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Review

Mitochondria in teleost spermatozoa

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ABSTRACT

There is an extraordinary diversity of reproductive modes in teleost and this variability is related to the phylogenetic relationships and adaption to very different biotopes. As in all vertebrates, sperm is produced as the end product of the process of spermatogenesis, and regarding teleost the spermatozoa lack an acrosome in almost all species and motility is activated as a response to osmolarity and ion content of the aquatic medium where the sperm is released. In this context, mitochondria possess a fundamental role for fish spermatozoa motility and integrity, hence, fertilizing potential; they are the energy supplier that allows flagellar movement and their dysfunction could play a main role in structural and functional damage to the spermatozoa. The ATP production through oxidative phosphorylation provides not only energy for cell activities, which includes Na^+/K^+ ATPase pump, endocytosis, protein synthesis and many other cell processes; but also produces reactive oxygen species, that under mitochondrial dysfunction causes oxidative stress.

The assessment of mitochondrial function (e.g. through measurement of mitochondrial membrane potential) as well as ATP content (mostly supplied by mitochondrial respiration) can be useful as quality markers of fish spermatozoa. Also quantification of ROS and antioxidant status, strongly influenced by mitochondria, are used as complementary measurements.

There is much information about sperm mitochondria and their function but studies of these aspects on fish reproduction are still required for applications in aquaculture. The real role of fish sperm mitochondria under short and long term storage and in vitro manipulation is not fully understood yet. Thus future research should focus on these matters.

Contents

1. Introduction

Mitochondria are organelles found in the great majority of eukaryotic cells playing a fundamental role in metabolism and ATP production

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through oxidative phosphorylation (Devenish et al., 2008). Because of this, great interest has been paid to its function on high energy-demanding cell types, including spermatozoa. These highly specialized cells, produced as the end product of spermatogenesis proceeding through successive mitotic, meiotic and postmeiotic phases within the seminiferous tubules of testis, possess an array of novel structural features and functional characteristics, jointly providing it with the capability of delivering male genome to the oocyte (Eddy, 1998). Spermatozoa are responsible of reproduction in most sexual-reproductive animals and its function relays mainly on its displacement capacity supported by tail movement. Mitochondria provide the energy to the flagellum, and lots of animals developed spermatozoa with large number of mitochondria (p.e. humans) and their number and function have been positively correlated with sperm motility and fertilization capacity (Ferramosca et al., 2013). Fish, on the other hand, except viviparous fish (Huang et al., 2004), exhibit structurally simplified spermatozoa: a small head lacking acrosome, probably as a result of secondary simplification during evolution because the development of the egg envelopes (Jamieson and Leung, 1991), a uniflagellar tail in most cases and a small mid-piece with a very few mitochondria, ranging from 1 to 10 depending on species (Lahnsteiner and Patzner, 2008).

The vast majority of extant fish are bony fish, which are classified under the *Teleostei* infraclass clade in the taxonomic tree (Betancur et al., 2013). In teleosts, sperm quality and fertilization capacity are also connected to the bio-energetic metabolisms of the mitochondria (Cartón-García et al., 2013). However, little research has been centered on ultrastructure, genome, and function of the spermatic mitochondria, which would allow understanding and integration of the physiology and biophysics in fish reproduction. This is particularly important for aquaculture industry where in-vitro fish sperm management is a key step, and the implementation of efficient methods to control and enhance sperm quality is a necessary manoeuvre. As an example, long-term preservation of fish sperm simplifies the production of selected strains and facilitates genetic selection of beneficial traits for commercial farming (Chen, 2002), but rudimentary selection methods are affecting several intensive-farming facilities due to constant sperm quality losses, causing lower fertilizing rates. Additionally, sperm conservation techniques, such as cryopreservation, are emerging tools for fish reproduction, but these procedures have been also associated with mitochondrial dysfunction, resulting in lower motility and thus decreased fertilization capacity (Liu et al., 2007).

Taking into account all the aspects mentioned above, the purpose of this review is to describe the mitochondria in teleosts spermatozoa as well as its role and importance in fish reproduction.

2. Diversity in the spermatozoa of teleost

2.1. Classification of teleost

There is an extraordinary diversity of reproductive modes in teleost. This variability is related to the phylogenetic relationships and adaption to very different biotopes. This means that, even though sperm cells in most fish species are built on the same principle, spermatozoa from each species have a particular morphology and function according to its phylogenetic lineage, reproductive modes (e.g. external or internal reproduction), gender systems (e.g. genetic sex determination or environmental sex determination), spawning dynamics (e.g. reproduction season and breed capacity), spawning site (e.g. fresh or salt-water), and others (Wootton and Smith, 2015). Osmolarity and ion content of the aquatic medium are central factors in activating motility in fish spermatozoa (Cosson, 2012b; Figueroa et al., 2014), so it is important to identify the spawning site and the seminal plasma composition of the fish species in study to understand its motility behaviour, since this is crucial for fertilization.

Most teleost reproduce by external fertilization, and a few by internal fertilization such as some *Poeciliids* (Mattei, 1991). Until about the eighties, several authors classified fish spermatozoa according to their fertilization modes. The hypothesis that sperm cells of species employing external fertilization have a simple structure, in contrast to more developed structures associated with internal fertilization, holds true for teleost spermatozoa according to Franzen (1970) (Stoss, 1983). The *Neopterygii* ancestors showed two new characters in the sperm that made Franzen hypothesis come true: a reduction in the size of the nucleus and the disappearance of the acrosome, whose simplified structure is close to that of the gamete of aquatic invertebrates with external fertilization (Mattei, 1991). Fig. 1 shows a simplified classification of all the family species of teleost.

Teleost comprises a wide variety of species of different taxonomic orders as shown in Fig. 1, but when the gametes of teleost are studied, investigation should not be restricted only to teleost models since a lot of non-teleost, such as chondrosteans and even marine invertebrates, share features with some teleost species (Kazama et al., 2012; Fedorov et al., 2015).

2.2. Teleost spermatozoa

The great diversity of teleost spermatozoa was first studied exhaustively by Mattei (1991) and reviewed by Lahnsteiner and Patzner (2008) with advances in ultrastructure. Fig. 2 summarizes these findings in sperm morphology and ultrastructure in teleost. Spermatozoa are subdivided into head, neck, neck-piece, mid-piece and tail. The length of a spermatozoon ranges between 25 and 100 μm and its width is about 2 μm in the middle of the head. The head piece lacks the acrosome observed in all other vertebrate groups, being a functional adaptation to the presence of a micropyle on the teleost oocyte (a single canal, which allows the entrance of spermatozoa). The shape of the nucleus is highly variable and appears to be related to the complexity of

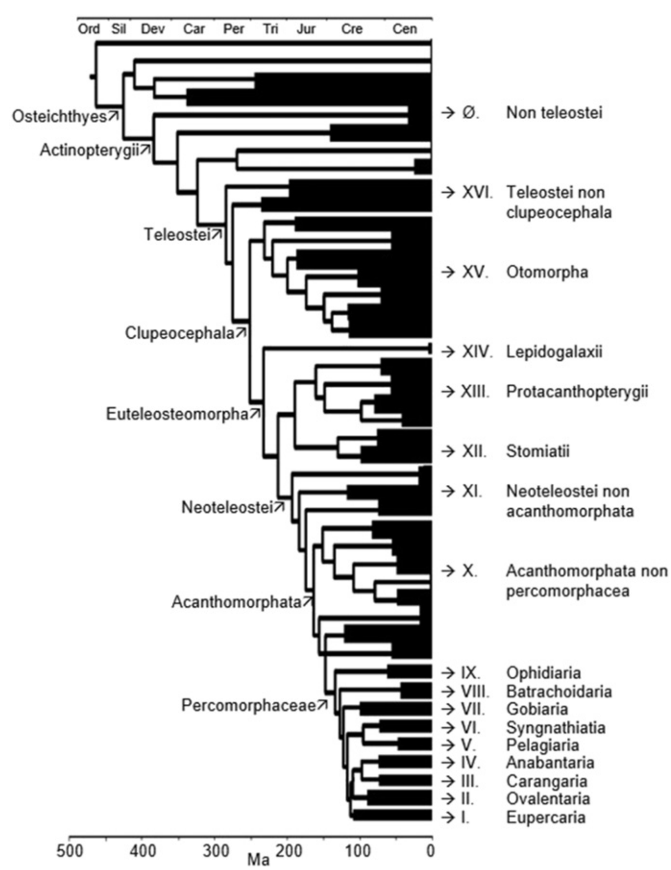

Fig. 1. Simplified phylogenetic tree adapted from Betancur et al. (2013). The classifications with Roman numerals are proposed by the author of this review.