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Morphofunctional organization of the male reproductive system of the catfish *Iheringichthys labrosus* (Lütken, 1874) (Siluriformes:Pimelodidae)

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Abstract. An anatomical, histological and ultrastructural study was made of the reproductive system and spermatogenesis of *Iheringichthys labrosus*. The testis are digitiform and consist of a spermatogenic cranial region, a spermatogenic/secretory medial (transition) region, and a strictly secretory caudal region. The cranial region represents 66% of the total length of the maturing testis and its fringes or lobes have a length of 5.59 ± 0.73 mm. The medial and caudal regions represent each 17% of the testicular length and their fringes have a length of 5.37 ± 0.69 mm and 3.12 ± 0.38 mm, respectively. Histologically, the cranial region of the testis is made up of seminiferous tubules with spermatogenic cells contained in cysts. These cells undergo synchronous development, inside the cysts where spermatogenesis is completed. The secretory caudal region does not constitute an individualized gland. Ultrastructurally, its secretory cells have a vesiculous nucleus and a cytoplasm with abundant dilated cisternae of rough endoplasmic reticulum. The caudal region produces a glycoproteic secretion and exhibits variable electron density during maturation. During the resting period, these cells are poor in synthesis organelles. The spermatozoa are of the primitive type, with a round head (1.56 ± 0.11 μm), a rudimentary middle piece, and a long flagellum with a 9+2 axonemal arrangement.

Keywords: Siluriformes, *Iheringichthys labrosus*, reproduction, spermatogenesis, testicular secretion

Introduction

The morphology of the reproductive system of male Siluriformes is highly diversified. In some families, spermatogenic cells are present along the entire length of the testis, whereas in other families the caudal region contains seminal vesicles or accessory structures that have no spermatogenic activity, but can store spermatozoa (Legendre et al., 1996). Also, the caudal region of the testis of some Siluriformes shows secretory activity, but does not store spermatozoa (Loir et al., 1989). Some Pimelodidae exhibit fringed testis during reproductive activity, with the spermatogenic cells being in asynchronous stages of development (Loir et al., 1989; Bazzoli et al., 1997). Knowledge of the anatomical differences between the reproductive systems of different teleosts may help in establishing the phylogenetic relationships between the species (Meisner et al., 2000). Furthermore, the morphology of the spermatozoa has been used for studying fish taxonomy and phylogeny (Jamieson, 1991; Mattei, 1991).

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The testis of teleosts have two compartments: a tubular compartment, which is made up of Sertoli cells and germinative cells, and an interstitial compartment, which is formed by connective tissue and Leydig cells (Grier, 1981). The Sertoli cells perform several functions to providing support and nutrition to the spermatogenic cells and, in addition they phagocytize residual spermatozoa (Billard, 1970). Neighboring Sertoli cells show membrane specializations such as interdigitations, desmosomes, and tight junctions, the latter being part of the blood-testis barrier (Abraham, 1980; Silva & Godinho, 1989; Pudney, 1993). The Leydig cells of teleosts, as in other vertebrates, have typical characteristics of steroid-secreting cells and increase in number over the period of gonodal development (Van Vuren & Soley, 1990; Arbuzova, 1995).

In this study, the morphofunctional pattern of the testis and the spermatogenesis of *I. labrosus* were analyzed using anatomical, histological and ultrastructural techniques, with a view to providing support to understand the reproduction of this species.

Materials and methods

Animals

One hundred and twenty-five males of *I. labrosus* captured bimonthly during 1998 in the Furnas reservoir (20°40'S; 46°19'W), state of Minas Gerais, southeast Brazil, were used. The specimens were fixed in 10% formaldehyde.

Anatomy

Maturing and resting testis were each divided into a cranial, a medial and a caudal region. The number and length of the fringes or lobes in each of these three regions of the maturing testis were determined using a pachymeter.

Light microscopy

Fragments of the cranial, medial and caudal regions of the testis were fixed in Bouin's fluid for 8–12 h, embedded in paraffin and glycol-methacrylate plastic resin, sectioned at 3–5 μm, and stained with hematoxylin-eosine and toluidine blue-1% sodium borate.

For detecting carbohydrates and proteins in the testis, classical histochemical techniques were used, i.e. PAS (Periodic Acid-Shiff), Alcian blue pH 0,5, Alcian blue pH 2.5 and ninhydrin-Schiff (Pearse, 1985).

The nuclear diameter of 100 spermatogenic cells in each stage of development was measured in 5 to 10 histological sections of maturing testis, using micrometry ocular lens associated with Zeiss microscopy.

Transmission electron microscopy

Fragments of the cranial, medial and caudal regions of testis in different stages of the reproductive cycle were fixed in 2.5% glutaraldehyde in 0.1M phosphate buffer at pH 7.2 and post-fixed in 1% osmium tetroxide and 1.5% potassium ferrocyanide. The specimens were embedded in epon/araldite, cut into ultrathin sections, stained with uranyl acetate and lead citrate, and examined under an EM-10 Zeiss microscope.

Statistical analysis

Significant differences in the length of the fringes between the three regions of the testis were determined using Student's *t*-test, with $P < 0.01$.

Results

The testis of *I. labrosus* are paired, digitiform organs which are anatomically related to the gaseous bladder cranially and to the kidneys caudally. Each maturing testis contains from 178 to 204 fringes or lobes ventrally oriented along its length (Fig. 1). The fringes communicate, singly or in pairs or groups of three, with the spermatic duct located in the central portion of each testis. The spermatic ducts of the right and left testis are joined at their caudal portion, forming the common spermatic duct, which extends to the urogenital papillae, situated caudally to the anal orifice.

The cranial region represents 66% of the total length of the maturing testis and its fringes have a length of 5.59 ± 0.73 mm. The medial (transition) and caudal regions represent each 17% of the testicular length and their fringes have a length of 5.37 ± 0.69 mm and 3.12 ± 0.38 mm, respectively. Student's *t*-test showed significant differences ($P<0.01$) between length of the fringes of the cranial and the caudal region ($t=30.03$) and between the medial and the caudal region ($t=28.6$); no significant differences were found between the cranial and medial regions.

In the maturing testis, the cranial region is spermatogenic (Fig. 2), the medial region is both spermatogenic and secretory (Fig. 3), and the caudal region is strictly secretory (Fig. 4). The secretion reacts positively to the PAS and ninhydrin-Schiff techniques, which indicates the presence of neutral glycoproteins. In the resting testis (Fig. 5), this secretion is absent (Figs 6, 7), and the lumen of the tubules becomes occluded.

The testis are surrounded by a tunica albuginea of connective tissue that emits septs to the interior of the organ, which delimit tubules. In the spermatogenic region, the wall of the seminiferous tubules is constituted by cysts, each of which contains spermatogenic cells in the same stage of development.

Primary spermatogonia (nuclear $\varnothing = 9.00 \pm 1.26$ μm): it is the largest of the spermatogenic cells, being only one per cyst. It has a central, vesiculous nucleus and a distinct nucleolus. Mitochondria, isolated or joined themselves by mitochondrial cementum (Fig. 8 and insert), are present in the cytoplasm.

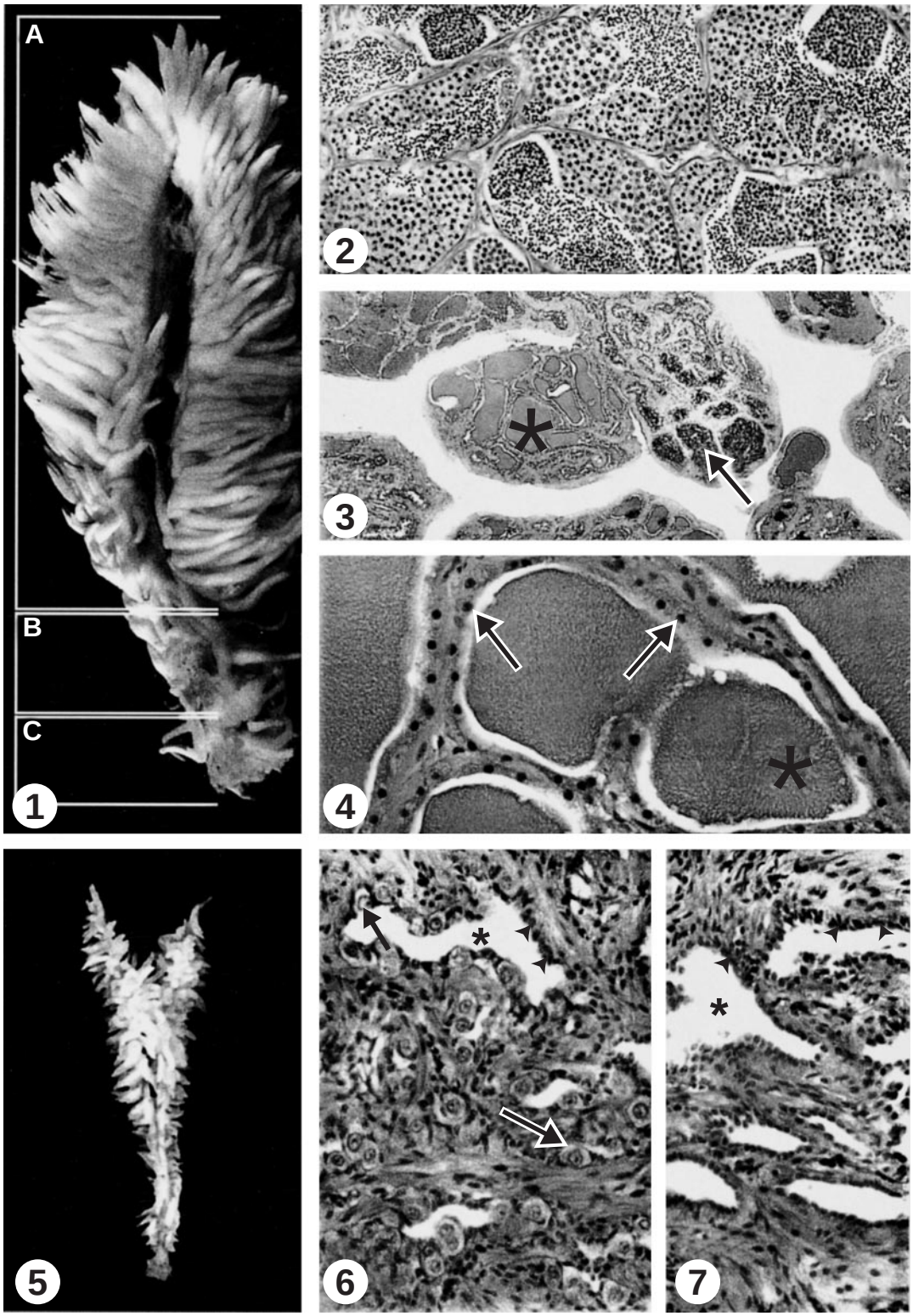

Fig. 1–7 Organization of the male reproductive system of *I. labrosus*. Toluidine blue-sodium borate (Figs 2–4) and hematoxylin-eosine (Figs 6–7). **Fig. 1** Fringed maturing testis with distinct regions: cranial (A), medial or transition (B), and caudal (C). ×2.8. **Fig. 2** Spermatogenic activity in seminiferous tubules of cranial region, with cysts of spermatogenic cells in different stages of development. ×78. **Fig. 3** Spermatogenic (arrow) and secretory (asterisk) activity in the fringes of the medial region. ×40. **Fig. 4** Strictly secretory activity in tubules of caudal region of testis: cubic cells in wall (arrow) and accumulation of secretion in lumen (asterisk). ×217. **Fig. 5** Fringed testis during resting period. ×2.8. **Fig. 6** Medial region of resting testis, with espermatogonia (arrow), secretory cells in tubule wall (arrowheads), and lumen with no secretion (asterisk). ×60. **Fig. 7** Caudal region of resting testis: tubule walls consisting of secretory cells only (arrowheads); lumen with no secretion (asterisk). ×60.

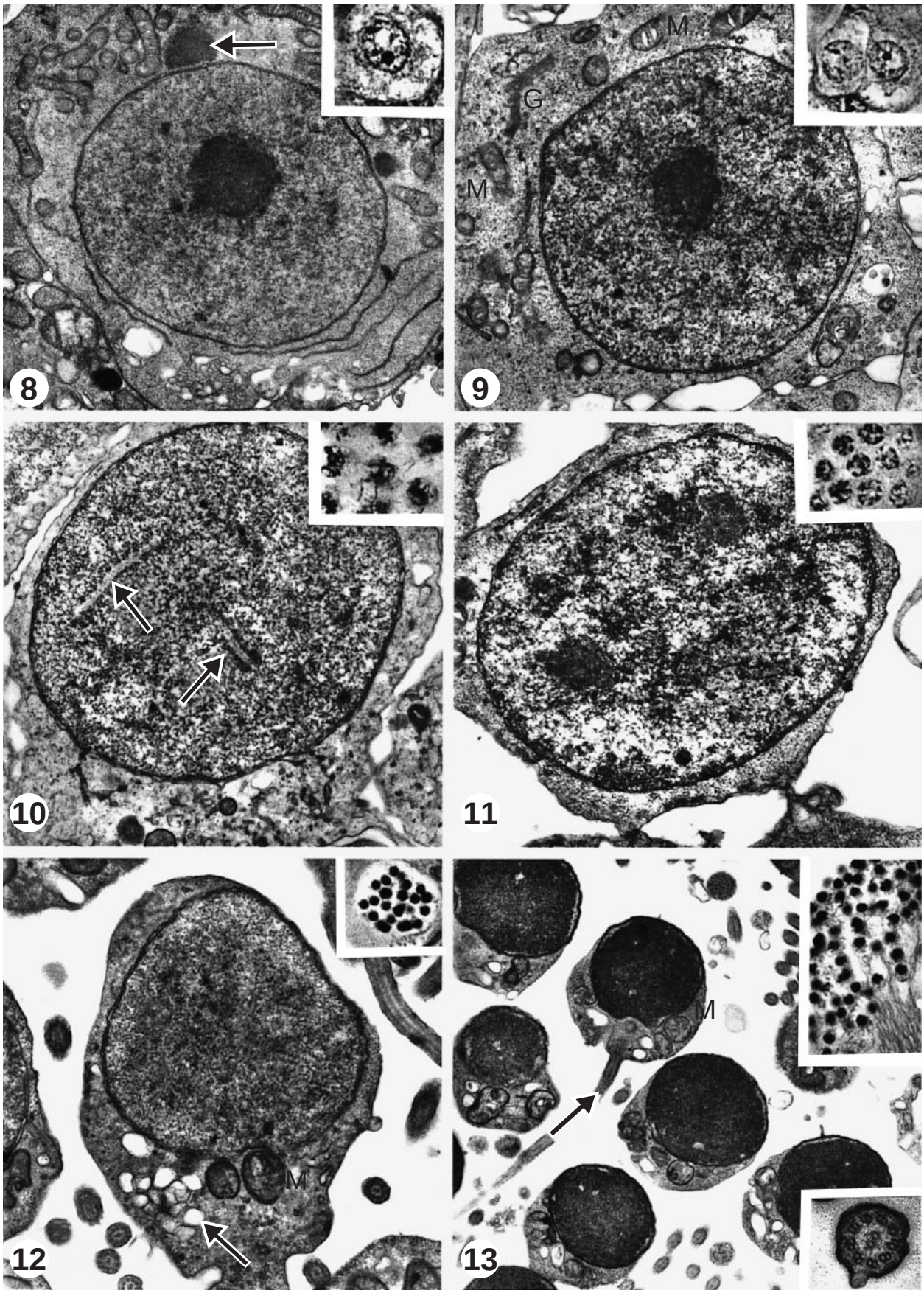
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Fig. 8–13 Ultrastructure of spermatogenic cells of *I. labrosus*. Insert: aspect of the nucleus in histological sections stained with hematoxylin-eosin. **Fig. 8** Primary spermatogonia: vesiculous nucleus and cytoplasm with mitochondria joined by mitochondrial cementum (arrow). ×10 680. Insert: ×880. **Fig. 9** Secondary spermatogonia: nucleus with loose chromatin and cytoplasm with few organelles. G = Golgi complex, M = mitochondria. ×13 440. Insert: ×880. **Fig. 10** Primary spermatocyte: nucleus with characteristic synaptonemal complexes (arrows). ×13 380. Insert: ×880. **Fig. 11** Secondary spermatocyte: nucleus with chromatin forming electron-dense clots. ×14 630. Insert: ×880. **Fig. 12** Intermediate-phase spermatid: eccentric nucleus and cytoplasm with electron-lucent vesicles (arrow) and mitochondria (M). ×17 116. Insert: ×880. **Fig. 13** Spermatozoa: round head with dense nucleus, middle piece with mitochondria (M), long flagellum (arrow). ×10 460. Insert: ×880. Lower insert: ultrastructure of flagellum showing microtubules in 9+2 axonemal arrangement. ×32 400.

Secondary spermatogonia (nuclear $\varnothing = 6.52 \pm 0.58\,\mu m$): these form cysts of two to four cells. They have a clear nucleus with loose chromatin, one or two nucleoli, and a cytoplasm with few organelles (Fig. 9 and insert).

Primary spermatocyte (nuclear $\varnothing = 4.34 \pm 0.55\,\mu m$): this cell originates from the last generation of secondary spermatogonia, after successive mitotic divisions. It has a dense cytoplasm, a nucleus with slightly condensed, granular chromatin and characteristic synaptonemal complexes. The latter consist each of two paralell, electron-dense strips referred as lateral arms and a medial electron-lucent strip (Fig. 10 and insert).

Secondary spermatocyte (nuclear $\varnothing = 3.21 \pm 0.41\,\mu m$): this originates from the first mitotic division of the primary spermatocyte. It has a scant cytoplasm, a central nucleus with chromatin forming electron-dense masses that may be scattered or clustered at either pole (Fig. 11 and insert).

Spermatid (nuclear $\varnothing = 2.36 \pm 0.48\,\mu m$): this cell has a scant cytoplasm with electron-lucent vesicles and a dense, round nucleus. Spermiogenesis is completed inside the spermatic cysts, releasing the spermatozoa intry the lumen of the seminiferous tubules. At the ultrastructural level, three stages of spermatid differentiation were observed: (1) initial stage: electron-dense nucleus and the cytoplasm shows intense vacuolization; (2) intermediate stage: the nucleus is eccentric, electron-lucent vesicles are present in the cytoplasm, and the implantation fossa has been formed (Fig. 12 and insert); and (3) advanced stage: the nucleus is very dense and the flagellum is in process of differentation.

Spermatozoon (nuclear $\varnothing = 1.56 \pm 0.11\,\mu m$): the smallest of the spermatogenic cells, the spermatozoon occurs in the lumen of the seminiferous tubules and testicular ducts. The spermatozoa have a round head and no acrosome. The middle piece is short and has few mitochondria. The flagellum is long and contains microtubules in 9+2 axonemal arrangement (Fig. 13 and insert).

Ultrastructurally, the secretory cells in the caudal region of the maturing testis exhibit a vesiculous nucleus and a cytoplasm with abundant distended cisternae of rough endoplasmic reticulum and lumen of the tubules is filled with secretion (Fig. 14 and insert). In the resting period, the cells of the caudal region show few synthesis organelles and the lumen of the tubules is empty or occluded (Fig. 15).

In general, the Sertoli cells have a triangular nucleus with chromatin often forming clots. The cytoplasm contains cisternae of rough endoplasmic reticulum, mitochondria, and free ribosomes. These cells emit cytoplasmic prolongaments that delimit the cysts (Fig. 16 and insert) and are connected by interdigitations, desmosomes, and tight junctions. In the spent testis, the Sertoli cells phagocytize residual spermatozoa (Fig. 17).

The interstitial tissue between the seminiferous tubules contains Leydig cells, connective tissue cells, myoid cells, collagenous fibrils, and blood capillaries. The myoid cells have an elongated shape and a fusiform nucleus and are arranged in discontinuous, concentric layers around the seminiferous tubules. The Leydig cells occur in groups and, at the ultrastructural level, exihibit a vesiculous nucleous and a cytoplasm with abundand smooth endoplasmic reticulum and mitochondria with tubular cristae (Figs. 18, 19).

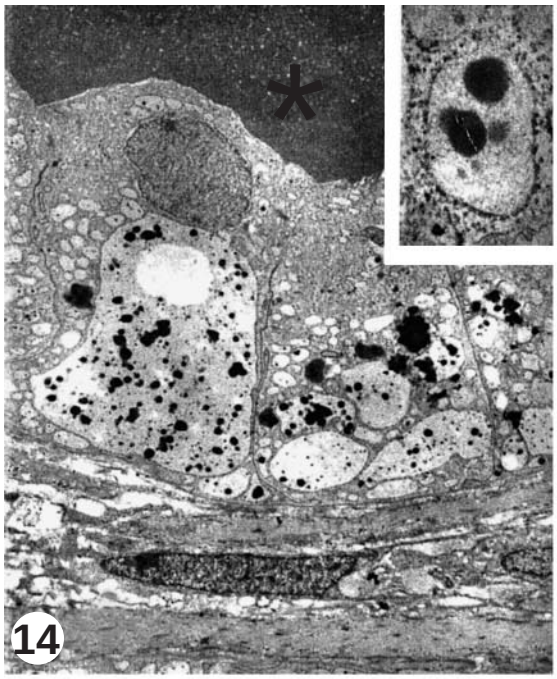
In testis in reproductive activity, the lumen of both the spermatic ducts of the caudal region and the common spermatic duct contains acidophilic secretion associated with the spermatozoa.

Discussion

Testis of *I. labrosus* present digitiform projections, or fringes, communicating with the spermatic duct. Fringed testis have been reported in several Siluriformes groups, including Ictaluridae (Sneed & Clemens, 1963); Clariidae (Siscar, 1970); Doradidae (Giese et al., 1999); Pimelodidae (Loir et al., 1989); and Auchenipteridae (Meisner et al., 2000).

In spite of its fringed aspect, the cranial region of the testis of *I. labrosus* is constituted by seminiferous tubules with spermatogenic cell cysts, similar to the pattern observed in the testis of most teleosts (Grier, 1981). Within the cysts, the spermatogenic cells undergo synchronous development, at which time they multiply, have their number of chromosomes reduced, and reorganize their cytoplasm, exhibiting a typical morphology in each stage of development (Pudney, 1993).

In *I. labrosus*, mitochondria were observed in the primary spermatogonia, isolated or joined themselves by mitochondrial cementum, which is made up of ribosomic RNA of nuclear origin (Clerot, 1979). The synaptonemal complexes in the primary spermatocytes are formed by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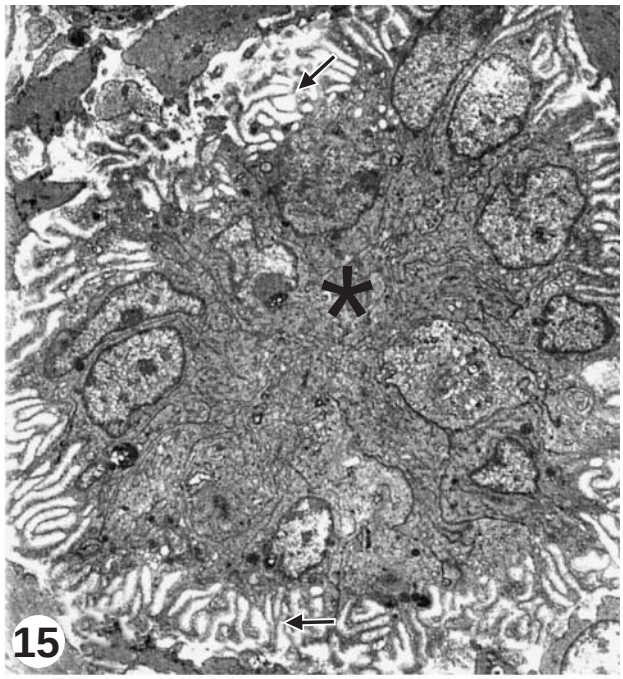
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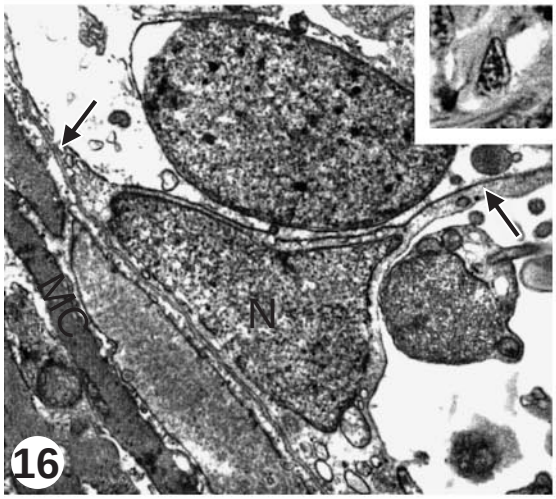
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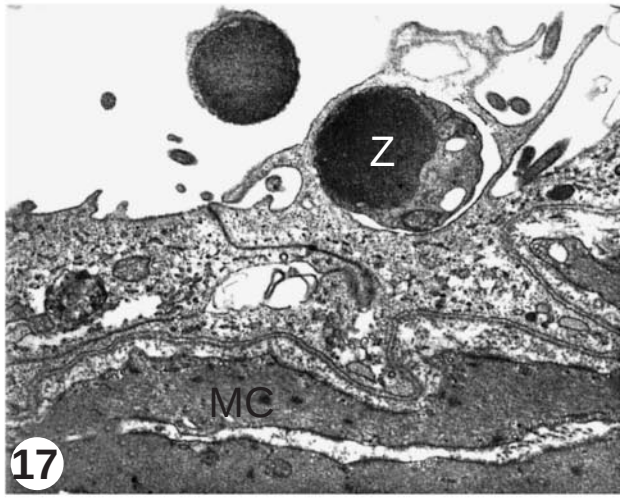
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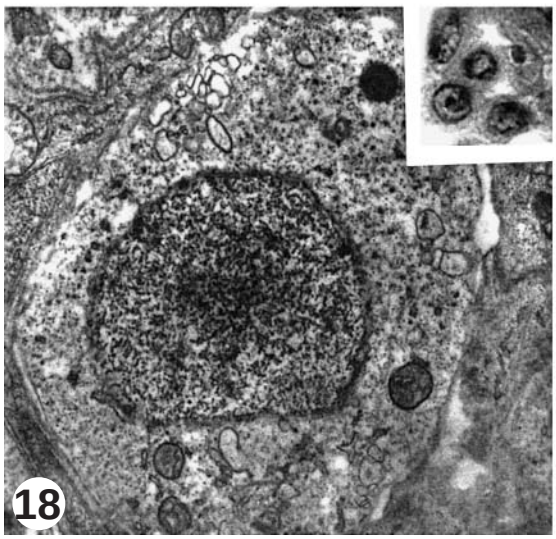
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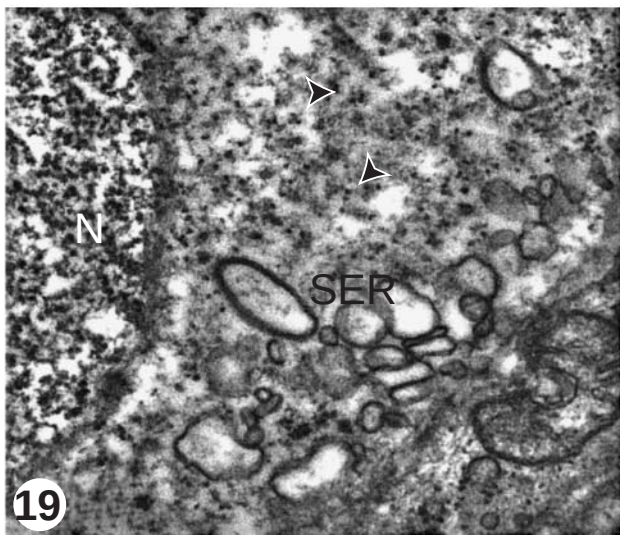
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Fig. 14–19 Ultrastructure of caudal region of testis, Sertoli cells and Leydig cells of *I. labrosus*. Inserts: histology of Sertoli and Leydig cells stained by hematoxylin-eosin. **Fig. 14** Secretory cells of caudal region of maturing testis. Vesiculous nucleus and cytoplasm with dilated cisternae of rough endoplasmic reticulum containing material of variable electron density. Lumen of tubule filled with secretion (asterisk). ×12 960. Insert: detail of rough endoplasmic reticulum cisternae. ×19 440. **Fig. 15** Tubule of caudal region of resting testis, with occluded lumen (asterisk) and wall consisting of secretory cells with cytoplasm containing few organelles, supported by a folded base membrane (arrows). ×2 480. **Fig. 16** Sertoli cell with a triangular nucleus (N) and cytoplasmic prolongaments (arrows) delimiting a cyst. MC = myoid cell. ×6980. Insert: ×880. **Fig. 17** Residual spermatozoon (Z) being phagocytized by Sertoli Cell. MC = myoid cell. ×9850. **Fig. 18** Leydig cell with vesiculous nucleus and cytoplasm containing smooth endoplasmic reticulum. ×11 700. Insert: ×350. **Fig. 19** Detail of cytoplasm of Leydig cell, with smooth endoplasmic reticulum (SER) and free ribosomes (arrowheads). N = vesiculous nucleus. ×25 050.

the pairing of homologous chromosomes during the first meiotic division (Grier, 1975). In the present study, similarly to the findings of Nagahama (1983), nuclear reorganization, cytoplasmic reduction, and formation of the flagellum were observed during spermiogenesis.

Based on its anatomical features – a round head, short middle piece with few mitochondria, and long flagellum – the *I. labrosus* spermatozoon can be considered as being of the primitive type, according to the classification criteria proposed by Billard (1970). Round-head spermatozoa occur in the Siluriformes exhibiting external fertilization, such as those of the family Pimelodidae, to which *I. labrosus* belongs, whereas spermatozoa with an elongated head occur in the families Ageneiosidae and Auchenipteridae, in which fertilization is internal (Loir et al., 1989).

The histological and ultrastructural characteristics of the Sertoli cells of *I. labrosus* suggest that, in addition to their supporting and synthesizing functions, these cells also phagocytize residual spermatozoa, which is in agreement with the reports of Pudney (1993). In *I. labrosus*, the wall of the cysts, which is made up of cytoplasmic prolongaments of the Sertoli cells, opens up to release the spermatozoa into the lumen of the seminiferous tubules. However, in some species, such release can occur in the secondary spermatocyte stage, as in *Notopterus notopterus* (Shrivastava, 1967), and in the spermatid stage, as in *Channa punctatus* (Srivastava & Singh, 1994). In the present study, tight junctions were observed in the membranes of adjacent Sertoli cells, which, according to Silva and Godinho (1989), constitute a blood–testis barrier that prevents macromolecules from migraty between neighboring Sertoli cell towards to the lumen of the seminiferous tubule, thus providing a micro-environment for the development of spermatogenesis (Abraham et al., 1980).

Spermatogenesis in fish is regulated by a neuroendocrine mechanism that involves interactions between Leydig cells, Sertoli cells and germ cells (Yaron, 1995; Miura, 1999). The Leydig cells of *I. labrosus* exhibit the cytological features normally associated with steroid–-secreting cells as an abundant smooth endoplasmic reticulum and mitochondria with tubular cristae. They can synthesize, produce or store secretion products that are necessary for spermatogenesis and expression of the secondary sexual characteristics (Payne et al., 1996).

The myoid cells of the testis of *I. labrosus* are arranged in discontinuous, concentric layers around the seminiferous tubules. The dense bodies and microfilaments contained in their cytoplasm may act in the contraction of the seminiferous tubules. The presence of desmine in the cytoplasm of the myoid cells of the testis of carp confirms the contractile nature of these cells (Yaron, 1995).

The secretory activity in the testis of some families of Siluriformes has been attributed to specialized structures or regions. The secretory tissue of the caudal region of the testis of *I. labrosus* is diffuse and does not form a conspicuous gland. In some Siluriformes of the families Pimelodidade, Loricariidae and Callichthyidae, secretory activity occurs also in the caudal portion, with or without a seminal vesicle being formed (Loir et al., 1989). In the families Heteropneustidae, Clariidae and Auchenipteridae, seminal vesicles occur also in the caudal region of the reproductive system (Siscar, 1970; Meisner et al., 2000). In fishes of other non-Siluriformes families, seminal vesicles in the Gobiidae (Lahnsteiner et al., 1992) and testicular glands in Blenniidae (Richtarski & Patzner, 2000) have been reported.

Glycoprotein secretion by the cells of the tubules in the caudal region of the testis of *I. labrosus* was observed during the period of maturation. Judging from its nature, this secretion may have similar functions to that of the seminal vesicles that occur in other groups of teleosts. The seminal vesicles can produce glycoproteins, steroid hormones, and pherormone that increase the volume of semen and may act in the fertilization and attraction of females (Van Den Hurk et al., 1987; Lahnsteiner et al., 1992). The morphology of epithelial cells of the testis and also its secretory aspect indicate that they are perhaps homologous to the Sertoli cells (Loir et al., 1989).

In summary, the unusual organization of the reproductive system of *I. labrosus* – presence of testicular fringes, distinct testicular regions, secretion stored in caudal region without constitute an individualized gland can provide useful criteria for phylogenetic analysis of the Siluriformes.

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