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Ultrastructure of Spermatogenesis of the Paradise Fish, *Macropodus opercularis*

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ABSTRACT: The intricate process of spermatogenesis in the paradise fish, *Macropodus opercularis*, was studied. In this species, the unrestricted or lobular type testes lining the caudal side of the body cavity are translucent and slender. Spermatogonia occur along the length of the tubules and the development of sperm takes place within cysts formed by Sertoli cells. Spermiogenesis involves preparatory morphological events followed by conspicuous modifications such as the movement of the centrioles, completion of the nuclear condensation, reduction of the cytoplasm, and the final differentiation of the flagellar complex. Mature spermatozoon has an oval nucleus, condensed chromatin, and typical 9 + 2 flagellar axoneme but lack acrosome. The role of the material in the nucleus and the cytoplasm as it reaches the Sertoli cell in the control of spermatogenesis is discussed.

KEY WORDS: Paradise fish, Testis, Ultrastructure, Spermatogenesis.

INTRODUCTION

The paradise fish (*Macropodus opercularis*) is a kind of Anabantoid fish where the male builds a foam nest before courtship. Although the agonistic and reproductive behavior had been documented (Hall, 1968; Davis and Kassel, 1975), the histological and ultrastructural process of spermatogenesis still lacks a detailed description.

Structures of the teleost testis can be divided into two basic types – 'tubular' and 'lobular' type – distinguished from each other by the distribution of spermatogonia. Only limited fine structural data are available on both spermatocytogenesis and spermiation of teleost (Pecio and Rafinski, 1999). Fine structural work on spermatogenesis continues to enhance our understanding of germ cell differentiation and provides insights into the relationships between various teleost groups, especially at or above the family level (Grier et al., 1980). Moreover, both light and electron microscopy of a wide spectrum of teleost spermatozoa have demonstrated that important morphological differences are found between different species (Grier, 1981). The present study details spermatozoon formation in the paradise fish, *M. opercularis*. The results of which will be the basis of future studies on the effects of reproductive behavior on gonadal development.

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MATERIALS AND METHODS

The male paradise fish (*Macropodus opercularis*) used in the present study were purchased from the aquarium and kept in a tank (30 × 18 × 25 cm^3) with water temperature at 30 ± 1℃. The photoperiod was light 16 hrs and dark 8 hrs. The body weights of the fish were between 2-4 g and the gonadosomatic indexes (GSI) were about 0.1%. The fish were fed with a daily diet of commercial pellets.

For histological observation, dissected testes were fixed in Bouin's fluid for 72 hrs, dehydrated in ascending series of alcohol, infiltrated in xylene and embedded in paraffin. Serial sections (5 μm thick) were double stained with Mayer's hematoxylin-alcoholic eosin (H and E) or stained with Periodic Acid Schiff's reagent (PAS) and then mounted for observation.

For transmission electron microscopy, samples were fixed and cut into pieces of 1 mm^3 in 2.5% glutaraldehyde in cacodylate buffer 0.1 M (pH 7.2) for 1 hr at 4℃. Specimens were washed in the same

buffer with 5% sucrose 3 times, and postfixed in 1% OsO_4 in the same buffer for 1 hr at room temperature. Samples were then washed 3 times and dehydrated through graded alcohol series and acetone and embedded in Spurr's resin (Spurr, 1969). Ultrathin sections were stained with uranyl acetate and lead citrate and were observed with a Hitachi H-7100 transmission electron microscope. Semithin sections, 0.5-1.0 μm thick, were stained with toluidine blue for light microscopy observation.

The Osmium-DMSO-Osmium method (Tanaka, 1989) was used in sample preparation for scanning electron microscopy. The testes were cut into small pieces and fixed in 1% OsO_4 in cacodylate buffer 0.1 M for 1 hr at 4℃. After washing with the same buffer containing 5% sucrose 3 times, the samples were immersed in 25% and 50% dimethyl sulfoxide (DMSO) for 30 min each and then quick-frozen in liquid nitrogen. The samples were cut into small pieces in liquid nitrogen and collected in 50% DMSO. Samples were then washed 3 times in 0.1 M cacodylate buffer and immersed in 1% OsO_4 at 20℃ for 1 hr followed by immersion in 0.1% OsO_4 at 20 ℃ for 18 hrs. After immersion in OsO_4, samples were transferred into 2% tannic acid in 0.1 M cacodylate buffer for 12 hrs. Finally the samples were treated in 1% OsO_4 again at room temperature for 1 hr and washed with distilled water. Then they were processed through a graded alcohol and acetone series, critical-point dried (Hitachi HCP-2 critical point dryer), fixed on stubs with double-sided adhesive tape and vacuum coated with gold (Hitachi 101 ion sputter), before being viewed with a Hitachi S-800 scanning electron microscope.

For comparison of the size of developing gametes during spermatogenesis and spermiation the diameters of 50 gametes of each developing stage were measured using transmission electron microscopy. Data were calculated and the means ± S.E.M. were used to show the changes in size.

RESULTS

Ultrastructure of the testes

The testis of the paradise fish consists of many branched and curved seminiferous tubules and the interstitial compartments (Fig. 1A). The seminiferous tubules are in 'lobular' form, which contain several to more than ten cysts (Fig. 1B). The cysts containing germ cells in different developing stages arranged in mosaic pattern in the seminiferous tubules (Fig. 1A). The cysts are surrounded by Sertoli cells connected to each other by desmosomes in the adjacent Sertoli cells (Fig. 1B). The interstitial tissues of the testis contain some blood vessels, the Leydig cells, and the myoid boundary cells (Fig. 1C).

Spermatocytogenesis (spermatogonium – spermatocyte – spermatid)

Depending on the status of mitosis, the spermatogonia are divided into primary and secondary phases. Primary spermatogonia (Figs. 2A and B) are the largest cells in the seminiferous tubules with diameters between 7.2-8.2 μm exhibiting a round nucleus with a prominent nucleolus (Fig. 8). The cytoplasm contains few organelles, but includes endoplasmic reticulum, free ribosomes, and round mitochondria with lamellar cristae (Figs. 2A and B). The diameters of the secondary spermatogonia are between 6.3-7.5 μm (Fig. 8), smaller than the primary spermatogonia. In the secondary spermatogonia the ultrastructures of the nucleus and cytoplasm are similar to that of the primary spermatogonia, but the organelles increase (Figs. 2C and D).

After mitosis, the secondary spermatogonium becomes a spermatocyte. Spermatocytes are separated into two phases: the primary and the secondary phase, according to the status of meiosis. The diameters of the primary spermatocytes are between 5.8-6.6 μm (Fig. 8). The mitochondria are abundant, and become smaller than that of the primary spermatogina (Fig. 3A). Moreover, microtubules are found to be closer to the centrosome (Fig. 3B). The secondary spermatocytes are much smaller in size due to meiosis: only 4.4-5.4 μm in diameter (Fig. 8). The chromosomes (2N) are sometimes found in the center of the nucleus (Fig. 3C).

Spermiogenesis (spermatid – spermatozoon)

(i) Early spermatids and flagellum formation

After meiosis, secondary spermatocytes become early spermatids. The spermatids often show irregular outlines because of intermittent connections to other cells (Fig. 4A). Due to meiosis, the size of the nucleus becomes smaller once again (Fig. 4A). The cytoplasm contains mitochondria, endoplasmic reticulum, and rosettes of ribosomes (Fig. 4A). The mitochondria are round or oval with lamellar cristae (Fig. 4B). Formation of the flagellum is the most significant change in the morphology of spermatids. In the phase of flagellum formation, the centrosome adjacent to the cell membrane forms the basal body that initiates the growth of flagellum (Fig. 4C). The microtubules in the basal body are 9 + 0 in structure, and then extend to form typical 9 + 2 structures in the flagellum (Fig. 4D).

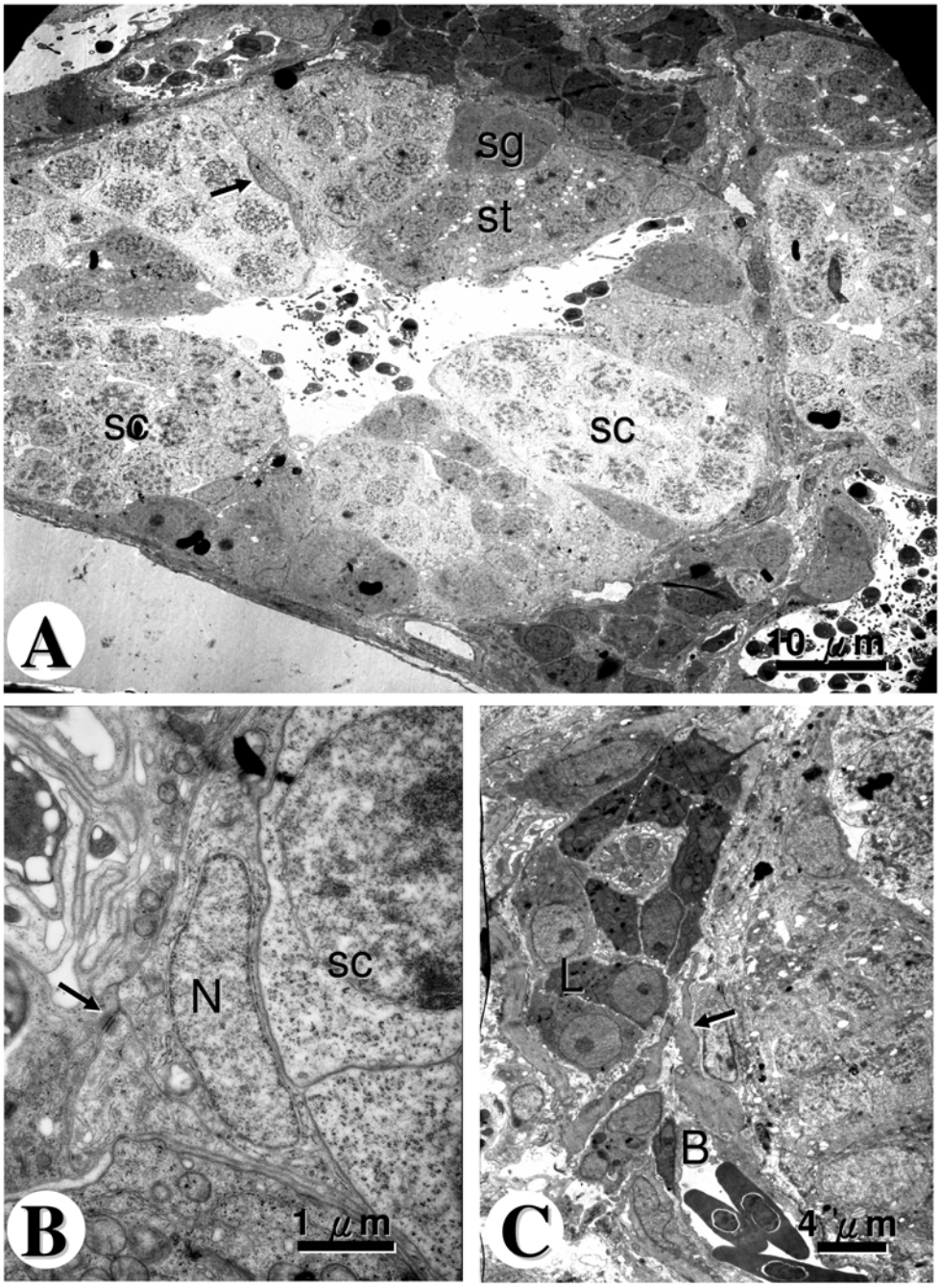

Fig. 1. Ultrastructures of the testes of *Macropodus opercularis*. A: Cross section of the seminiferous tubules revealed the 'lobular' type. Each lobule consists of several cysts. Each cyst surrounded by Sertoli cells (arrow) contains groups of developing germ cells, i.e., spermatogonia (sg), spermatocytes (sc), and spermatids (st). B: Nucleus of a Sertoli cell (N). Note that there is a desmosome (arrow) in the adjacent Sertoli cell. C: Leydig cells (L), blood vessels (B) and myoid boundary cells (arrow) were observed in the interstitial tissues.

(ii) Centrosome-nucleus complex formation

The flagellum-forming centrosome moves closer to the nucleus. The other centrosome is perpendicular to flagellum-forming centrosome and engulfed by the nuclear fossa, a concave part of the nucleus (Fig. 5A). The engulfed centrosome then connects to the nuclear envelope by many fibrous structures (Figs. 5B and 5C). Formation of the centrosome-nucleus complex reveals obvious polarity of the spermatids (Fig. 5D). Most organelles concentrate in the cytoplasm near the flagellum and condensed chromatin appears in the apical-located nucleus (Fig. 5D).

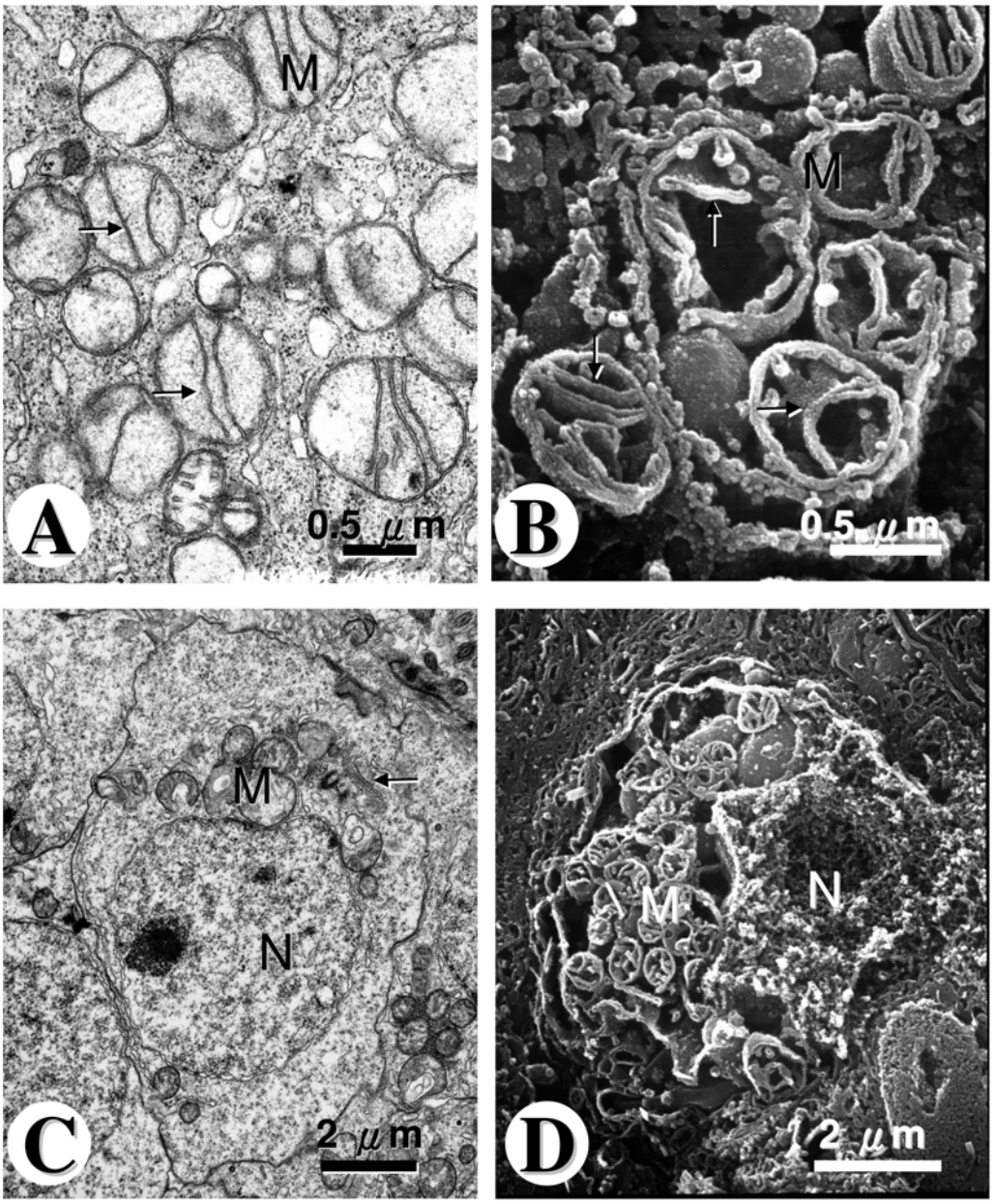

Fig. 2. Spermatogonia. TEM (A) and SEM (B) micrographs of the primary spermatogonium indicate that most of the cytoplasm is occupied by round mitochondria with few cristae (arrows). M. mitochondria. TEM (C) and SEM (D) micrographs of the secondary spermatogonium contains round to oval mitochondria (M) with more cristae. The smooth endoplasmic reticulum, the Golgi body (arrow), and abundant free ribosomes were also found in the cytoplasm. N, nucleus; M, mitochondria.

(iii) Cytoplasm depletion

Characteristic of this phase are the many vacuoles in the flagellar-side cytoplasm (Figs. 6A and B). The cytoplasm contains few mitochondria (Figs. 6A and B). The other organelles are not found.The Sertoli cell usually surrounds the spermatid in this phase (Fig. 6C). Many residual cytoplasm containing vacuoles together with cytoplasm-depleted spermatids were found in the central area of the cyst (Fig. 6D).

(iv) Spermatozoon

The spermatid discards most of its cytoplasm to form a mature spermatozoon. A spermatozoon can be divided into four parts: (1) the head, (2) the neck, (3) the middle piece, and (4) the tail (Figs. 7A and B). The head region consists of an oval nucleus and condensed chromatin. The centrosome, deeply engulfed by the nucleus in the nuclear fossa, forms the neck region. In the middle piece, the cytoplasm extends toward the flagellum and develops the collar

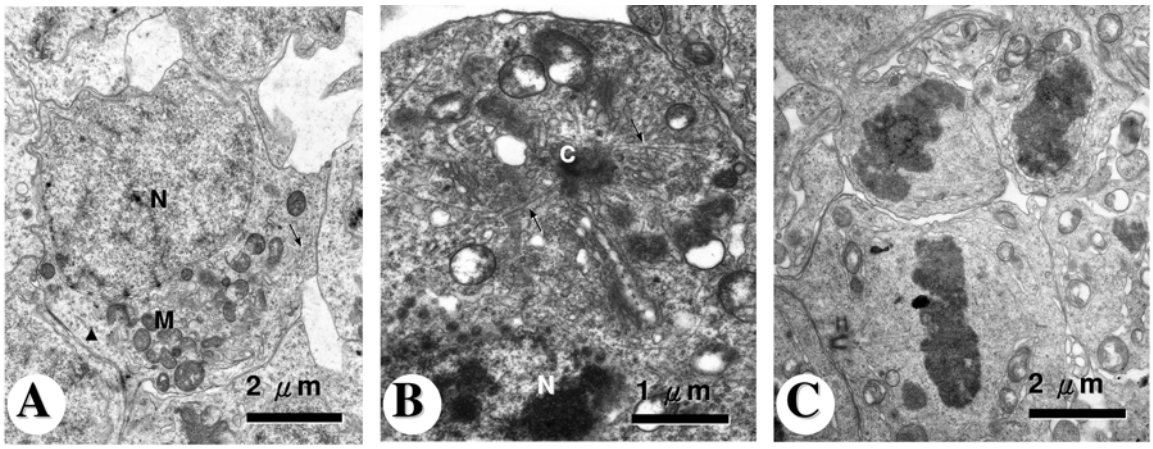

Fig. 3. Spermatocytes. A: The primary spermatocyte contains abundant mitochondria (M) in the cytoplasm. N, nucleus; smooth endoplasmic reticulum (arrow), rosettes of ribosomes (arrowhead). B: In the cytoplasm of the primary spermatocyte, microtubules (arrows) are found near the centrosome (C). C: The secondary spermatocyte is in the second meiosis.

structure. Very few mitochondria are present in the collar-shape cytoplasm (Figs. 7A and B). The tail part contains a flagellum arising from a centrosome with typical 9 + 2 microtubular structure.

The cell diameters decreased with development in spermatogenesis (Fig. 8).

DISCUSSION

The structures of the testis in teleosts are generally divided into unrestricted or restricted spermatogonia-testis type according to the intratubular distribution of spermatogonia (Grier, 1981). In the restricted spermatogonial testis-type the spermatogoina are totally restricted to the distal terminus of the tubule immediately beneath the tunica albuginea where they are associated with Sertoli cells (Grier, 1981). However, in the unrestricted spermatogonial testis-type the distribution of spermatogonia is similar to that observed within the mammalian testis in that they may occur along the entire length of the seminiferous tubule. The spermatogonia are limited to small, peripheral cysts within the tubule which consequently enlarge and extend toward the tubule lumen as spermatogenesis takes place (Grier et al., 1980). The type of testis in the paradise fish (*M. opercularis*) is unrestricted. The testis contains seminiferous tubules which form a branching network similar to the structures of the testis of the mullet (Mujil cephalus) (Grier et al., 1980). Within the tubules, various stages of the germ cells are confined to cysts formed by Sertoli cells subsequently heading for the lumen where sperms arise (Fig. 1).

The spermatogenesis of the paradise fish, like the other teleosts, starts from the primary spermatogonia. Primary spermatogonia are the largest germ cells and possess a prominent nucleolus (Fig. 2). Through a process of cell division and morphological changes, the primary spermatogonia developed into sperm with increasing number (Pudney, 1995) and decreasing cell diameters (Fig. 8). Although the size of cells at each stage of spermatogenesis varies among species of teleosts, the spermatogonia are the largest among the spermatogenic cells. However, the ultrastructures and the organelle distribution may change in different stages of the process (Lahnsteiner and Pztzner, 1990; Gwo and Gwo, 1993; Pudney, 1995). The primary spermatogonia divide mitotically, producing clusters of smaller secondary spermatogonia with less well-defined nucleoli (Fig. 2). Except for the nucleus, the organelles are similar to those in the primary spermatogonia with little modification as in the other teleosts (Bruslé and Bruslé, 1978; Burke and Leatherland, 1984).

After mitosis, the secondary spermatogonia become spermatocytes. Spermatocytes are separated into two phases: the primary and the secondary phase, according to the status of meiosis. Primary spermatocytes with oval nuclei are round to spherical in the testes of most teleosts (Bhatti and Al-Daham, 1978; Bruslé and Bruslé, 1978; Pudney, 1995). Large amounts of microtubules occurred in the cytoplasm of the primary spermatocytes of the killifish (Thiaw and Mattei, 1989). In the paradise fish, like the other teleosts, the chromatin in the nucleus condensed and the distribution and amounts of organelles changed due to meiosis. Very few papers stated the ultrastructures of secondary spermatocytes because of the short-term appearance of this stage (Grier, 1976; Bhatti and Al-Daham, 1978; Bruslé, 1981; Burke and Leatherland, 1984).

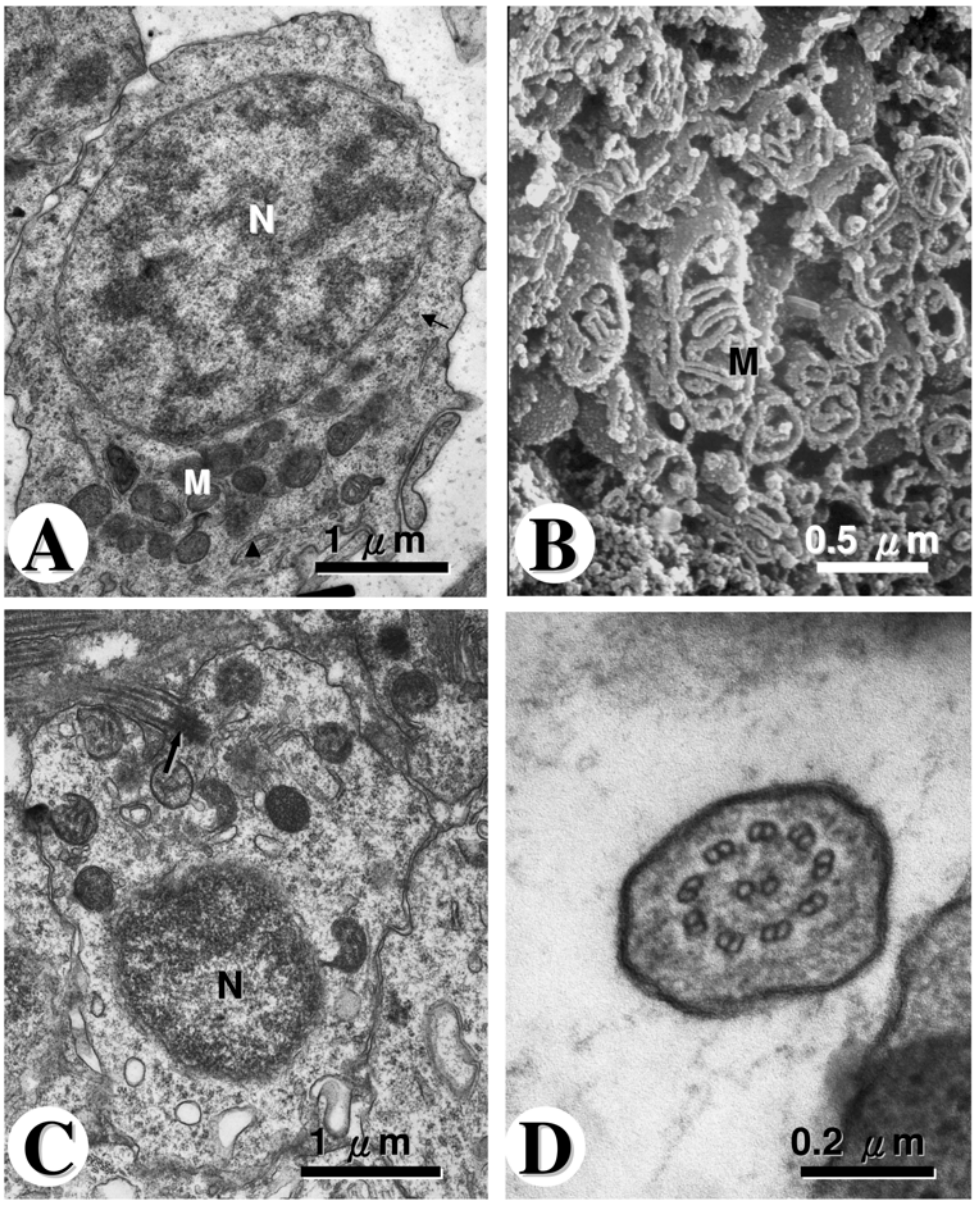

Fig. 4. Early spermatids and flagella formation. After meiosis, the nucleus of early spermatid becomes much smaller (A). Organelles are still found in the cytoplasm (A, B). M, mitochondria; N nucleus; rossettes of ribosomes (arrow) and endoplastic reticulum (arrowhead). C: The basal body (arrow) entends and initiates to form the flagellum. D: The microtubules keep growing to form the flagellum of the spermatid with typical structure of 9 + 2 microtubules.

Spermiogenesis generally involves preparatory morphological events followed by conspicuous modifications of the spermatids such as structural changes (e.g., nuclear chromatin become more homogeneous and form coarse dense granules; formation of the flagellum) and intracellular movements (e.g., centrosome-nucleus complex formation; cytoplasm depletion) (Zirkin, 1975; Bruslé, 1981; Billard, 1983; Jones and Butler, 1988; Lahnsteiner and Patzner, 1990; Gwo and Gwo, 1993). Developing stages from spermatids to sperms were divided according to the cell sizes as well as structural changes in previous reports (Grier, 1976; Bruslé, 1981; Billard, 1983; Jones and Butler, 1988; Lahnsteiner and Patzner, 1990). The present study described spermiogenesis of the paradise fish using the occurrence of the flagellum (Fig. 4), the location of the centrosomes (Fig. 5), and the depletion of the cytoplasm (Fig. 6) as indicators. Concomitant with the formation of the flagellum, the ultrastructures and distribution of the organelles changed. In most fish, including the paradise fish, the mitochondria move

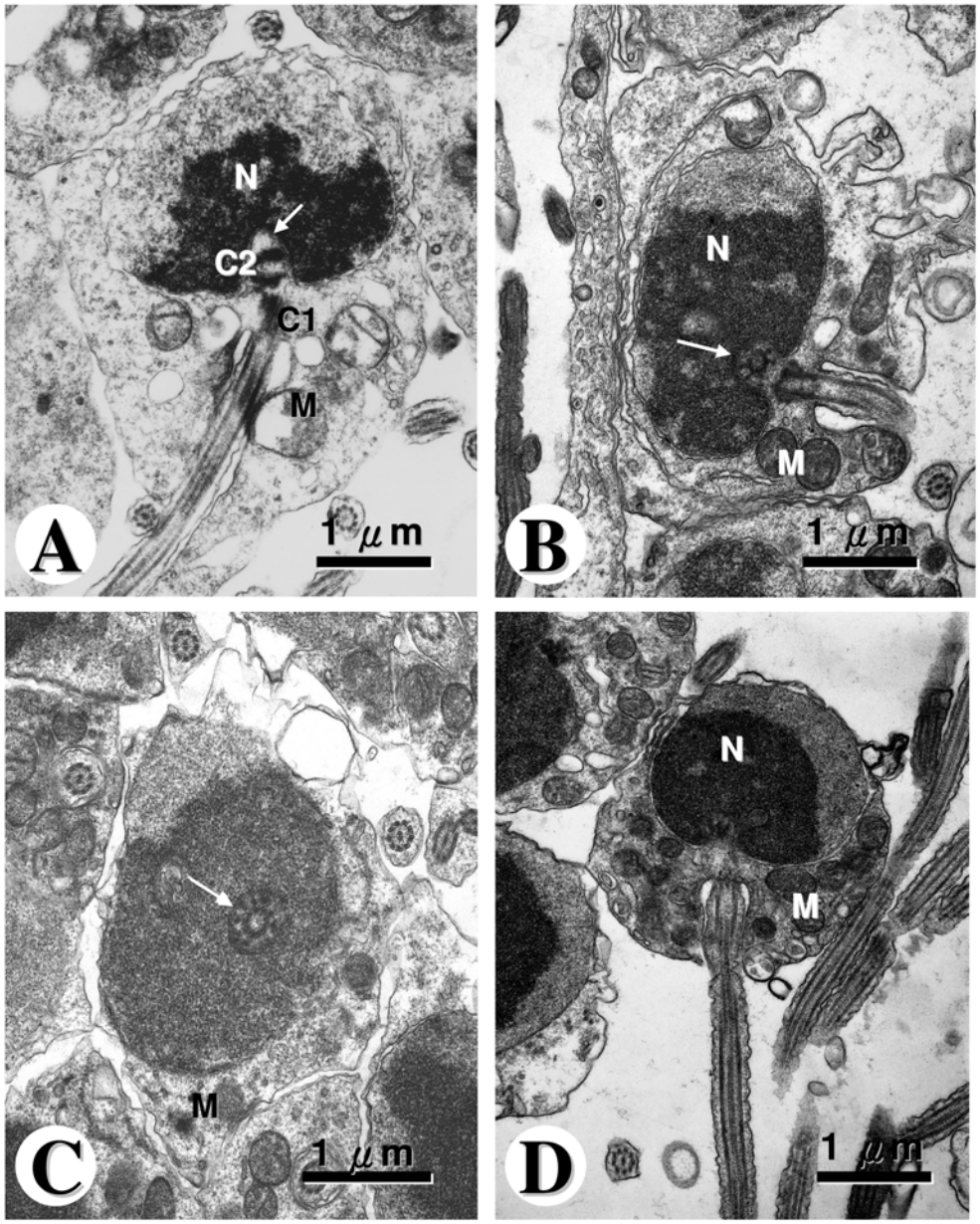

Fig. 5. Centrosome-nucleus complex formation. A: The flagellum-forming centrosome (C1) was found to be perpendicular to the other centrosome (C2) which is engulfed by the nuclear fossa (arrow). Meanwhile, the chromatin condenses. B: A centrosome (arrow) falls into the nuclear fossa. C: Transverse section of the engulfed centrosome in the nuclear fossa showed that the former is connected to the nucleus envelope by fibrous structures (arrow). D: Formation of the centrosome-nucleus complex indicates the obvious polarity of the spermatid. Condensed chromatin exhibits in the apical-located nucleus (N) and most organelles are found in the cytoplasm near the flagellum. M, mitochondria; N, nucleus.

toward the flagellum. But in several species the mitochondria lie within shallow depressions of the nuclear caudal surface (Jones and Butler, 1988; Lahnsteiner and Patzner, 1990). The number of mitochondria decrease in most fish studied. In some species the mitochondria even become reduced to a single large mitochondrion, possibly by fusion (Todd, 1976; Fishelson et al., 1990). However, fusion of mitochondria was not found in the paradise fish.

The head region of teleostean spermatozoon consists of nucleus containing condensed chromatin. Dependent upon the species, the spermatozoa diversify in their form (Grier, 1973; Van Deurs and Lastein, 1973; Mattei and Mattei, 1975; Todd, 1976). In the paradise fish, the head region of the spermatozoon consists of an oval nucleus with condensed chromatin (Fig. 7). Like the other teleosts, the tail part contains a flagellum with typical 9 + 2 microtubular structure in the

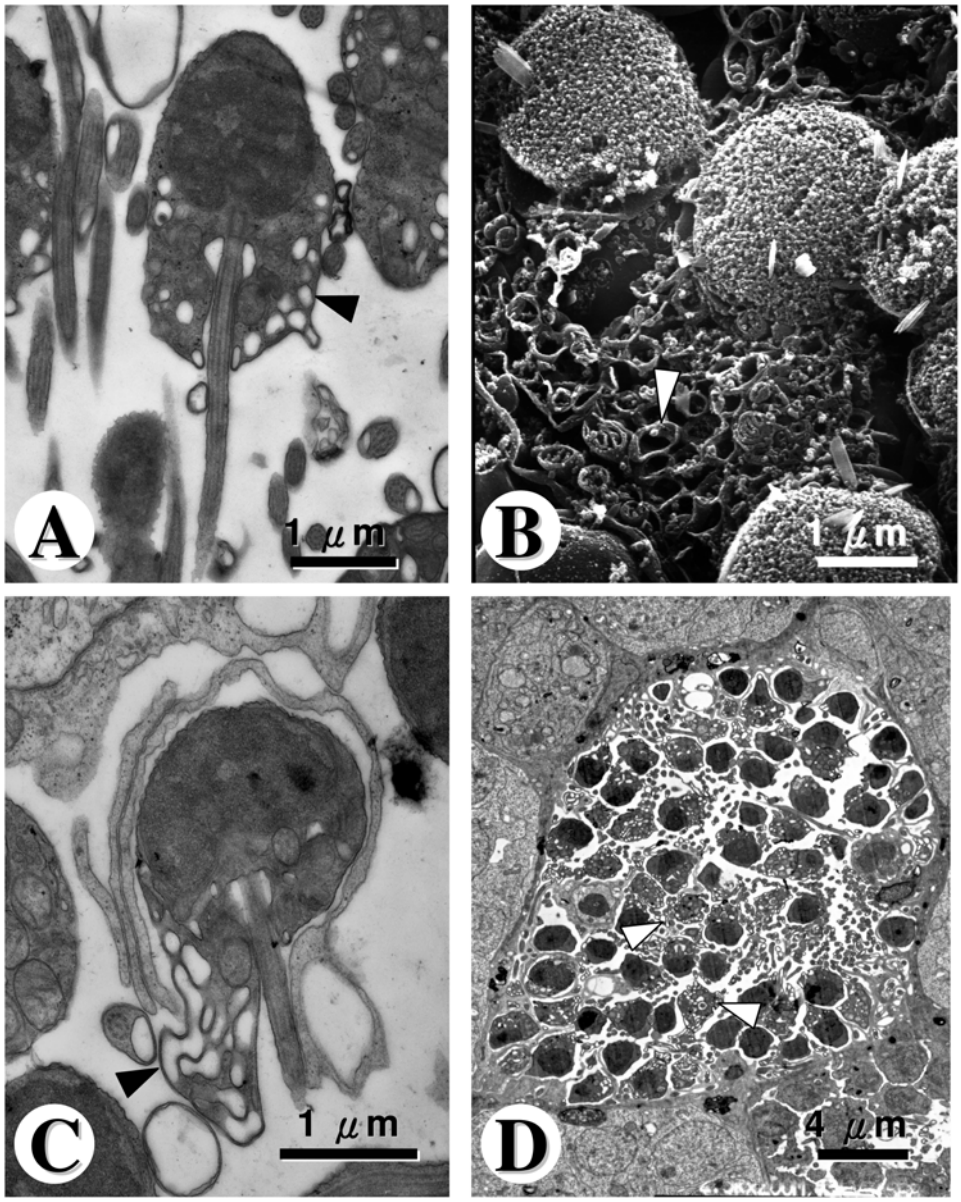

Fig. 6. Depletion of spermatid cytoplasm. TEM (A) and SEM (B) micrographs of this stage indicate many vacuoles (arrowheads) appear in the tail-side cytoplasm within which exhibit only a few mitochondria. C: The spermatid surrounded by the Sertoli cell showing depletion of the cytoplasm (arrowhead). D: There is depleted cytoplasm of the mature spermatids in the cyst (arrowheads).

spermatozoon of the paradise fish. Only a minimal number of species exhibit the 9 + 0 structure (Mattei and Mattei, 1975).

The spermatozoa of the paradise fish lack acrosome. The spermatozoa of fish have been categorized into acrosomal type (with an acrosome) and anacrosomal type (lacking an acrosome) (Jamieson, 1991). It is well known that the loss of the acrosome in teleostean spermatzoa is accompanied by the development of the micropyle in mature oocytes. The micropyle is a channel structure through which an anacrosomal sperm can enter the egg without proteolytic decomposition of the zona pellucida of the egg. Thus, our finding indicates that the micropyle-dependent fertilization is the approach by which this species prevent the egg from polyspermy.

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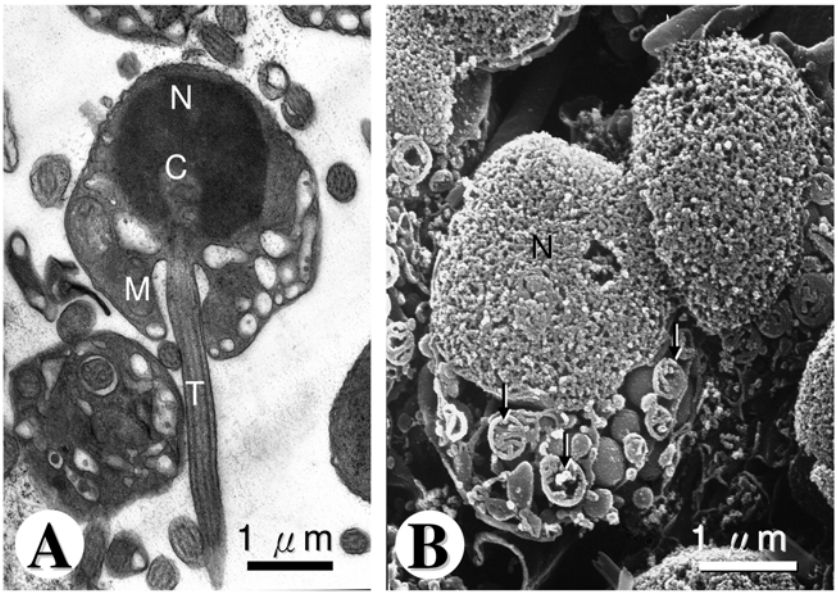

Fig. 7. TEM (A) and SEM (B) micrographs reveal the ultrastructures of the spermatozoon. A mature spermatozoon could be separated into four parts: (1) head region (N) with oval nucleus and condensed chromatin; (2) neck region (C) with tight connection of the centrosome and the nuclear fossa; (3) middle piece (M) with collar structure formed by the remaining cytoplasm containing some vacuoles and mitochondria of the spermatid; (4) tail region (T) with typical microtubular structures. Mitochondria (arrows).

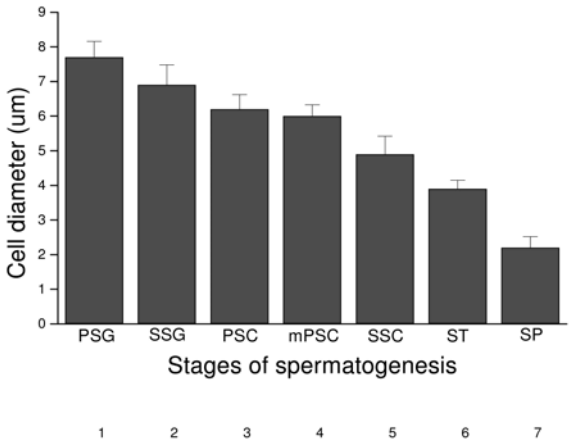

Fig. 8. Cell diameters (μm) of the germ cells in different stages of spermatogenesis. PSG, primary spermatogonium; SSG, secondary spermatogonium; PSC, primary spermatocyte; mPSC, meiosis primary spermatocyte; SSC, secondary spermatocyte; ST, spermatid; SP, spermatozoon. Sample size: 50 cells per stage.

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蓋斑鬥魚精子生成之組織超微研究

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摘　　要

報告中我們以蓋斑鬥魚 (*Macropodus opercularis*) 精子生成做組織學上的精微探究。此物種之精巢組織構造為小葉狀形式、外觀呈半透明之細長狀器官，緊貼於近尾端之體腔側壁。精細胞分布於細精管內側，並以支持細胞環繞而成的囊胞為發育單位。精子形變包括許多形態上的顯著改變，如中心粒的位移、細胞核的濃縮、細胞質的減少和鞭毛構造的形成。成熟精子的細胞核為卵圓形，內含有濃縮後的染色質，鞭毛中有典型的 9 + 2 微管結構但無頂體。文中也對精子發育過程中細胞核質與細胞質胞器所扮演的角色有所討論。

關鍵詞：蓋斑鬥魚、精巢、超微結構、精子發育。

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