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Spermatological characteristics of the Trypanorhyncha inferred from new ultrastructural data on species of Tentacullariidae, Eutetrarhynchidae, and Progrillotiidae

Caractéristiques spermatologiques des Trypanorhyncha inférées de nouvelles données ultrastructurales d'espèces de Tentacullariidae, Eutetrarhynchidae et Progrillotiidae

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ABSTRACT

The present study focuses on the ultrastructural characteristics of both spermiogenesis and the spermatozoon in the order Trypanorhyncha. New ultrastructural data are presented for two species of the unexplored superfamily Tentacularioidea, *Nybelinia queenslandensis*, and *Kotorella pronosoma*. The present study also provides supplementary data on the superfamily Eutetrarhynchoidea, with the analysis of spermiogenesis and spermatozoon of two progrillotiids, *Progrillotia dasyatidis* and *Pro. pastinacae*, and new ultrastructural data concerning spermiogenesis in the eutetrarhynchids *Dollfusiella spinulifera* and *Parachristianella trygonis*. Spermiogenesis in trypanorhynchs follows the Bâ and Marchand's type I and the ultrastructural organisation of the mature spermatozoon corresponds to the Levron et al.'s type I. The most remarkable characters concerns the number of electron-dense plates constituting the intercentriolar body during spermiogenesis and in the variability of the arc-like row of thick cortical microtubules present in the anterior areas of the spermatozoon because of its variability according to the species.

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RÉSUMÉ

Cette étude porte sur les caractéristiques ultrastructurales de la spermiogenèse et du spermatozoïde dans l'ordre Trypanorhyncha. Des nouvelles données sont présentées pour deux espèces, *Nybelinia queenslandensis* et *Kotorella pronosoma*, de la super-famille précédemment non explorée Tentacularioidea. Cette étude fournit aussi des informations supplémentaires sur la super-famille Eutetrarhynchoidea, avec une analyse de la spermiogenèse et du spermatozoïde de deux Progrillotiidae, *Progrillotia dasyatidis* et *Pro. pastinacae*, et de nouvelles données ultrastructurales concernant la spermiogenèse chez les Eutetrarhynchidae *Dollfusiella spinulifera* et *Parachristianella trygonis*. La

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spermiogenèse chez les Trypanorhynques suit le Type I de Bâ et Marchand et l'organisation ultrastructurale du spermatozoïde correspond au type I de Levron et al. Les caractères les plus remarquables concernent le nombre de plaques denses aux électrons qui constituent le corps intercentriolaire pendant la spermiogenèse et la variabilité de la rangée en arc de microtubules corticaux épais présents dans les régions antérieures du spermatozoïde, à cause de la variabilité parmi les espèces.

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1. Introduction

Trypanorhynchs are polyzoic cestodes, readily recognised by their rhyncheal apparatus, and are common metazoan parasites of marine fish. Adult worms parasitize elasmobranch fishes while their larval stages occur in a variety of teleosts, elasmobranchs and marine invertebrates (crustaceans, cephalopods and bivalves), including zooplankton [1]. Trypanorhynchs possess a scolex with two or four bothria [2] and also a tentacular apparatus consisting of four retractile tentacles armed with hooks that are attached to four bulbs [3]. This rhyncheal apparatus is unique within the cestodes, and provides a strong synapomorphy that supports the monophyly of this order [4].

This order has been considered to be one of the most chaotic and confusing tapeworm groups, but recent work has shed considerable light on their systematics [5]. Morphological evidence strongly supports the monophyly of trypanorhynchs [1,5]. Although Waeschenbach et al. [6] presented molecular data that support the monophyly of the Trypanorhyncha, other molecular studies have suggested that this order is paraphyletic and consists of two well-supported clades [4,7–9]. The first clade groups together the superfamilies Eutetrarhynchoidea and Tentacularioidea while the second clade groups together the Gymnorhynchoidea, the Lacistorhynchoidea and the Otobothrioidea. Recently, Olson et al. [10], in a combined analysis of molecular and morphological data, identified two clades with each one occurring in the two principal clades of the elasmobranch definitive hosts (rays or sharks) and they proposed the suborders Trypanobatoida and Trypanoselachoida for these two major clades according to the primarily hosts parasitized, rays and sharks, respectively. The Trypanobatoida contains the Tentacularioidea (including the eutetrarhynchoids) and the Trypanoselachoida contains the Lacistorhynchoidea, the Otobothrioidea and the Gymnorhynchoidea.

The ultrastructural studies on cestode spermatozoa have proved useful in interpreting their phylogenetic relationships within the Platyhelminthes and could, therefore, provide useful morphological indicators of the phylogeny and/or classification of trypanorhynchs [11–19]. However, in the Trypanorhyncha, studies of spermiogenesis and/or spermatozoa are limited to species belonging to three of the five superfamilies, namely Gymnorhynchoidea, Lacistorhynchoidea and Eutetrarhynchoidea. These are *Grillotia erinaceus* and *Lacistorhynchus tenuis* [20–22] (Lacistorhynchoidea), *Aporhynchus menezesi* [23] (Gymnorhynchoidea), and *Dollfusiella spinulifera* and *Parachristianella trygonis* [24,25] (Eutetrarhynchoidea).

The aim of this present study is to analyse, for the first time, the spermatological patterns of two species of the unexplored superfamily Tentacularioidea, *Nybelinia queenslandensis* and *Kotorella pronosoma*. The present study also provides supplementary data on the superfamily Eutetrarhynchoidea, with the analysis of spermiogenesis and mature spermatozoon of two progrillotiids, *Progrillotia dasyatidis* and *Progrillotia pastinacae*, and new ultrastructural data concerning spermiogenesis in the eutetrarhynchids *Dollfusiella spinulifera* and *Parachristianella trygonis*. These new ultrastructural observations are focussed in the number of plates, constituting the intercentriolar body during spermiogenesis and in the variability of the arc-like row of thick cortical microtubules present in the anterior areas of the spermatozoon. In fact, these two characters are showed as the most interesting in this order because of its variability according to the species.

2. Materials and methods

Live adult specimens of *N. queenslandensis* and *K. pronosoma* were collected by Prof. Ian Beveridge, University of Melbourne, from *Carcharhinus melanopterus* and *Himantura granulata*, respectively, caught off Lizard Island (Queensland, Australia). *D. spinulifera* was provided by Prof. Malcolm K. Jones from *Rhinobatos typus* collected on the reef flats at Heron Island (Queensland, Australia). *Pro. dasyatidis* and *Pro. pastinacae* were collected from *Dasyatis tortonesei* and *Dasyatis pastinaca*, respectively, caught off Sidi Mansour and Zarzis (Gulf of Gabès, Tunisia). Finally, *P. trygonis* was collected from *Dasyatis pastinaca* caught off Sidi Mansour (Gulf of Gabès, Tunisia). All the three species isolated from Tunisian elasmobranchs were collected in collaboration with Dr Lassad Neifar (University of Sfax).

After dissection, the mature proglottids from these cestodes were routinely processed for transmission electron microscopy examination. Thus, they were fixed in cold (4 °C) 2.5% glutaraldehyde in a 0.1 M sodium cacodylate buffer at pH 7.4 for a minimum of 2 h, rinsed in a 0.1 M sodium cacodylate buffer at pH 7.4, post-fixed in cold (4 °C) 1% osmium tetroxide (OsO_4) with 0.9% potassium ferricyanide [$K_3Fe(CN)_6$] in the same buffer for 1 h, rinsed in milliQ water, dehydrated in an ethanol series and propylene oxide, and finally, embedded in Spurr's resin. Ultrathin sections (50–60 nm thick) were obtained using a Reichert–Jung Ultracut E ultramicrotome, placed on copper grids and double-stained with uranyl acetate and lead citrate. The ultrathin sections were examined using a JEOL 1010 TEM operated at an accelerating voltage of 80 kV.

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