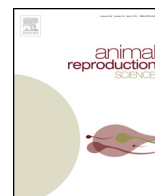




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A comparative overview of the sperm centriolar complex in mammals and birds: Variations on a theme

John T. Soley

Department of Anatomy and Physiology, Faculty of Veterinary Science, University of Pretoria, Private Bag X04, Onderstepoort 0110, South Africa

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ABSTRACT

This paper presents an overview of the structure, function and anomalies of the sperm centriolar complex (CC) on a comparative basis between mammals and birds. The information is based on selected references from the literature supplemented by original observations on spermiogenesis and sperm structure in disparate mammalian (cheetah and cane rat) and avian (ostrich, rhea and emu) species. Whereas the basic structure of the CC (a diplosome surrounded by pericentriolar material) is similar in Aves and Mammalia, certain differences are apparent. Centriole reduction does not generally occur in birds, but when present as in oscines, involves the loss of the proximal centriole. In ratites, the distal centriole forms the core of the entire midpiece and incorporates the outer dense fibres in addition to initiating axoneme formation. The elements of the connecting piece are not segmented in birds and less complex in basic design than in mammals. The functions of the various components of the CC appear to be similar in birds and mammals. Despite obvious differences in sperm head shape, the centrosomal anomalies afflicting both vertebrate groups demonstrate structural uniformity across species and display a similar range of defects. Most abnormalities result from defective migration and alignment of the CC relative to the nucleus. The most severe manifestation is that of acephalic sperm, while angled tail attachment, abaxial and multiflagellate sperm reflect additional defective forms. The stump-tail defect is not observed in birds. A comparison of defective sperm formation and centrosomal dysfunction at the molecular level is currently difficult owing to the paucity of relevant information on avian sperm.

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1. Introduction

Since their identification in the late nineteenth century through the pioneering work of Theodor Boveri, Edouard van Beneden, Walther Flemming and others (Bornens and Gönczy, 2014; Scheer, 2014; Schatten and Sun, 2015), the structure and function of centrosomes and centrioles have intrigued scientists. An extensive amount of data has been generated on this complex organelle during the past 120

years, both in terms of its morphology and in respect of its role in cell division, ciliogenesis and fertilization. This topic has been comprehensively reviewed with more recent studies focussing on the molecular basis of centriole-centrosomal structure and dysfunction (Schatten and Sun, 2009, 2012). The ultrastructural features of the centrosome have been documented in numerous publications. It consists essentially of a pair of centrioles aligned perpendicular to each other (forming a diplosome) and surrounded by an osmiophilic, fibro-granular matrix, the pericentriolar material (PCM) (Avidor-Reiss et al., 2015; Bornens and Gönczy, 2014; Chemes, 2012; Manandhar et al., 2005;

E-mail address: john.soley@up.ac.za

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Sathananthan, 2012; Sathananthan et al., 1996). Each centriole forms a hollow cylinder, the walls of which are composed of nine circularly arranged sets of triplet microtubules (Avidor-Reiss et al., 2015; Sathananthan, 2012; Sathananthan et al., 1996; Winey and O'Toole, 2014). In the centrosome a distinction can be made between the older (mother) centriole and the newly formed daughter centriole, although both organelles remain attached to each other (Bornens and Gönczy, 2014; Avidor-Reiss et al., 2015)

Early ultrastructural studies on sperm from diverse species revealed the presence of a pair of centrioles located in the neck region of the cell. This observation initiated an intense and ongoing study on the structure and role of the centrosome during spermiogenesis and fertilization (Fawcett, 1971, 1975). Much of the early work focussed on the morphology of rodent sperm (Fawcett, 1971, 1975; Fawcett and Phillips, 1969; Woolley and Fawcett, 1973), although the structural abnormalities affecting fertility in various commercially important production animals (see Chenoweth and McPherson, 2014) as well as the fine structure of human and primate sperm was also investigated (Afzelius, 1996; Dadoune, 1988; Holstein and Roosen-Runge, 1981; Zamboni, 1992; Zamboni and Stefanini, 1971). In response to the growing incidence of human infertility, and prompted by the need to fully understand sperm pathologies for the application of assisted reproductive technologies (ART), research on human sperm structure expanded exponentially. In respect of the role of the centrosome in fertility studies, two focus areas soon emerged. For successful *in vitro* fertilisation (IVF) a thorough knowledge of sperm abnormalities was required and, based on patient studies, a number of obvious centriolar defects were identified that adversely affected fertility (Afzelius, 1996; Chemes, 2012; Chemes and Sedo, 2012; Moretti and Collodel, 2012; Zamboni, 1992). With the advent of intracytoplasmic sperm insemination (ICSI) it became clear that more subtle changes to the composition of the centrosome at a molecular level, not reflected as obvious structural anomalies, could adversely affect successful zygote formation and subsequent embryogenesis (Avidor-Reiss et al., 2015; Chemes, 2012; Chemes and Rawe, 2003, 2010; Sathananthan, 2012; Sathananthan et al., 1996).

Compared to the amount of data generated on mammalian sperm, very little information is currently available on this topic in birds. However, recent work on the characterisation of sperm defects in ratites (Du Plessis and Soley, 2011a,b, 2012a,b; Du Plessis et al., 2014) has highlighted the importance of understanding the role of the sperm centriolar complex (CC) in birds, particularly those of commercial value.

This paper presents an overview of the structure, function and anomalies of the sperm CC on a comparative basis between mammals and birds, excluding its role in fertilization and zygote formation. The information is based on selected references from the literature supplemented by original observations on sperm structure and spermiogenesis in disparate mammalian (cheetah and cane rat) and avian (ostrich, rhea and emu) species. The cheetah (*Acinonyx jubatus*) is listed as vulnerable in the Red List of Threatened Species of the International Union for

Conservation for Nature (IUCN 2015), while the greater cane rat or grasscutter (*Thryonomys swinderianus*) is viewed as a potentially valuable unit of microlivestock. Ratites, in particular the ostrich (*Struthio camelus*) and emu (*Dromaius novaehollandiae*), are commercially exploited and form important niche industries world-wide. The overview is not exhaustive and the reader is referred to key references in the text for specific points of interest, particularly regarding the advances made in determining the molecular basis for centrosome dysfunction.

2. General features of the sperm centriolar complex

In mammalian and avian sperm the CC or paternal centrosome (Sathananthan, 2012) consists of a pair of centrioles (a diplosome) that form the core of the complex neck region of the cell. This region constitutes the vital connection between the head and the flagellum. In addition, the diplosome initiates the formation, via the free end of the distal centriole (DC), of the axial filament complex (axoneme) which forms the motile apparatus of the tail. The concentration of pericentriolar material (PCM) that surrounds the diplosome in somatic cells is present in the form of ordered structures that contribute towards attaching the flagellum to the sperm head. The structure and development of the neck region of mammalian sperm has been described in detail (Barth and Oko, 1989; Brito et al., 2010; Fawcett, 1971, 1975; Fawcett and Phillips, 1969; Holstein and Roosen-Runge, 1981; Manandhar and Sutovsky, 2007; Pesch and Bergmann, 2006; Phillips, 1974; Sathananthan, 2012; Zamboni, 1992) and recently summarised for birds (Aire, 2007, 2014; Jamieson, 2007).

During spermiogenesis in mammals and birds spermatids typically display both proximal and distal centrioles. However, in mature sperm of some species this arrangement varies. In the oscine clade of passerine birds, for example, the proximal centriole (PC) is generally considered to be absent (Jamieson, 2007) whereas no centrioles are reportedly present in rat sperm (Woolley and Fawcett, 1973). These variations clearly do not influence the motility of sperm which reinforces the observation that a basal body (effectively the DC which forms the axoneme), is not required for flagellar movement (Fawcett and Phillips, 1969).

The orientation of the centrioles may also differ. In most species the paired centrioles are typically aligned at right angles to each other, as also observed in the cane rat and cheetah (Fig. 1) and in ratites (Fig. 2). However, in some non-passerine birds such as the quail (Jamieson, 2007) and Guineafowl (Aire, 2014; Aire and Soley, 2003) the PC and DC lie almost inline. Why this preferential arrangement is reflected in mature sperm when the normal centriolar alignment persists in early round and elongating spermatids (Aire and Soley, 2003), remains unexplained. In some oscine birds such as the Masked weaver (Aire and Ozegbe, 2012) and Eurasian bullfinch (Birkhead et al., 2007) the PC is inclined at a 45° angle to the DC. Whereas these deviations in the orientation of the PC are “normal” features in some avian species, incorrect alignment of the CC during spermiogenesis results in a number of sperm pathologies and is discussed below.

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