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Review

Novel clathrin/actin-based endocytic machinery associated with junction turnover in the seminiferous epithelium

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ABSTRACT

Tubulobulbar complexes are elaborate clathrin/actin related structures that form at sites of intercellular attachment in the seminiferous epithelium of the mammalian testis. Here we summarize what is currently known about the morphology and molecular composition of these structures and review evidence that the structures internalize intercellular junctions both at apical sites of Sertoli cell attachment to spermatids, and at basal sites where Sertoli cells form the blood–testis barrier. We present updated models of the sperm release and spermatocyte translocation mechanisms that incorporate tubulobulbar complexes into their designs.

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1. Introduction

1.1. Spermatogenesis and organization of the seminiferous epithelium

Spermatogenesis involves the differentiation of relatively generalized diploid cells (spermatogonia) into specialized haploid cells (spermatids) that are released as spermatozoa into the duct system of the male reproductive tract. The process occurs in one of the most complex epithelia of the body known as the seminiferous epithelium. This stratified epithelium consists of two populations of cells, Sertoli cells and spermatogenic cells. The Sertoli cells form

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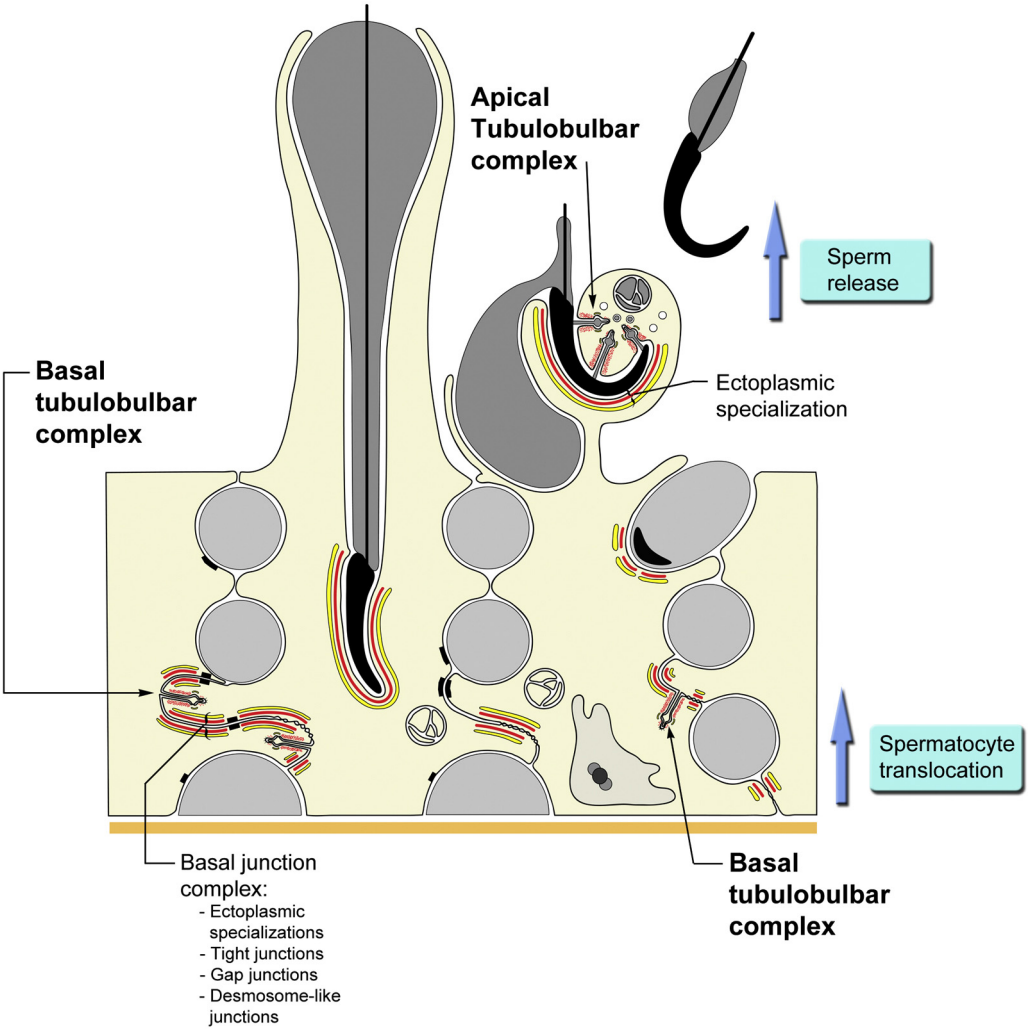

Fig. 1. Shown here is a diagram of the rat seminiferous epithelium illustrating the locations of tubulobulbar complexes. The figure progresses through spermatogenesis from stages IV/V on the left to stages VIII/IX on the right. Tubulobulbar complexes develop at apical sites where Sertoli cells are attached to spermatids and at basal sites where neighboring Sertoli cells are attached to each other. The appearance of tubulobulbar complexes is correlated with a reduction in intercellular junctions that ultimately results in sperm release at apical sites and spermatocyte translocation at basal sites.

the architectural elements of the epithelium. These cells are irregularly columnar in shape and extend from the base to the apex of the epithelium. Through an elaborate junction complex near their bases, they divide the epithelium into two compartments—a basal compartment below the junctions and an adluminal compartment above. The spermatogenic cells lie between and are attached to the Sertoli cells. These cells ultimately give rise to the male gametes during the process of spermatogenesis. The process begins with spermatogonia in the basal compartment. Through a series of mitotic divisions in the basal compartment, these cells give rise to spermatocytes that enter meiosis, cross the junction complexes between Sertoli cells and move into the adluminal compartment to complete meiosis and become haploid spermatids. These latter cells undergo a series of elaborate morphological changes to become mature cells that ultimately are released from the epithelium as spermatozoa.

1.2. Organization of intercellular junctions

Morphologically identifiable intercellular junctions occur at two major locations in the epithelium and their function is absolutely essential to spermatogenesis (Fig. 1). The first location is near the base of the epithelium where massive homotypic junction complexes consisting of adhesion, tight, gap and desmosome-like junctions link together neighboring Sertoli cells. The adhesion junctions are unique to the seminiferous epithelium and are termed 'ectoplasmic specializations'. They are characterized by a layer of hexagonally packed actin filaments situated between the plasma membrane and a cistern of endoplasmic reticulum, and are mainly nectin- and integrin-based attachments [1–3]. Tight and gap junctions to some extent overlap with, or are contained within, regions occupied by ectoplasmic specializations. Desmosome-like junctions, that are predominantly intermediate filament related, are intercalated amongst the ectoplasmic specializations where they appear in discontinuities or breaks in the adhesion zones. Tight junctions within the basal junction complexes [4], together with the bodies of the Sertoli cells, form the 'blood–testis' or Sertoli cell' barrier that sequesters post-meiotic spermatogenic cells in an immuno-privileged and physiologically distinct environment above the junctions. This adluminal compartment is essential for spermatogenic cells to progress through spermatogenesis.

The second major location where junctions occur is between Sertoli cells and spermatids (Fig. 1). Here, the junctions are heterotypic and consist almost entirely of ectoplasmic specializations. As with ectoplasmic specializations in basal junction complexes, those at apical sites are nectin- and integrin-based [1–3,5]. Unlike

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