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Zoological Research

A Novel Type of Spermiogenesis in the Nile Catfish *Chrysichthys auratus*（Siluriformes：Bagridae）in Egypt，with Description of Spermatozoon Ultrastructure

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Abstract：Spermiogenesis and spermatozoon ultrastructure in the Nile catfish *Chrysichthys auratus* are described using transmission electron microscopy．Spermiogenesis involves some unique peculiarities such as：the development of the centriolar complex and the initial segment of the flagellum in a position directly perpendicular to the basal pole of the nucleus，as a result of absence of nuclear rotation；lack of a cytoplasmic canal during differentiation of the spermatids into spermatozoa；the base of the basal body is not traversed by the basal plate；a basal foot anchors the basal body to the nucleus；and the presence of numerous vesicles around the midpiece and base of the flagellum．In addition，spermiogenesis includes some common features such as：chromatin compaction；formation of a medial shallow nuclear fossa；and elimination of excess cytoplasm．The mature spermatozoon has an elongate conical-shaped head with no acrosome or acrosomal vesicle，a long midpiece with numerous vesicles that continue backwards around the base of the flagellum and a long tail or flagellum，which has no lateral fins or a membranous compartment．The mitochondria lie close to the nucleus basal pole and surround the initial segment of the axoneme and are separated from the flagellum by the inner mitochondrial envelope due to disappearance of the cytoplasmic canal．The flagellum has the classical axoneme structure of a 9＋2 microtubular pattern．On the basis of the peculiar features mentioned above，it is concluded that spermiogenesis in this Nile catfish is a synapomorphic type derived from types I and II spermiogenesis，which are common among teleosts．Accordingly，this type could be considered as a novel type of spermiogenesis and could be termed as“type III”．

Key words：Sperm；Novel spermiogenesis；Ultrastructure；Siluriformes

埃及尼罗鲶鱼精子形成及精子超微结构

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摘要：用透射电镜观察了埃及尼罗鲶鱼（*Chrysichthys auratus*）精子形成及精子超微结构。精子形成过程除了具有鱼类精子形成的共同特征外，还具有一些特点：由于细胞核没有转动，中心粒复合体和鞭毛的起始部分位于细胞核的后端，并与核垂直；精子细胞变态过程中未产生袖套腔；基板未跨越基体的基部；基足将基体固定于细胞核；中段和鞭毛的基部具大量囊泡。成熟精子头部呈长锥状，没有顶体；中段长并含大量囊泡，向后延伸并包围鞭毛的基部；鞭毛细长，无侧鳍；线粒体位于核的后端附近，并包围轴丝；轴丝具典型的“9＋2”模式。总之，埃及尼罗鲶鱼的精子形成有别于硬骨鱼类的常见的精子形成类型——I 型和 II 型，可以称为 III 型。

关键词：精子；精子形成；超微结构；Siluriformes
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There are two types（I and II）of spermiogenesis in teleosts resulting in two types of spermatozoa（Mattei，1970；Jamieson，1991）．In type I spermiogenesis，rotation of the nucleus occurs，the diplosome en-

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ters the nuclear fossa and the flagellum is symmetrically located, while in type II spermiogenesis there is no nuclear rotation, the diplosome remains outside the fossa and the flagellum is asymmetrically located. Depending upon the variation in these features, fish spermatozoa are widely divergent in form and structure (Mattei, 1970; Nicander, 1970; Stein, 1981; Jamieson, 1991) and their structure is essentially controlled by the mode of reproduction (Gardiner, 1978; Grier et al, 1978). Generally, they vary from aflagellate to biflagellate and have an enormous range of shapes, sizes and structures; the number and location of organelles also vary (Baccetti et al, 1984; Baccetti, 1986; Jones & Butler, 1988; Jamieson, 1991; Mattei, 1991). Jamieson (1991) classified fish spermatozoa into two types, aquasperm and introsperm, based on their external or internal mode of fertilization. With few exceptions (Billard, 1983), both types of spermatozoa in telosts have no acrosome, but the eggs have a micropyle, which allows entry of the spermatozoon.

Mattei (1970) recognized two types of spermatozoa depending upon variations in the process of spermiogenesis. The major difference between these two spermatozoan types is related to the flagellar axis position, which may be perpendicular or parallel to the nucleus (Mattei, 1970; Jamieson, 1991). These positions result from the presence or absence of the nuclear rotation during spermiogenesis (Mattei, 1970). Most externally fertilized teleosts have a simple type of spermatozoon, called the type I aquasperm, which is characterized by a roundish head and a short midpiece with few mitochondria (Jamieson, 1991; Mattei, 1991). However, many internally fertilized teleosts, which include both oviparous and viviparous species, have a complex sperm called the type II introsperm, which has an elongated head and other derived features such as the absence of the midpiece, no nuclear rotation, the head runing more or less parallel to the flagellum and the mitochondria located on the posterior tip of the head (Jamieson, 1991; Mattei, 1991).

Electron microscopy of a wide spectrum of teleost spermatozoa has demonstrated that important ultrastructural characteristics can be identified between different species (Ginzburg, 1968; Franzen, 1970; Mattei, 1970, 1988, 1991; Gwo & Arnold, 1992; Gwo et al, 1993, 1994b, 1995; Gwo, 1995) and can be used for inferring both the taxonomic and phylogenetic relationships between taxa (Billard, 1970; Franzen, 1970; Mattei & Mattei, 1974; Jamieson, 1981, 1991; Baccetti et al, 1984; Baccetti, 1985; Lahnsteiner & Patzner, 1990; Mattei, 1991; Jamieson, 1991; Justine, 1991; Gwo & Arnold, 1992; Gwo et al, 1992, 1993, 1994a, b, 1995; Gwo & Gwo, 1993; Gwo, 1995).

Although Jamieson (1991) and Mattei (1988, 1991) provided data on the spermatozoa ultrastructure of practically all major extant fish groups, the spermatozoa of neotropical teleosts, especially the Siluriformes, are still not well known (Poirier & Nicholson, 1982; Maggese et al, 1984; Jamieson, 1991; Mattei, 1991; Quagio-Grassiotto & Carvalho, 2000). Within the Siluriformes, the family Bagridae is one of the most common families in the Nile River in Egypt. The Nile bagrid catfishes are comprised of four genera: *Bagrus*, *Chrysichthys*, *Clarotes* and *Auchenoglanis*. Of these genera, the first two are common at the Nile River, while the others are very rare. *Bagrus bajad* and *Chrysichthys auratus* are the most widespread species in the Nile and its channels in Egypt.

Despite the numerous studies on fish spermatozoa, to date there is no published data describing the fine structure of the spermatozoa of the Nile bagrid catfishes. In this paper the ultrastructure of spermatozoon and spermiogenesis of *C. auratus*, belonging to the family Bagridae, is described and compared with those of other teleosts to find out the specific characters of spermiogenesis and spermatozoa in the family Bagridae. This information will help in the construction of the phylogenetic relationship between the bagrid catfishes and other catfish families, and between the catfishes and other teleost fishes.

1 Materials and Methods

The breeding season of the long fin catfish *Chrysichthys auratus*, Geoffroy 1809 runs from April to September. In May 2005, three mature males with a total length of 24 cm were collected from the Nile at El Minia (Middle Egypt). Samples of testis were fixed in 3% glutaraldehyde made in 0.12 mol/L phosphate buffer (pH 7.4) for 1 h at 4℃ and post-fixed in 1% osmium tetroxide made in the same buffer for 1 h. After fixation, the samples were dehydrated in a graded series of ethyl alcohols, cleared in propylene oxide and then embedded in low viscosity Epoxy resin. Thick plastic sections were cut using a LKB ultramicrotome with a glass knife and then stained with toluidine blue. Ultra-thin sections were made of appropriate regions

and stained with drops of 2% uranyl acetate followed by lead citrate for 30 min. Sections were examined and photomicrographs were taken at an 80 kV accelerating voltage using JEOL JEM-100CX II TEM.

Germ cells and spermiogenic stages were identified according to the criteria given by Gwo & Gwo (1993) and sizes of germ cells, organelles and other structures were attained on the basis of 15 to 20 measurements from each category. Mean and standard deviation values are given.

2 Results

2.1 Spermatogenesis

Spermatogenesis occurs in cysts located in the seminiferous tubules. Each cyst consists of a group of germ cells, which are usually at the same stage of development and surrounded by the cytoplasmic processes of the Sertoli cell. Earlier stages of spermatogenesis do not show any specific peculiarities in *Chrysichthys auratus*. Primary spermatogonia are relatively large cells with extensive cytoplasm and a prominent rounded central nucleus of $1.6 \pm 1.02\ \mu m$ in diameter (Fig. 1A). The nucleus contains granular chromatin that exhibits some irregular condensed patches and one distinct nucleolus with darkly stained fibrilar chromatin. The cytoplasm contains numerous irregular-shaped mitochondria with inconspicuous cristae; one side of the matrix is very dark, while the other side is very light. In addition, the cytoplasm shows few primary Golgi vesicles, dispersed highly electron-dense particles, which are either free (nuage) or associated with mitochondria (cement), and a centriole that is very close to the nucleus. However, secondary spermatogonia, produced by mitotic division of the primary spermatogonia, are relatively

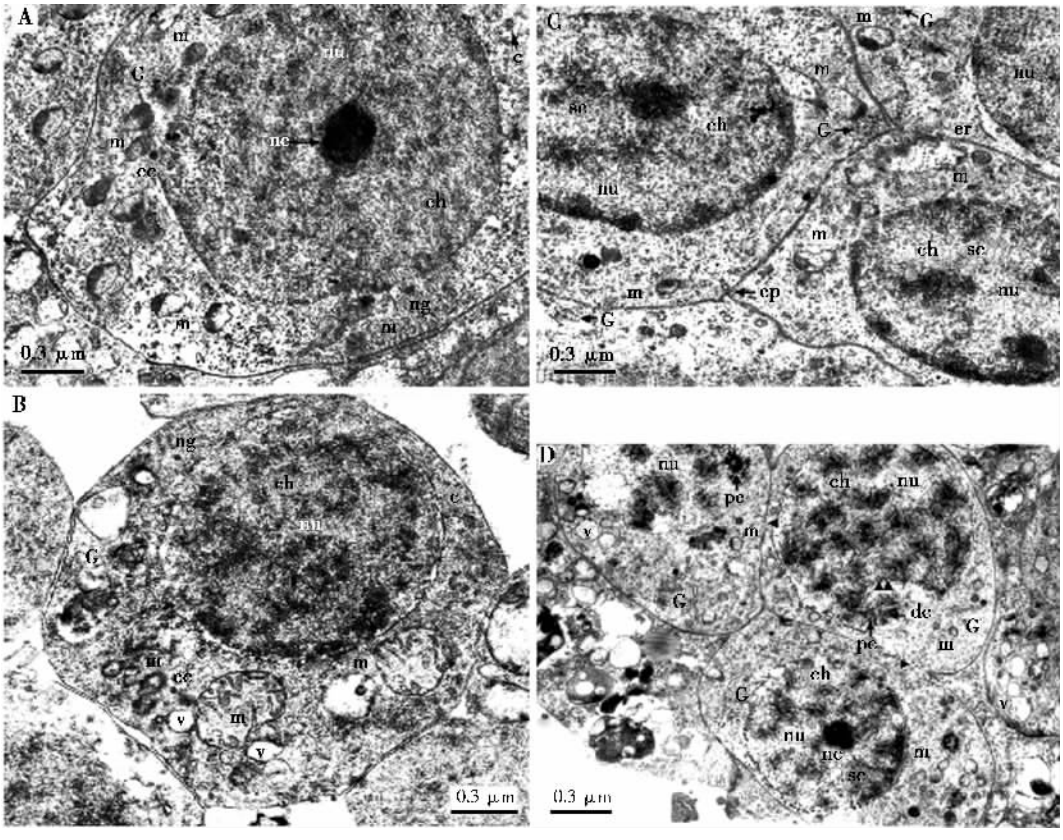

Fig. 1　Transmission electron micrographs through the spermatogenic cells of *Chrysichthys auratus*

A, Primary spermatogonium showing nucleus (nu), nucleolus (nc), granular chromatin (ch), mitochondria (m), Golgi vesicles (G), nuage (ng), cement (ce) and a centriole (c).

B, Secondary spermatogonium with a conspicuous nucleus (nu), heterogonous chromatin (ch) variable-sized mitochondria (m), Golgi vesicles (G), nuage (ng), cement (ce), vesicles (v) and a centriole (c).

C, Primary spermatocyte with a prominent nucleus (nu), nucleolus (nc), clumped or slightly mottled chromatin (ch) and synaptonemal complexes (sc). The cytoplasm shows mitochondria (m), endoplasmic reticulum (er) and Golgi vesicles (G). The cytoplasmic processes (cp) of the Sertoli cell surround the cells.

D, Secondary spermatocyte (shown in the lower part of Figure) with a small rounded nucleus (nu) nucleolus (nc), granular chromatin (ch), synaptonemal complexes (sc), mitochondria (m) and Golgi vesicles (G).

small cells (Fig. 1B). Each cell has a nucleus of 1.3 ± 0.09 μm in diameter and less well-defined nucleolus. The nucleus chromatin is heterogeneous with irregularly distributed patches. Mitochondria are variable in size; large mitochondria show a homogeneous matrix and well-defined cristae. Golgi primary vesicles, nuage, cement and few vesicles are distributed in the cytoplasm, in addition to the centriole, which is clearly visible in a position perpendicular to the nucleus basal pole. In addition, spermatocytes are either spheroid or elongated small cells and their shape changes subsequently into ovoid during later stages of spermiogenesis. The nucleus of the primary spermatocyte is relatively small and oval in shape, measuring 1.2 ± 0.05 μm in diameter, and contains synaptonemal complexes, a less well-defined nucleolus and clumped or slightly mottled chromatin (Fig. 1C), which changes gradually into more evenly dense granular and patching chromatin typical of the early spermatids. The cytoplasm shows numerous mitochondria, endoplasmic reticulum and Golgi apparatus. The cytoplasmic processes of the Sertoli cell surround numerous (up to three) spermatocytes. The size of the secondary spermatocyte, produced by the first meiotic division of the primary spermatocyte, is slightly smaller than the primary cell size. The cell is elongated in shape, while the nucleus is spherical and measures 1.0 ± 0.13 μm in diameter. The nucleus shows more patching chromatin than the primary spermatcyte, a clearly visible nucleolus and synaptonemal complexes. The cytoplasm contains numerous vesicles, mitochondria and Golgi apparatus, which lie close to the centrioles (Fig. 1D).

2.2 Spermiogenesis

Spermiogenesis begins with the polarization of the germ cells; the nucleus moves to an eccentric position, while the other organelles migrate and concentrate at the opposite pole of the cell (Figs. 1D, 2A – D, 3A – D, 4A). The early spermatids are relatively elongated cells that remain interconnected by cytoplasmic bridges resulting from the incomplete cytokinesis of mitotic and meiotic divisions (Fig. 1D). Each spermatid has a small round nucleus (1.0 ± 0.01 μm in diameter) with granular chromatin distributed in small electron-dense patches of heterogeneous density, reduced cytoplasm and inconspicuous ribosomes (Fig. 1D). A small number of mitochondria are located around the centriolar complex, which appears close to the plasma membrane in a position perpendicular to the basal pole of the nucleus, i.e. there is no nuclear rotation (Fig. 1D). The centriolar complex consists of proximal and distal centrioles, which are arranged perpendicular to each other and are interconnected by fine osmiophilic filaments (Figs. 2: A, B, D). The distal centriole differentiates into the basal body, which starts to form the initial segment of the flagellum (Figs. 2A, B, D). In transverse sections, both of the centrioles show the typical nine triplet microtubules construction, while the initial segment of the flagellum reveals the typical axonemal configuration with nine double peripheral and two single central microtubules (Figs. 2C; 3A, B; 4A – C). During this stage, chromatin compaction begins progressively in the center of the nucleus to form coarse, dense granules, which gradually aggregate together into a coarse, compact highly electron-dense homogeneous matrix characteristic to the nucleus of the early spermatozoa (Figs. 2AD; 3A, B). Meanwhile, a depression appears medially in the nuclear outline very close to the centriolar complex, initiating the formation of the nuclear fossa, into which the centriolar complex later enters the nucleus (Figs. 1D; 2A – D; 3A, B).

During later stages of spermiogenesis, the nuclear fossa deepens and the centriolar complex, including the proximal and distal centrioles, gradually moves into the nuclear fossa bringing with it the basal body that forms the initial segment of the flagellum and the plasma membrane. The plasma membrane invaginates to form a space, the cytoplasmic canal, between the flagellar and plasma membranes (Figs. 2D; 3C, D; 4B). In transverse sections, the sheath enveloping the microtubules of the proximal centriole appears connected to the nucleus by relatively thick anchoring fibrils (Figs. 2D, 3B). In addition, a basal foot extends laterally from the midregion of the basal body and anchors it to the nucleus (Fig. 2D). Simultaneously, most of the cytoplasm around the nucleus moves toward the region surrounding the cytoplasmic canal to establish the formation of the midpiece of the future spermatozoon (Figs. 3C, D; 4A). In this region, which forms the initial segment of the axoneme, several mitochondria are located and surrounded by numerous vesicles (Fig. 4A). As a result of movement of the cytoplasm to the midpiece region, a perinuclear space is formed around the nucleus, which later disappears in the mature spermatozoon when the plasma membrane adheres tightly to the nucleus membrane (Figs. 3C, D).

At the end of spermiogenesis, the residual cyto-

plasm and the cytoplasmic bridges interconnecting the spermatids disintegrate and the cytoplasmic processes of the Sertoli cells move away leaving the spermatozoa in the lumen of the seminiferous tubules.

2.3 Spermatozoon

The mature spermatozoon has an elongated conical-shaped head, a long midpiece and a long tail or flagellum. The head has no acrosome or acrosomal vesicle (Figs. 4D; 5A, B). The nucleus, measuring 1.8 ± 0.01 μm in diameter and 2.1 ± 0.01 μm in length, has the form of an inverted U in longitudinal section and is surrounded by a narrow strip of cytoplasm with no organelles. It is covered by a nuclear envelope underlying the plasma membrane (Figs. 4D; 5A, B). The posterior medial region of the nucleus is penetrated by a shallow nuclear fossa, the length of

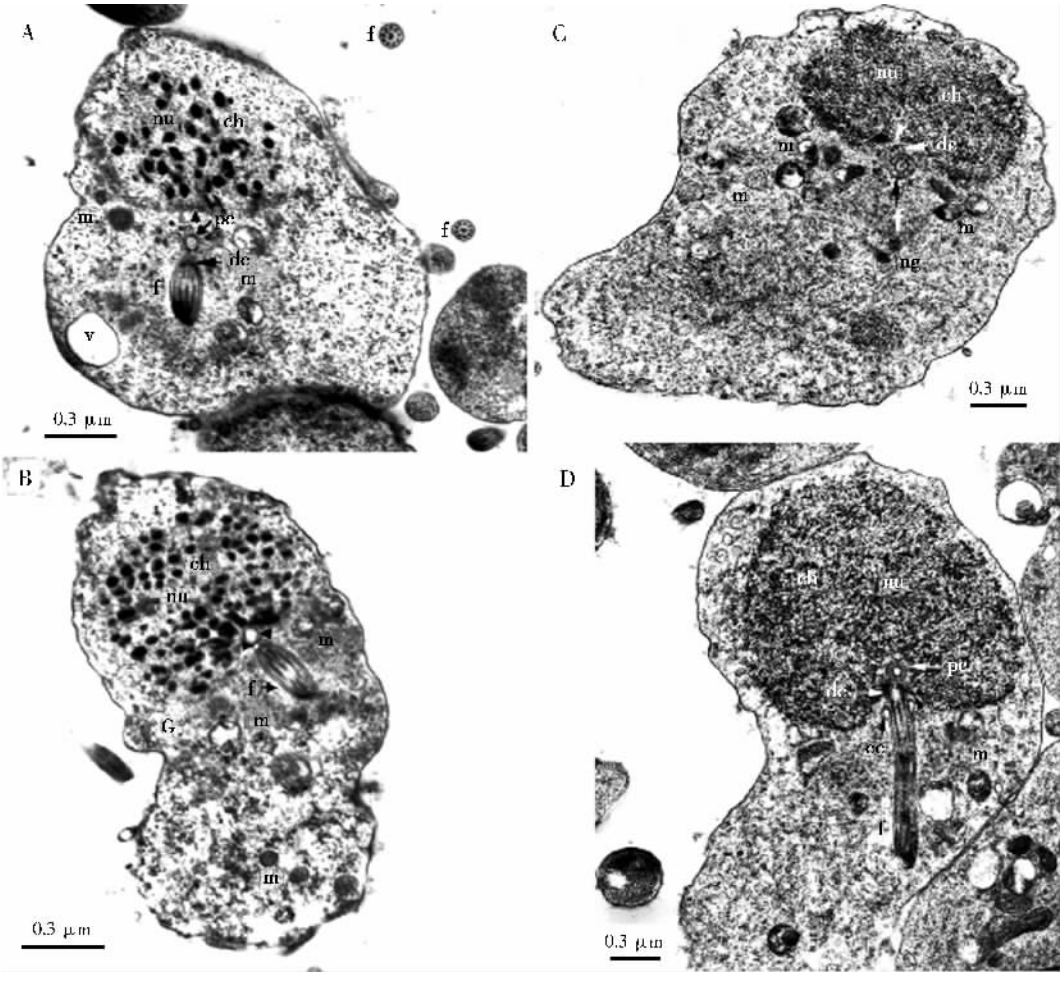

Fig. 2　Transmission electron micrographs through the stages of spermiogenesis in *Chrysichthys auratus*

Early spermatid cells (as shown in the upper part of Fig. 1D) that show a spherical nucleus (nu) with condensed patches of chromatin (ch) and the proximal (pc) and distal (dc) centrioles, which are located just close to the basal pole of the nucleus in a depression formed on the outline of the nucleus as a sign of nuclear fossa formation (double arrowheads). Mitochondria (m), vesicles (v) and Golgi flattened cisternae (G) are clearly visible in the cytoplasm. Arrowhead refers to the cytoplasmic bridges between cells.

A, Early spermatid (longitudinal section) showing the nucleus (nu) with its chromatin (ch) that is condensed into electron-dense large granules, the proximal centriole (pc) and the distal centriole (dc) which forms the initial segment of the flagellum (f). Note the indentation in the nucleus margin above the centriolar complex (arrowhead) as a sign of nuclear fossa formation. Several mitochondria (m) and a single large vesicle (v) are situated close to the centriolar complex.

B, Early spermatid (longitudinal section) showing the proximal centriole (right arrowhead), the distal centriole (left arrowhead), which forms the initial region of the flagellum (f), and the electron-dense large granules of nucleus chromatin (ch). Note the presence of mitochondria (m) and Golgi vesicles (G) around the centriolar complex and the initial region of the axoneme.

C, Early spermatid (cross section) showing the microtubular pattern (9 + 2) of the initial region of the flagellum (f) and the distal centriole (dc) which is located in the nuclear fossa (arrowhead). Nuage (ng) and several mitochondria (m) are unevenly distributed in the cytoplasm.

D, Longitudinal section in middle phase spermatid showing the proximal centriole (pc), the differentiation of the distal centriole (dc) into the basal body, which forms the flagellum (f), and the formation of the cytoplasmic canal (cc) around the developing midpiece. Note the nucleus (nu) has a heterogeneous chromatin (ch) and the presence of a basal foot on both sides of the basal body that attaches the latter to the nucleus (arrowhead).

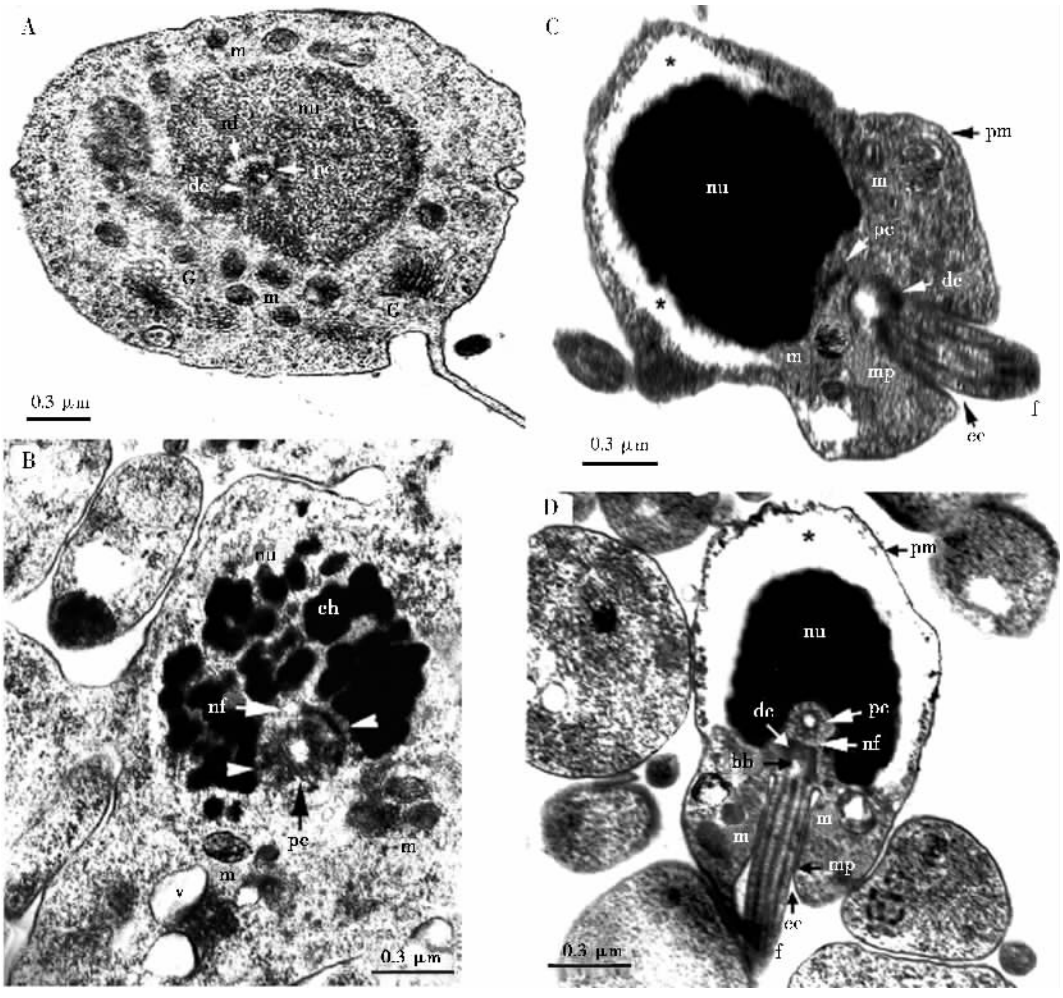

Fig. 3 Transmission electron micrographs through the stages of spermiogenesis in *Chrysichthys auratus*

A, Transverse section in middle phase spermatid at the level of the nucleus (nu) showing the proximal (pc) and distal (dc) centrioles which are located in the nuclear fossa (nf). Note the presence of numerous mitochondria (m) and Golgi apparatus (G) in the cytoplasm.

B, Transverse section in middle phase spermatid showing the microtubular pattern (9 + 0) of the proximal centriole (pc) that is located in the nuclear fossa (nf). Note the anchoring fibrils (arrowheads) which attach the proximal centriole to the nucleus (nu), the condensed electron-dense granules of the nucleus chromatin (ch) and the mitochondria (m) and vesicles (v) which are unevenly distributed in the cytoplasm.

C, Oblique longitudinal section in late spermatid showing the perinuclear space (stars) formed around the nucleus (nu) as a result of migration of the residual cytoplasm to the basal part of the nucleus to establish the formation of the midpiece (mp) of future spermatozoon and the condensation of chromatin granules (ch) into an electron-dense compact mass in the nucleus. Note the presence of the proximal (pc) and distal (dc) centrioles and the cytoplasmic canal (cc), which is formed by the plasma membrane (pm) around the midpiece (mp) and the initial region of the flagellum (f) and separates the midpiece from the mitochondria (m).

D, Longitudinal section in late spermatid showing that the nucleus chromatin (ch) is more electron-dense and compacted into a homogeneous matrix. Note that the proximal (pc) and distal (dc) centrioles are located in the nuclear fossa (nf) and interconnected with osmiophilic filaments (of), the basal body (bb) is well developed, the plasma membrane (pm) invaginates around the initial region of the flagellum (f) to form a space, the cytoplasmic canal (cc) and most of the cytoplasm around the nucleus moves backwards toward the region surrounding the cytoplasmic canal to establish the formation of the midpiece (mp) of future spermatozoon.

which is about one-third of the nucleus length. The nuclear fossa contains the centriolar complex and the basal body of the axoneme and is filled by an electron-dense material (Figs. 4D; 5A, B). The nuclear fossa appears bell-shaped in longitudinal section and circular in transverse section. The chromatin is highly electron-dense and consists of compact coarse granular patches, with irregularly-shaped electron-dense thick fibers and electron-lucent lacunae. The proximal and distal centrioles are connected to each other by osmiophilic filaments. The proximal centriole is anchored to the nucleus by numerous anchoring fibrils (Figs. 4D; 5A, B), while the basal body is attached laterally to the nucleus on both sides by the basal foot (Fig. 5B). Each centriole exhibits the classical (9 + 0) nine-microtubular triplet pattern. The basal part of the basal body is not

traversed by a basal plate and the axes of the two centrioles are perpendicular to each other and to the flagellar axis (Figs. 4D；5A，B).

The midpiece measures 1.9 ± 0.02 μm in diameter and 1.8 ± 0.01 μm in length and contains numerous (up to six) unequal spherical mitochondria [approximately (0.1 – 0.6) ± (0.05 – 0.03) μm in diameter] and several peripheral vesicles, which are circular or elongate in shape (Figs. 4D；5A – C). Some of the peripheral vesicles continue backwards to surround the base of the flagellum (Figs. 4D；5B，C). The mitochondria lie close to the base of the nucleus and surround the initial segment of the axoneme and are separated from the flagellum by the inner mitochondrial envelope, which is closely applied to the flagellar plasma membrane due to the disappearance of the cytoplasmic canal. The axoneme in this region has the same microtubular pattern (9 + 2) as the flagellum (Figs. 4D；5A，B).

The flagellum is 30.1 ± 0.03 μm in length and 0.3 ± 0.01 μm in diameter, composed of a typical 9 + 2 microtubular doublet structure and surrounded by the flagellar plasma membrane (Figs. 4D；5B – D). The central tubules are interconnected by a single strand, while the outer doublets are connected to the flagellar plasma membrane by short Y-shaped bridges. Each of the nine outer doublets consists of subfibers A and B. Two dynein arms arise from subtubule A of each doublet and extend towards the next tubule (Figs. 5C，D). The flagellum has neither lateral fins nor a membranous compartment；however its base is surrounded by a backward extension of the peripheral vesicles located in the midpiece (Figs. 4D；5B-D).

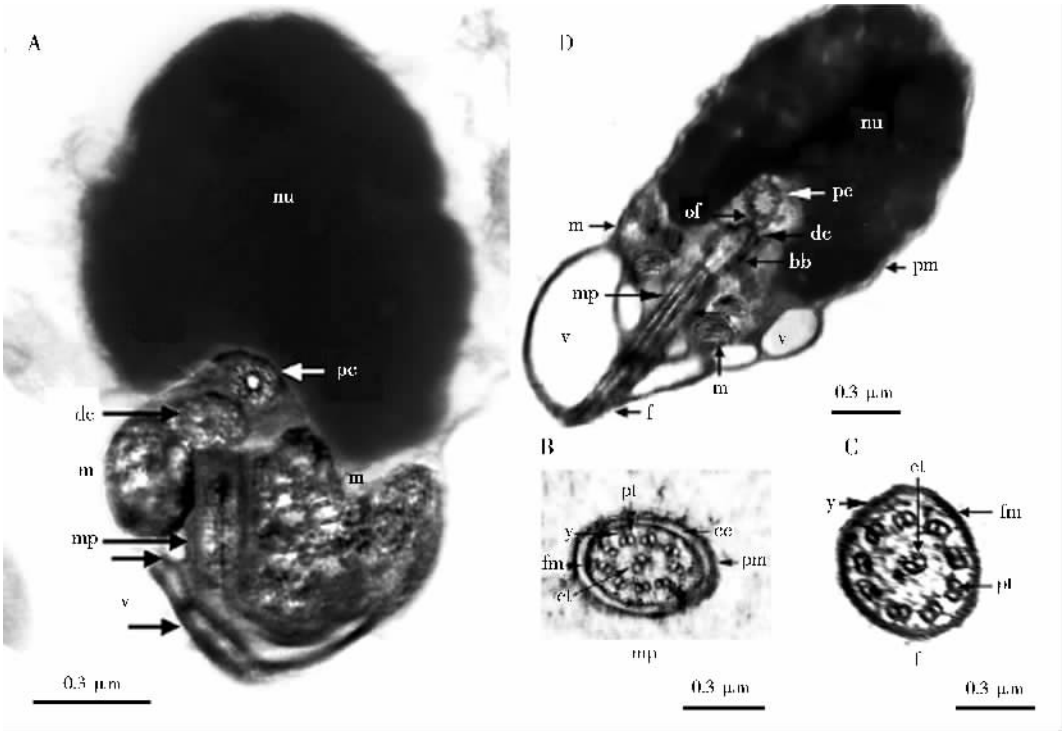

Fig. 4　Transmission electron micrographs in late spermatids and spermatozoa of *Chrysichthys auratus*

A, Oblique longitudinal section in late spermatid showing the inverted U-shaped nucleus (nu), the disappearance of the cytoplasmic canal separating mitochondria (m) from the flagellum in the midpiece region (mp) and the proximal (pc) and distal (dc) centrioles that are located in the nuclear fossa. Note the presence of vesicles (v) and four mitochondria (m), one at the left side and three at the right side of the midpiece region.

B, Transverse section through the midpiece (mp) of late spermatid showing the presence of the cytoplasmic canal (cc) between the plasma membrane (pm) and the flagellar membrane (fm) and the microtubular pattern (9 + 2) of the flagellum (f). Note that each of the peripheral microtubular doublets (pt) is connected to the plasma membrane by a Y-shaped link (y) and the central tubules (ct) are interconnected by a thin filament.

C, Transverse section through the flagellum (f) of late spermatid showing its microtubular pattern of two central microtubular doublets (ct) and nine peripheral microtubular doublets (pt), which are surrounded by the flagellar membrane (fm), and the peripheral microtubular doublets (pt) that are connected to the plasma membrane by a Y-shaped link (y).

D, Oblique longitudinal section through the whole sperm showing the inverted U-shaped nucleus (nu) surrounded by the plasma membrane (pm), which is closely applied to the nuclear membrane, the proximal (pc) and distal (dc) centrioles that are interconnected by osmiophilic filaments (of), the basal body (bb) that is not traversed by a basal plate and the midpiece (mp) which is surrounded by mitochondria (m) and vesicles (v). Note that the vesicles surrounding the midpiece extend backwards to enclose the base of the flagellum (f).

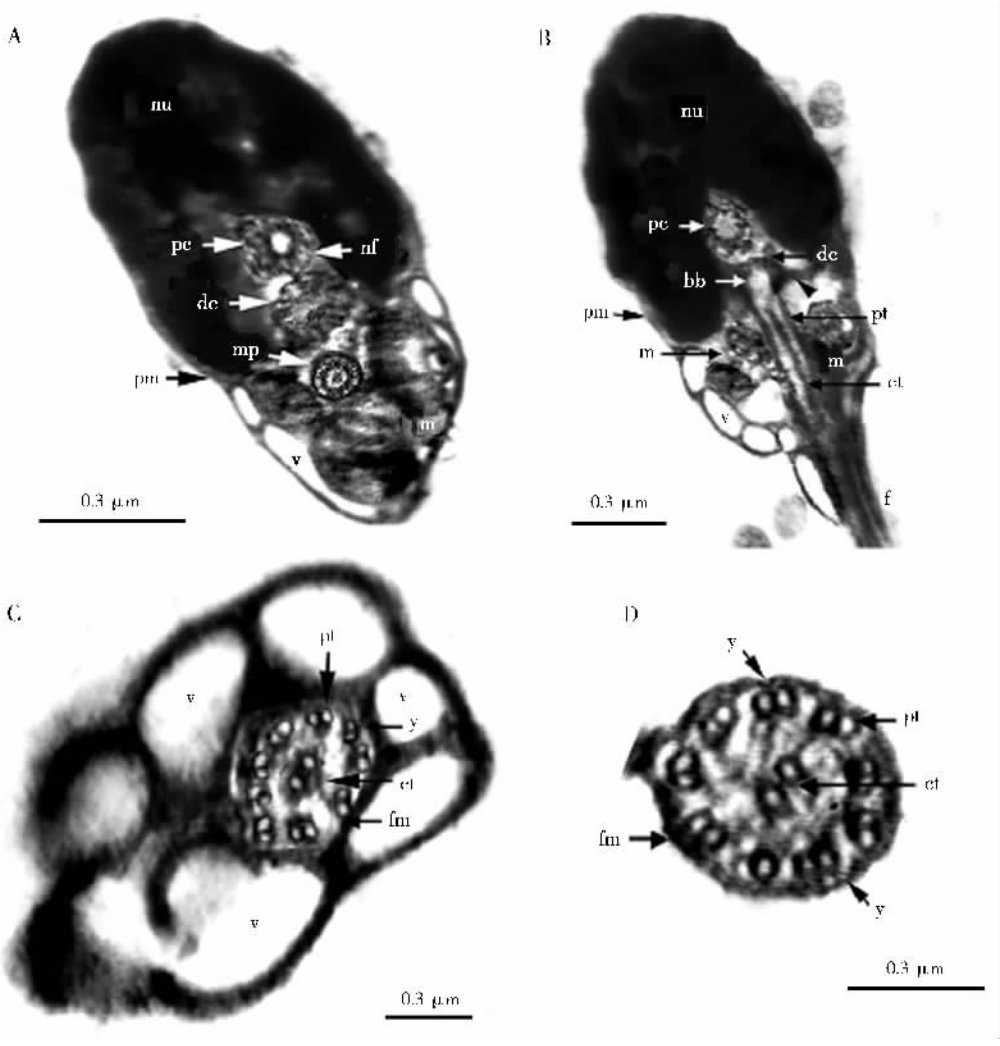

Fig. 5 Transmission electron micrographs in the mature spermatozoon of *Chrysichthys auratus*

A, Oblique longitudinal section in the head and midpiece regions showing the inverted U-shaped nucleus (nu) surrounded by the plasma membrane (pm) that is applied very tightly to the nuclear envelope, the proximal (pc) and distal (dc) centrioles, which are located in the nuclear fossa (nf), and the midpiece region (mp) where there are three mitochondria (m) and numerous vesicles (v). Note the anchoring fibrils connecting the proximal centriole to the nucleus and the microtubular structure of the axoneme in the midpiece region.

B, Longitudinal section showing the inverted, conical U-shaped nucleus (nu) surrounded by the plasma membrane (pm), which is closely applied to the nuclear envelope, the medial shallow nuclear fossa (nf) that contains both the proximal (pc) and distal (dc) centrioles and part of the basal body (bb), which is attached to the nucleus on both sides by the basal foot (arrowhead), a short midpiece (mp) with no cytoplasmic canal, the mitochondria, which are separated from the flagellum by the flagellar membrane, and a long tail, of which its base is enclosed by the vesicles extending backwards from the midpiece.

C, Transverse section in the initial region of the flagellum showing the numerous vesicles (v), which are in close contact with the flagellar plasma membrane (fm), and the central (ct) and peripheral microtubular doublets of the flagellum. Note the Y-shaped link (y) that connects the peripheral doublets to the flagellar membrane.

D, Transverse section in the flagellum showing its basic structure of nine peripheral (pt) and two central (ct) microtubular doublets. Note that each of the nine outer doublets is connected to the flagellar plasma membrane (fm) by a Y-shaped link (y) and consists of subfibers A and B.

3 Discussion

Among members of the Teleostei with external fertilization, the flagellum generally develops laterally to the nucleus in the early spermatids. In addition, the flagellar axis may be either perpendicular or parallel to the nucleus depending on whether or not nuclear rotation occurs (Matei, 1970). The resulting sperm is type I aquasperm, which has a head containing a spherical nucleus with no acrosome, a midpiece of variable dimensions with or without a cytoplasmic canal and a long tail or flagellum (Jamieson, 1991; Mattei, 1991). In *Chrysichthys auratus*, spermiogenesis lacks nuclear rotation since the diplosome-flagellar axis appears directly perpendicular to the nucleus. This type of

spermiogenesis leads to the formation of a peculiar type of spermatozoa with an elongate conical-shaped nucleus, a long midpiece without a cytoplasmic canal and a long flagellum. The absence of nuclear rotation and origin of the flagellum directly perpendicular to the nucleus pole have also been described in the siluriformes *Malapterurus electricus* and *Synodontis schall* (Shahin, 2006b, c). In addition, lack of nuclear rotation has been reported in the mugilid *Liza aurata* (Brusle, 1981) and characids *Diapoma speculiferum* and *Diapoma* sp. (Burns et al, 1998), *Mimagoniates barberi* (Pecio & Rafiński, 1999), *Acestrorhynchus falcatus* (Matos et al, 2000) and *Merluccius merluccius* (Medina et al, 2003). However, in these species the diplosome remains outside the nuclear fossa and the flagellum is asymmetrically located, i. e. it inserts laterally to the head (type II ; Mattei, 1970). On the other hand, it has been reported that the rotation of the nucleus may occur only to a slight degree as in the cyprinid *Cyprinus carpio*, esocid *Esox lucius* (Billard, 1986), cichlid *Oreochromus niloticus* (Lou & Takahashi, 1989) and characid *Paracheirodon innesi* (Jamieson, 1991). Furthermore, it can occur at 90° as in the centrarchid *Lepomis macrochirus* (Sprando et al, 1988), sparid *Acanthopagrus schlegeli* (Gwo & Gwo, 1993 ; Gwo et al, 1993), poeciliid and zenarchopterid species (Jamieson & Grier, 1993), diplomystid *Diplomystes mesembrinus* (Quagio-Grassiotto et al, 2001a), erythrinid *Hoplias malabaricus* (Quagio-Grassiotto et al, 2001b), characid *Alestes dentex* (Shahin, 2006a) and curimatid species (Quagio-Grassiotto et al, 2003).

It is recognized that nuclear rotation greatly affects the position of the nuclear fossa and accordingly the attachment of the flagellum to the nucleus (Quagio-Grassiotto et al, 2003). For example, when rotation is absent, the nuclear fossa is either medial in position and the flagellum is perpendicular to the nucleus (Shahin, 2006b, c), or is lateral or absent, and thus the flagellum is parallel to the nucleus (Burns et al, 1998 ; Matos et al, 2000). If rotation is incomplete, the nuclear fossa is eccentric and so is the flagellum, which is perpendicular to the nucleus (Matos et al, 1998 ; Jamieson, 1991 ; Burns et al, 1998 ; Magalhães, 1998 ; Andrade et al, 2001 ; Quagio-Grassiotto et al, 2001b, 2003). But if rotation is complete (90°), the nuclear fossa is medial and the flagellum is medial and perpendicular to the nucleus (Mattei et al, 1995 ; Aires, 1998 ; Romagosa et al, 1999 ; Zaiden, 2000 ; Veríssimo-Silveira, 2003 ; Shahin, 2006a). Quagio-Grassiotto et al (2003) pointed out that the position of the centriolar complex is related to the shape of the nuclear fossa. When the nuclear fossa is deep, as in *C. auratus*, the centriolar complex is located inside it. If the nuclear fossa is of the moderate type, it may contain the entire centriolar complex, as in *M. electricus* and *S. schall* (Shahin, 2006b, c), part of the complex, or only one of the centrioles, while the other one lies outside. However, if the nuclear fossa is completely absent, the centriolar complex usually lies close to the nucleus. For more details on the absence and occurrence of a shallow to deep nuclear fossa in the spermatozoa of many viviparous and some oviparous taxa, see Shahin (2006a).

The arrangement of the centriolar complex is quite variable among teleosts and is considered a species-specific feature in the Cypriniformes (Mansour et al, 2002). The proximal centriole may be anterior or lateral to the distal centriole. In either case, it may be coaxial, parallel, oblique or perpendicular to the distal centriole. In *C. auratus* spermatozoa, the two centrioles are arranged perpendicular to each other and the proximal centriole lies anterior to the distal one. Similar conditions have been described in *A. schlegeli* (Gwo & Gwo, 1993 ; Gwo et al, 1993), *A. latus* (Gwo, 1995), *Chanos chanos* (Gwo et al, 1995), *D. mesembrinus* (Quagio-Grassiotto et al, 2001a), *M. merluccius* (Medina et al, 2003), *A. dentex* (Shahin, 2006a) and *M. electricus* and *S. schall* (Shahin, 2006b, c). Nevertheless, the two centrioles are oriented at right angles to each other in *Anguilla japonica* (Gwo et al, 1992), *Plecoglossus altivelis* (Gwo et al, 1994a), *Epinephelus malabaricus* and *Plectropomus leopardus* (Gwo et al, 1994b) and *Oncorhynchus masou formosanus* (Gwo et al, 1996). Among the Characiformes variable orientation of the centrioles has been reported. For example, the proximal centriole can be antero-lateral and slightly oblique to the basal body (Jamieson, 1991) or lateral, oblique and distant from the distal centriole (Mattei et al, 1995). It may also be anterior, coaxial and slightly oblique to the basal body (Quagio-Grassiotto et al, 2001b) or anterior, lateral and perpendicular to the basal body (Matos et al, 2000). Furthermore, it may be anterior, medial and perpendicular to the basal body (Aires, 1998 ; Burns et al, 1998 ; Pecio & Rafinski, 1999 ; Romagosa et al, 1999 ; Zaiden, 2000 ; Shahin, 2006a) or anterior, medial to slightly lateral, and at a right or slightly oblique angle relative

to the distal centriole (Quagio-Grassiotto et al, 2003).

It is worth mentioning that in *C. auratus*, the basal section of the distal centriole is not traversed by a basal plate; a case which seems to be uncommon among Siluriformes, Characiformes and Cypriniformes (for review, see Shahin, 2006a, b). It is however normal in some Salmoniformes (Gwo et al, 1994, 1996) and Gonorynchiformes (Gwo et al, 1995) of which data are available.

The midpiece exhibits two situations among teleosts, one of which is at the posterior end of the nucleus as in *C. auratus*, many teleosts (Jamieson, 1991; Mattei, 1991; Shahin, 2006b, c) and some Characiformes (Jamieson, 1991; Matos et al, 1993, 1998; Mattei et al, 1995; Burns et al, 1998; Andrade et al, 2001; Quagio-Grassiotto et al, 2001b, 2003; Shahin, 2006a). In the alternative possibility, the midpiece is located laterally to the nucleus as in some members of Characiformes (Burns et al, 1998; Pecio & Rafinski, 1999; Matos et al, 2000).

In *C. auratus*, the midpiece is long and lacks the cytoplasmic canal and cytoplasmic sheath or collar, although the canal is clearly formed in the early spermatids. Similar findings have been found in the Siluriformes *D. mesembrinus* (Quagio-Grassiotto et al, 2001a) and Sorubim lima (Quagio-Grassiotto & Carvalho 2000) and in the Characiformes *H. malabaricus* (Nagrão, 1999) and *Macropsobrycon uruguayanae* (Burns et al, 1998). Conversely, a long midpiece with a long cytoplasmic canal enveloped by the cytoplasmic sheath or collar, which is formed by the plasma membrane as a thin cytoplasmic projection, has been recorded in some characids (Jamieson, 1991; Matos et al, 1993; Aires, 1998; Romagosa et al, 1999; Zaiden, 2000; Veríssimo-Silveira, 2003; Shahin, 2006a) and in the siluriform *M. electricus* (Shahin, 2006b). However, a short midpiece and a short cytoplasmic canal have been observed in some of the Siluriformes (Jaspers et al, 1976; Poirier & Nicholson, 1982; Jamieson, 1991; Shahin, 2006c) and the majority of the Characiformes (Magalhães, 1998; Matos et al, 1998, 2000; Andrade et al, 2001; Quagio-Grassiotto et al, 2003; Shahin, 2006a) as well as in many teleosts (see Jamieson, 1991; Mattei, 1991; Gwo & Gwo, 1993; Gwo, 1995; Gwo et al, 1993, 1994b, 1995, 1996; Quagio-Grassiotto et al, 2001a, 2003). Moreover, long midpiece and long cytoplasmic sheath attached to one side of the nucleus have been found in the species of Glandulocaudinae (Burns et al, 1998) except for species of *Mimagoniates* (Burns et al, 1998; Pecio & Rafinski, 1999) that have a short cytoplasmic sheath. The cytoplasmic sheath has a variable length among teleosts (for review, see Quagio-Grassiotto et al, 2001a).

The situation of mitochondria shows considerable variation among teleosts. They are located either adjacent to the caudal pole of the nucleus and surround the initial segment of the axoneme and separated from it by the cytoplasmic canal as in many teleosts (see Shahin, 2006a, b, c). However, they can be situated in the nuclear indentation as in the flounder (Jones & Butler, 1988), many blenniid species (Lahnsteiner & Patzner, 1990; Silveira et al, 1990) and several eels (Mattei & Mattei, 1974; Todd, 1976; Gwo et al, 1992), close to the nucleus near the centriolar complex (Mattei et al, 1995) or close to the nucleus and laterally in relation to the flagellum as in *P. altivelis* (Gwo et al, 1994a). In *C. auratus*, the mitochondria lie close to the base of the nucleus and surround the initial segment of the axoneme and are separated from the flagellum by the inner mitochondrial envelope, which closely adheres to the flagellar plasma membrane due to the disappearance of the cytoplasmic canal.

Progressive condensation and compaction of chromatin occur in *C. auratus* during spermiogenesis. In early stages, the chromatin appears as irregular, coarse, dense granules, which gradually aggregate together into a coarse, compact highly electron-dense homogeneous matrix characteristic to the nucleus of the early spermatozoa. Changes in the pattern of nuclear chromatin condensation during spermiogenesis have previously been reported in many teleosts (Billard, 1983; Lou & Takahashi, 1989; Silveria et al, 1990; Gwo & Gwo, 1993; Pecio & Rafiński, 1999; Quagio-Grassiotto et al, 2001a, b; Shahin, 2006a, b, c). Iatrou & Dixon (1978) interpreted the progressive alterations of chromatin packing as the result of the transformation of nuclear basic proteins.

The nuclear chromatin in spermatozoan heads is widely different in appearance among fishes (for more details see Tab. 1.).

Chrysichthys auratus possesses heterogeneously compact coarse granular patches, with irregularly shaped electron-dense thick fibers and electron-lucent lacunae. Similar chromatin has been found in some Characiformes (see Matos et al, 1993; Mattei et al,

Tab. 1 Species of teleost possessing different types of chromatin

Chromatin type	Species name	Literature reference
Dense, homogeneous and compact	*Cyprinus carpio*	Billard (1970)
	Carassius auratus	Fribourgh et al (1970) and Baccetti et al (1984)
	Rhodeus sericeus sinensis	Guan & Afzelius (1991)
	Goodeidae	Grier et al (1978)
	Poecilia latipinna	Grier (1973)
	Gambusia affinis	Grier (1975)
	Blenniidae	Lahnsteiner & Patzner (1990) and Silveira et al (1990)
	Argyropelecus gigas	Thiaw et al (1990)
	Cymatogaster aggregate	Gardiner (1978)
	Characoden lateralis	Grier et al (1978)
	Jenysia lineate	Dadone & Narbaitz (1967)
	Labidesthes sicculus	Grier et al (1990)
	Acanthopagrus schlegeli	Gwo et al (1993) and Gwo & Gwo (1993)
	Acanthopagrus latus	Gwo (1995)
	Diplomystes mesembrinus	Quagio-Grassiotto et al (2001a)
	Anguilla japonica	Gwo et al (1992)
	Merluccius merluccius	Medina et al (2003)
Granular and heterogeneous	*Liza aurata*	Brusle (1981)
	Oreochromis niloticus	Lou & Takahashi (1989)
	Oncorhynchus tshawtscha	Zirkin (1975)
	Salvelinus fontinalis	Fribourgh (1978)
	Coregonus wartmanni	Stein (1981)
	Oncorhynchus mykiss	Billard (1983)
	Micropongius undulates	Gwo (1989) and Gwo & Arnold (1992)
	Chanos chanos	Gwo et al (1995)
	Oncorhynchus masou formosanus	Gwo et al (1996)
	Epinephelus malabaricus and *Plectropomus leopardus*	Gwo et al (1994b)
	Plecoglossus altivelis	Gwo et al (1994a)

1995；Aires, 1998；Burns et al, 1998；Romagosa et al, 1999；Zaiden, 2000；Veríssimo-Silveira, 2003；Shahin, 2006a) as well as in the siluriformes *M. electricus* and *S. schall* (Shahin, 2006b, c), however, in *M. electricus* the chromatin is condensed only in the posterior part of the nucleus.

In the present study, the midpiece of *C. auratus* was found to contain several spherical and elongate vesicles located around the mitochondria and extending backwards around the base of the flagellum. Similar findings have been found in the midpiece of many Characiformes spermatozoa (for details, see Quagio-Grassiotto et al, 2003；Shahin, 2006a) and in the siluriform *M. electricus* (Shahin, 2006b), however the vesicles do not extend beyond the midpiece around the flagella. However, *C. auratus* entirely lacks the "lattice tubule" described by Mattei et al (1995) in *Citharinus* sp., or the membranous compartment found in the initial region of the flagellum of some Characiformes (Quagio-Grassiotto et al, 2003) as well as some Cypriniformes (Baccetti et al, 1984；Kim et al, 1998；Lee & Kim, 1998) and also the flagellar lateral fins or intratubular differentiations occurred in some teleosts (Mattei, 1988, 1991；Jamieson, 1991). In addition, the alar sheets radiating from the basal body triplets and joining it to the plasma membrane, which have been observed in *E. malabaricus* and *P. leopardus* (Gwo et al, 1994b) and *A. latus* (Gwo, 1995), are not present in *C. auratus*. Nevertheless, the basal body is anchored to the nucleus on both sides by a basal foot. Similar occurrence of the basal foot has also been described in *A. dentex* (Shahin, 2006a), *E. malabaricus* and *P. leopardus* (Gwo et al, 1994b) and *A. latus* (Gwo, 1995). The nuclear notch and the fibrous bodies observed in some teleosts (see Shahin, 2006a) that serve to attach the centriolar complex to the nucleus are totally absent in *C. auratus*, however the proximal centriole is anchored to the nucleus with numerous anchoring fibrils. This is the same as is reported for both *M. electricus* and *S. schall* (Shahin, 2006b, c). It is probable that both the anchoring fibrils, and the basal foot, function in the attachment and stabilization of the tail, thereby enabling the centriole to withstand the torque generated by the movement of the flagellum (Gwo, 1995).

It is evident that both the spermiogenic stages and mature spermatozoon of *C. auratus* have many compound features, which seem to be derived from those of

types I and II spermiogenesis (Mattei, 1970, 1988). The most peculiar of these features are: 1) the absence of nuclear rotation and development of the centriolar complex and the initial region of the flagellum directly perpendicular to the basal pole of the nucleus; 2) the absence of the basal plate in the base of the basal body; and 3) the presence of numerous peripheral vesicles, which surround the midpiece and the base of the flagellum. These features could be regarded as unique for this species, although some of them, such as the formation of the cytoplasmic canal in the spermatids and its disappearance in the mature spermatozoon, have been previously mentioned in some species of the Siluriformes (Quagio-Grassiotto & Carvalho, 2000; Quagio-Grassiotto et al, 2001a) Until now, some of these features have been found in either Cypriniformes, Characiformes or even in Salmoniformes and Gonorynchiformes, except the development of the centriolar complex and the initial region of the flagellum directly perpendicular to the basal pole of the nucleus which has been recently scored in *M. electricus* and *S. schall* (Shahin, 2006b, c). None of these features have been described in the other Siluriformes. Therefore, it can be concluded that spermiogenesis in *C. auratus* is a synapomorphic type derived from types I and II spermiogenesis of Mattei (1970). In addition, it can be regarded as a novel type, designated as type III. The considerable similarities of spermiogenic stages and some spermatozoan features of this species to those of *M. electricus* and *S. schall* (Shahin, 2006b, c) indicate that they are closely related to each other. The similarities to some members of the Cypriniformes, Characiformes and Gonorynchiformes, support the hypothesis that the Otophysi, the Siluriformes and Characiformes, are sister-groups to the Cypriniformes (Fink & Fink, 1996) and to the Gonorynchiformes (Fink & Fink, 1981).

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References:

Aires ED. 1998. Características Morfológicas e Histofisiológicas da via Espermática da Piracanjuba, *Brycon orbignyanus* (Pisces, Teleostei) [M]. Ph. D. Dissertation, Botucatu: Universidade Estadual Paulista.

Andrade RF, Bazzoli N, Rizzo E, Sato Y. 2001. Continuous gametogenesis in the neotropical freshwater teleost, *Bryconops affinis* (Pisces: Characidae) [J]. *Tissue Cell*, **33**: 524–532.

Baccetti B. 1985. Evolution of the sperm cell [A]. In: Metz CB, Monroy A. Biology of Fertilization, Vol 2 [M]. Orlando: Academic Press, 3–58.

Baccetti B. 1986. Evolutionary trends in sperm structure [J]. *Comp Biochem Physiol*, **85**: 29–36.

Baccetti B, Burrini AG, Callaini G, Gibertini G, Mazzini M, Zerunian S. 1984. Fish germinal cells: I. Comparative spermatology of seven cyprinid species [J]. *Gamete Res*, **10**: 373–396.

Billard, R. 1970. Ultrastructure comparee de spermatozoides de quelques poissons teleosteens [A]. In: Baccetti B. Comparative Spermatology [M]. New York: Academic Press, 71–79.

Billard R. 1983. Ultrastructure of trout spermatozoa: Changes after dilution and deep freezing [J]. *Cell Tissue Res*, **228**: 205–218.

Billard R. 1986. Spermatogenesis and spermatology of some teleost fish species [J]. *Reprod Nutr Dev*, **26**: 877–920.

Brusle S. 1981. Ultrastructure of spermatogenesis in *Liza aurara* Risso, 1810 (Teleostei, Muglidae) [J]. *Cell Tissue Res*, **217**: 415–424.

Burns JR, Weitzman SH, Lange KR, Malabarba LR. 1998. Sperm ultrastructure in characid fishes (Teleostei: Ostariophysi) [A]. In: Malabarba LR, Reis RE, Vari RP, Lucena ZM, Lucena CAS. Phylogeny and Classification of Neotropical Fishes [M]. Porto Alegre: Edipucrs, 235–244.

Dadone L, Narbaitz R. 1967. Submicroscopic structure of spermatozoa of a cyprinodontiform teleost, *Jenysia lineata* [J]. *Z Zellforsch*, **80**: 214–219.

Fink SV, Fink WL. 1981. Interrelationships of Ostariophysan teleost fishes [J]. *Zool J Linn Soc London*, **72**: 297–353.

Fink SV, Fink WL. 1996. Interrelationships of Ostariophysan fishes [A]. In: Stiassny MLJ, Parenti LR, Johnson GD. Interrelationships of Fishes [M]. San Diego: Academic Press, 209–249.

Franzen A. 1970. Phylogenetic aspects of the morphology of spermatozoa and spermatogenesis [A]. In: Bacaetti B. Comparative Spermatology [M]. New York: Academic Press, 26–46.

Fribourgh JH. 1978. Morphology of the brook trout spermatozoon as determined by scanning and transmission electron microscopy [J]. *Prog Fish-Cult*, **40**: 26–29.

Fribourgh JH, McClendon DE, Soloff BL. 1970. Ultrastructure of the goldfish, *Carassius auratus* (Cyprinidae) spermatozoa [J]. *Copeia*, **2**: 274–279.

Gardiner DM. 1978. Fine structure of the spermatozoon of the viviparous teleost, *Cymatogaster aggregata* [J]. *J Fish Biol*, **13**: 435–438.

Ginzburg AS. 1968. Fertilization in Fishes and the Problem of Polyspermy, 1st ed [M]. Moscow: Academy of Science.

Grier HJ. 1973. Ultrastructure of the testis in the teleost *Poecilia latipinna* spermatogenesis with reference to the intercentriolar lamellated body [J]. *J Ultrastruct Res*, **45**: 82–92.

Grier HJ. 1975. Spermatogenesis in the teleost *Gambusia affinis* with particular reference to the role played by microtubules [J]. *Cell Tissue Res*, **165**: 89–102.

Grier HJ, Fitzsimons JM, Linton JR. 1978. Structure and ultrastructure of the testis and sperm formation in goodeid teleosts [J]. *J Morphol*, **156**: 419–438.

Grier HJ, Moody HJ, Cowell BC. 1990. Internal fertilization and sperm morphology in the brook silverside, *Labidesthes sicculus* [J]. *Copeia*, **1**: 221–226.

Guan TL, Afzelius BA. 1991. The spermatozoon of the Chinese bitterling, *Rhodeus sericeus sinensis* (Cyprinidae, Teleostei) [J]. *J Submicrosc Cytol Pathol*, **23**: 351–356.

Gwo JC. 1989. Cryopreservation of Atlantic croaker spermatozoa: Optimization of procedures, evaluation of morphological changes and sssessment of motility [D]. Ph. D. Dissertation, Texas: Texas A and M University, College Station.

Gwo JC. 1995. Spermatozoan ultrastructure of the teleost fish *Acanthopagrus latus* (Perciformes: Sparidae) with special reference to the basal body [J]. *J Submicrosc Cytol Pathol*, **27**: 391–396.

Gwo JC, Arnold CR. 1992. Cryopreservation of Atlantic croaker spermatozoa: Evaluation of morphological changes [J]. *J Exp Zool*, **264**: 444–453.

Gwo JC, Gwo HH. 1993. Spermatogenesis in the black porgy (Teleostei, Perciformes, Sparidae) [J]. *Mol Reprod Dev*, **36**: 75–83.

Gwo JC, Gwo HH, Chang SL. 1992. The spermatozoon of the Japanese eel, *Anguilla japonica* (Teleostei, Anguilliformes, Anguillidae) [J]. *J Submicrosc Cytol Pathol*, **24**: 571–574.

Gwo JC, Gwo HH, Chang SL. 1993. The ultrastructure of *Acanthopagrus schlegeli* spermatozoon [J]. *J Morphol*, **216**: 29–33.

Gwo JC, Lin XW, Kao YS, Chang HH. 1994a. The ultrastructure of ayu, *Plecoglossus altivelis*, spermatozoon (Teleostei, Salmoniformes, Plecoglossidae) [J]. *J Submicrosc Cytol Pathol*, **26**: 467–472.

Gwo JC, Gwo HH, Kao YS, Lin BH, Shih H. 1994b. Spermatozoan ultrastructure of two species of grouper *Epinephelus malabaricus* and *Plectropomus leopardus* (Teleostei, Perciformes, Serranidae) from Taiwan [J]. *J Submicrosc Cytol Pathol*, **26**: 131–136.

Gwo JC, Lin XW, Kao YS, Chang HH, Su MS. 1995. The ultrastructure of milkfish, *Chanos chanos* (Forsskål), spermatozoon (Teleostei, Gonorynchiformes, Chanidae) [J]. *J Submicrosc Cytol Pathol*, **27**: 99–104.

Gwo JC, Lin XW, Gwo HH, Wu HC, Lin PW. 1996. The ultrastructure of Formosan landlocked salmon, *Oncorhynchus masou formosanus*, spermatozoon (Teleostei, salmoniformes, salmonidae) [J]. *J Submicrosc Cytol Pathol*, **28**: 33–40.

Iatrou K, Dixon GH. 1978. Protamine messenger RNA: Its life history during spermatogenesis in rainbow trout [J]. *Fed Proc*, **37**: 2526–2533.

Jamieson BGM. 1981. The Ultrastructure of the Oligochaeta [M]. London: Academic Press.

Jamieson BGM. 1991. Fish Evolution and Systematics: Evidence from Spermatozoa [M]. Cambridge: Cambridge University Press.

Jamieson BGM, Grier HJ. 1993. Influences of phylogenetic position and fertilization biology on spermatozoal ultrastructure exemplified by exocoetoid and poeciliid fish [J]. *Hydrobiologia*, **271**: 11–25.

Jaspers EJ, Avault JW, Russell JD. 1976. Spermatozoal morphology and ultrastructure of channel catfish, *Ictalurus punctatus* [J]. *Trans Am Fish Soc*, **105**: 475–480.

Jones PR, Butler RD. 1988. Spermatozoon ultrastructure of *Platichthys flesus* [J]. *J Ultrastruct Mol Struct Res*, **98**: 71–82.

Justine JL. 1991. Phylogeny of parasitic platyhelminthes: A critical study of synapomophies proposed on the basis of the ultrastructure of spermiogenesis and spermatozoa [J]. *Can J Zool*, **69**: 1421–1440.

Kim KH, Kwon AS, Lee YH. 1998. Spermatozoal ultrastructure and phylogenetic relationship of the subfamily Gobioninae (Cyprinidae) 2. Ultrastructure of spermatozoa in the Korean gudgean, *Squalidus chankaensis tsuchigae* [J]. *Korean J Limnol*, **31**: 159–164.

Lahnsteiner F, Patzner RA. 1990. Spermiogenesis and structure of mature spermatozoa in bleniid fishes (Pisces, Blenniidae) [J]. *J Submicrosc Cytol Pathol*, **22**: 565–576.

Lee YH, Kim KH. 1998. Ultrastructure of spermatozoa in *Pungtungia herzi* [J]. *Dev Reprod*, **2**: 141–148.

Lou YH, Takahashi H. 1989. Spermatogenesis in the Nile tilapia *Oreochromis niloticus* with notes on a unique pattern of nuclear chromatin condensation [J]. *J Morphol*, **200**: 321–330.

Magalhães ALB de. 1998. Gametogénesis e reproducão de Galeocharax knerii (Steindachner, 1879) (Pisces, Characidae) nos reservatórios de Furnas e Itumbiara: Estudo biométrico, histológico e ultra-estrutural [M]. M. Sc. Dissertation, Belo Horizonte: Universidade Federal de Minas Gerais.

Maggese MC, Cukier M, Cussac VE. 1984. Morphological changes, fertilizing ability and motility of *Rhamdia sapo* (Pisces, Pimelodidae). Sperm induced by media of different salinities [J]. *Revista Brasil Biol*, **44**: 541–546.

Mansour N, Lahnsteiner F, Patzner CA. 2002. The spermatozoon of the African catfish: Fine structure, mobility, viability and behavior in seminal vesicle secretion [J]. *J Fish Biol*, **60**: 545–560.

Matos E, Matos P, Oliveria E, Azevedo C. 1993. Ultraestrutura do espermatozóide do pacu, *Metynnis maculates* Kner, 1860 (Pisces, Teleostei) do rio Amazonas [J]. *Revista Brasil Cién Morfol*, **10**: 7–10.

Matos E, Matos P, Santos MNS, Azevedo C. 1998. Aspectos morfológicos e ultraestruturais do espermatozóide de *Curimata inornata* Vari, 1989 (Pisces, Teleostei) do rio Amazonas [J]. *Acta Amaz*, **28**: 449–453.

Matos E, Matos P, Corral L, Azevedo C. 2000. Estrutura fina do espermatozóide de *Acestrorhyncus falcatus* Bloch (Teleostei, Characidae) da região norte do Brasil [J]. *Revista Brasil Zool*, **17**: 747–752.

Mattei C. 1970. Spermiogeneses comparee des poisons [A]. In: Baccetti B. Comparative Spermatology [M]. New York: Academic Press, 57–69.

Mattei X. 1988. The flagellar apparatus of spermatozoa in fish: Ultrastructure and evolution [J]. *Biol Cell*, **63**: 151–158.

Mattei X. 1991. Spermatozoon ultrastructure and its systematic implications in fishes [J]. *Can J Zool*, **69**: 3038–3055.

Mattei C, Mattei X. 1974. Spermiogenesis and spermatozoa of the elopomorpha (teleost fish) [A]. In: Afzelius BA. The Functional Anatomy of the Spermatozoon [M]. New York: Pergamon Press, 211–221.

Mattei X, Marchand B, Thiaw OT. 1995. Unusual midpiece in the spermatozoon of the teleost fish, *Citharinus* sp [J]. *J Submicrosc Cytol Pathol*, **27**: 189–191.

Medina A, Megina C, Abascal FJ, Calzada A. 2003. The sperm ultrastructure of *Merluccius merluccius* (Teleostei, Gadiformes): Phylogenetic considerations [J]. *Acta Zool* (*Stockholm*), **84**: 131–137.

Negrão JNC. 1999. Aspectos Ultraestruturais da Espermatogĕnese da Traira, *Hoplias malabaricus* (Pisces, Erythrinidae) [M]. M. Sc. Dissertation, Botucatu: Instituto de Biociĕncias, Universidade Estadual Paulista.

Nicander L. 1970. Comparative studies on the fine structure of vertebrate spermatozoa [A]. In: Baccetti B. Comparative Spermatology [M]. New York: Academic Press, 47–62.

Pecio A, Rafiński J. 1999. Spermiogenesis in *Mimagomiates barberi* (Teleostei: Ostariophysi: Characidae), an oviparous, internally fertilizing fish [J]. *Acta Zool* (*Stockholm*), **80**: 35–45.

Poirier GR, Nicholson N. 1982. Fine structure of the testicular spermatozoa from the channel catfish, *Ictalurus punctatus* [J]. *J Ultrastruct Res*, **80**: 104–110.

Quagio-Grassiotto I, Carvalho ED. 2000. Ultrastructure of *Sorubim lima* (Teleostei, Siluriformes, Pimelodidae) spermiogenesis [J]. *J Submicrosc Cytol Pathol*, **32**: 629–633.

Quagio-Grassiotto I, Oliveira C, Gosztonyi AE. 2001a. The ultrastructure of spermiogenesis and spermatozoa in *Diplomystes mesembrinus* [J]. *J Fish Biol*, **58**: 1623–1632.

Quagio-Grassiotto I, Negrão JNC, Carvalho ED, Foresti F. 2001b. Ultrastructure of spermatogenic cells and spermatozoa in *Hoplias mal-*

abaricus (Teleostei, Characiformes, Erythrinidae) [J]. *J Fish Biol*, **59**: 1494–1502.

Quagio-Grassiotto I, Gameiro MC, Schneider T, Malabarba LR, Oliveira C. 2003. Spermiogenesis and spermatozoa ultrastructure in five species of the Curimatidae with some considerations on spermatozoal ultrastructure in the Characiformes [J]. *Neotrop Ichthyol*, **1**: 35–45.

Romagosa E, Narahara MY, Borella MI, Barreira SF, Fenerich-Verani N. 1999. Ultrastructure of the germ cells in the testis of matrinxã, *Brycon cephalus* (Teleostei, Characidae) [J]. *Tissue Cell*, **31**: 540–544.

Shahin AAB. 2006a. Spermatogenesis and spermatozoon ultrastructure in the Nile Pebblyfish *Alestes dentex* (Teleostei: Characiformes: Alestidae) in Egypt [J]. *World J Zool*, **1** (1): 1–16.

Shahin AAB. 2006b. Semicystic spermatogenesis and biflagellate spermatozoon ultrastructure in the Nile electric catfish *Malapterurus electricus* (Teleostei: Siluriformes: Malapteruridae) [J]. *Acta Zool* (*Stockholm*), **87**: 215–227.

Shahin AAB. 2006c. Spermatogenesis and spermatozoon ultrastructure in the Nile catfish *Synodontis schall* (Teleostei: Siluriformes: Mochokidae) in Egypt [J]. *Acta Zool Sinica* (In press).

Silveira H, Rodrigues P, Azevedo C. 1990. Fine structure of the spermatogenesis of *Blennius pholis* (Pisces, Blenniidae) [J]. *J Submicrosc Cytol Pathol*, **22**: 103–108.

Sprando RL, Heidinger RC, Russell LD. 1988. Spermiogenesis in the bluegill (*Lepomis macrochirus*): A study of cytoplasmic events including cell volume changes and cytoplasmic elimination [J]. *J Morphol*, **198**: 165–177.

Stein H. 1981. Licht-und elektronenoptische Untersuchungen an der Spermatozoen verschiedener Susswasserknochenfische (Teleostei) [J]. *Z Angew Zool*, **68**: 183–198.

Thiaw OT, Thiaw D, Mattei X. 1990. Extension of proximal centriole in a teleost fish spermatozoon [J]. *J Submicrosc Cytol Pathol*, **22**: 357–360.

Todd PR. 1976. Ultrastructure of spermatozoa and spermatogenesis in New Zealand freshwater eels (Anguillidae) [J]. *Cell Tissue Res*, **171**: 221–232.

Veríssimo-Silveira R. 2003. Ciclo Reproductivo e Cinética da Espermatogénese do Dourado (*Salminus maxillosus*, 1849) [M]. M. Sc. Dissertation, Jaboticabal: Universidade Estadual Paulista.

Zaiden SF. 2000. Morfologia Gonadal e Metabolismo Energético da Piraputanga *Brycon hilarii* (Cuvier e Valenciennes) (Pisces, Characidae) em Cativeiro, Durante o ciclo Reproductivo Annual [M]. Ph. D Dissertation, Jaboticabal: Universidade Estadual Paulista.

Zirkin BR. 1975. The ultrastructure of nuclear differentiation during spermatogenesis in the salmon [J]. *J Ultrastruct Res*, **50**: 174–184.

本刊编委徐林研究员简介

徐林研究员

徐 林，男，1963 年生于四川泸州，博士，中国科学院昆明动物研究所研究员，博士生导师，所动物模型和人类疾病机理重点实验室主任，所学术委员会主任。1985 年于四川南充师范学院生物系获学士学位；1989 年于中国科学院昆明动物研究所脑与行为实验室获硕士学位，1990—1992 年任研究实习员，1992—1994 年任助理研究员；同年到英国伦敦大学药学院药理系做访问学者，1995 年于爱尔兰三一学院攻读博士，1998 年获得博士学位。现任云南大学神经行为学、中南大学精神卫生研究所、中国科技大学博士生导师；中国科学院上海神经研究所客座研究员；中国神经科学学会“神经药理学专业委员会”副主任，中国生物物理学会理事，中国生理学会“生理心理学委员会”副主任；国家自然科学基金委、国家科技部聘任项目评审专家；十多种国际神经科学 SCI 杂志的评审专家。

其研究团队主要从事学习记忆机理和神经系统疾病药理学研究。系统研究了应激生活事件和应激异常记忆在精神疾病发生发展中的重要作用及其作用机制。其研究揭示了心理应激破坏了大脑某个脑区自身（如海马，杏仁核等）和多脑区间的神经可塑性稳态。神经可塑料稳态的丧失很可能是精神疾病（抑郁症、PTSD、精神分裂症、毒品成瘾等）行为/情绪异常表现的重要机制；同时利用各种精神疾病动物模型进行天然活性成分筛选及药理药效学研究。相关研究成果已发表在 *Nature*, *PNAS*, *Neuro Science Letters*, *J of Neurosci*, *Molecular Psychiatry* 等国际权威学术杂志。目前，已取得国际国内专利 2 项，发表 SCI 论文 27 篇，撰写和编辑专著 2 部；参加的国家 1035 新药攻关项目酚克络酮新药已获得国家一类新药临床试验证书。1994 年在英国药学院药理系参加 Lamotrigine 抗癫痫新药药理学研究，已获美国 FDA 批准临床新药。

徐林研究员曾获得科学院“百人计划”和杰出青年基金的资助。主持过国家 973 计划，多项国家自然科学基金、省市级项目数项，荣获 973 先进个人等多项荣誉。