the current knowledge regarding the bovine placenta and attempts to define terms. In this process, conventional terminology is presented, and contemporary and novel terms are proposed from a biological perspective. For example, use of terms such as syndesmochorial, retained placenta, and large offspring syndrome should be revisited. Furthermore, the clinical relevance of the structure and function of the bovine placenta is reviewed. Finally, terms discussed in this review are summarized (in table format).

1. Introduction

An excellent review published in 2000 [1] focused on the ontogeny of the most important cellular populations of the bovine placenta from the utero-fetal defense perspective and stressed the importance of placentology and placental pathology. The review identified the etymological origin of the word “placenta.” It is derived from Latin, meaning “flat cake,” due to the apparent gross similarity of the human discoid placenta to round, flat loaves of unleavened bread common in ancient times. Although differentiation of the early conceptus is very similar in humans and cattle in size [2], the initial establishment with the uterine epithelium and subsequent growth and differentiation of the placenta are very different between these two species [1].

Defining and adopting terminology used in bovine reproduction that is clear, precise, understandable, and available in a single source would make the exchange of clinical and research information and outcomes more efficient. Furthermore, diagnoses and inference of results between and among studies can be correctly interpreted and substantiated or negated, and therapy and hypotheses can be formulated without unnecessary confusion and redundancy in treatments and experiments. On the basis of these objectives, a series of articles on ovarian dynamics [3], biology of the preattachment embryo [4], and production and manipulation of preattachment embryos [5] have been published. This article will review the development and clinically relevant features associated with the bovine placenta. As in the previous reviews [3–5], the focus is on terminology and its application in clinical and research settings. Clinical management of specific placental conditions is beyond the scope of this review; however, this information is readily available in standard Theriogenology textbooks.

The term placenta points to the structure that has both maternal (endometrium) and fetal components [6,7]. These are identified as maternal placenta and fetal placenta,

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respectively [6,7]. The term fetal placenta refers to the chorioallantois [7], whereas the term fetal membranes includes the amnion and chorioallantois [8]. These distinctions will be applied to the clinical conditions that are discussed in this review. This review will attempt to define the terms applicable to the morphology, components, and defects of the bovine placenta, whereas endometrial defects are beyond the scope of this review.

2. Morphology

Currently, the bovine placenta is described as "cotyledonary synepitheliochorial," on the basis of its morphology that is established at approximately Days 40 to 50 of pregnancy. Earlier classification as syndesmochorial was on the basis of a misunderstanding of the number and form of the layers intervening between the fetal and maternal circulation and needed correction. The earlier assumption that the uterine epithelium is lost in the process of placentation resulting in direct apposition of trophectoderm to the maternal connective tissue is no longer tenable. It is now known that the uterine epithelium persists although initially modified to a variable degree into patches of a hybrid fetomaternal syncytium formed by the migration and fusion of a particular type of trophectodermal cells with uterine epithelial (UE) cells. These trophoblastic binucleate/giant cells (TGCs) migrate and modify the uterine epithelium by apical fusion to form fetomaternal hybrid syncytial plaques, with up to eight nuclei at the junction of fetal and maternal tissue [9–11]. These syncytial plaques are replaced by regrowth of UE cells by Day 40 and subsequently TGC-UE fusion produces only transient trinucleate minisyncytia (Fig. 1) throughout the remainder of pregnancy. These studies have necessitated a change in the morphological terminology of placentation and defined the bovine placenta as synepitheliochorial. The "syn" indicates the contribution of TGC to the fetomaternal syncytium and contrasts with the simple microvillar interdigitation between trophoblast and uterine epithelium (epitheliochorial) over the rest of the placenta [12]. Trophoblast cells from Days 15 to 20 embryos have been grown in tissue culture and can form spherical hollow balls of cells referred to as "trophoblastic cell vesicles" or "trophoblastic vesicles" [13–16].

The term "cotyledonary" refers to the presence of localized areas of trophectodermal proliferation forming "cotyledons" in the placenta; each cotyledon is the fetal part of a placentome. The placentome is formed by the tuft of chorionic villi from the cotyledon enmeshed with corresponding maternal crypts of the caruncles. These crypts develop from the preformed flat endometrial caruncles, present in the nonpregnant cow, which are aligned along the uterine horns. Normally, there are 80 to 90 caruncles (range, 75–120) [7]. A corresponding number of cotyledons are apparent on the chorioallantoic surface [17]. These two structures form the placentomes. Placentome formation with a synepitheliochorial interhemal barrier provides the vast increase in surface area necessary for the continuously increasing substance exchange between the dam and the fetus. The gross morphology and the pattern of fetomaternal interdigitation (villus/crypt architecture of the mid- to late-pregnant placenta) differ considerably among bovid species [18], but the detailed cellular structure of the materno-fetal interface is the same throughout pregnancy [19]. In summary, the three characteristics of a synepitheliochorial placenta are the presence of TGC in fetal trophectoderm, formation of fetomaternal syncytia, and development of a placentomal chorioallantoic placental organization.

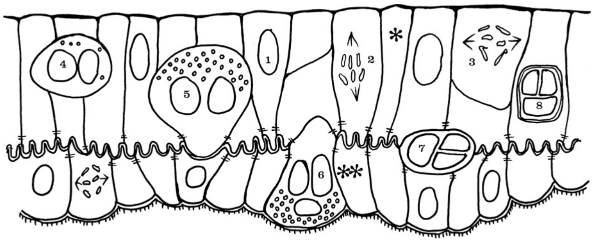

Fig. 1. Migration (1 and 2), fusion and injection (3) of TGC, and formation of a trinucleate cell (4 and 5). Courtesy of Dr. Wooding and Springer.com.

3. Components

3.1. Fetal membranes

An arrangement of transporting epithelia between maternal and fetal circulations more vividly encapsulates the functional aspects of the placenta. It is primarily made up of fetal membranes, which include the amnion, allantois, and chorion (collectively termed extraembryonic membranes). The trophectoderm and the nonvascular mesoderm form the chorion, which is also known as "somatopleur." The chorion produces folds to enclose the embryo to form a fluid-filled sac, the amnion. A Day-35 embryo with a well-formed amnion is referred to as an "amniotic vesicle," which can be identified either by transrectal palpation or by transrectal ultrasonographic examination of the uterus (described later under pregnancy diagnosis). Inside the amnion, the embryo develops free of asymmetric constraints in a shock-absorbing and compression-resistant environment. Once the amnion is formed, an endodermal vesicle grows from the hind-end of the embryonic gut to form the allantoic vesicle, covered from its inception by vascular splanchnopleuric mesoderm (Fig. 2). The "splanchnopleur" is the name given to the definitive yolk sac wall. The allantois is continuous with the developing urogenital system of the embryo and acts as a site for waste deposition. Much more importantly, its rich blood supply also allows it to develop as an organ of respiratory exchange when it grows through the exocoelom to fuse with the chorion, which surrounds the embryo to form the chorioallantois. Thus, the chorioallantois is enormously expanded in cotyledon formation.

Recent works [17,20] reported the gross development and cellular nature of these membranes from Days 20 to 70 of pregnancy. At approximately Days 20 to 25, the membranes appear transparent and occupy both uterine horns. At this time, the allantois is separated from the chorion with noticeable yet discrete blood vessels appearing on the side facing the ventral part of the embryo. The amniotic membrane appears smooth, forming a thin film that envelops the