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ULTRASTRUCTURAL CHANGES IN SERTOLI CELLS IN OHRID TROUT – *SALMO LETNICA* (KARAMAN) DURING THE PRESPAWNING AND POSTSPAWNING PERIOD

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Summary

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A cytological analysis based on ultrastructural findings in some regions of Ohrid trout` testes – *Salmo letnica* (Karaman) in the prespawning and postspawning period, with a special emphasis of Sertoli cells, was performed.

Sertoli cells, being an integral part of the seminiferous lobules underwent considerable changes, which influenced their cytomorphological features. The cells with endotheliomorphic appearance, characteristic for the prespawning period, gradually increase their dimensions. Lipid vacuoles of different size were noticed in their cytoplasm, while the nuclei acquired a polymorphic appearance.

In the seminiferous lobules with rare sperm residues Sertoli cells underwent further changes which caused their involution. The degenerative changes of Sertoli cells were manifested by an extreme vacuolisation, mitochondria with desintegrated crysts or mitochondria in degeneration (with widened crysts and thickened matrix), by desorganised endoplasmic reticulum, digestive vacuoles (autophagosomes), "myeline-like" structures and lysed cytoplasmic regions. The above mentioned changes were followed by karyopyknosis, complete degeneration and delamination of cells from the wall of the seminiferous lobules, lysis and detritus formation (Sertoli necrotic material) in the lumen of the lobules.

The degeneration of Sertoli cells was followed by destruction of the basal membrane of the lobules.

Key words: Ohrid trout, *Salmo letnica* (Karaman), Sertoli cells

INTRODUCTION

The number of authors having described the structural and functional characteristics of Sertoli cells in different Teleostei species is noticeable (Billard, 1970; Bilard *et al.*, 1972; Nicols & Graham, 1972; Gresik *et al.*, 1973; Hurk *et al.*, 1975; Grier & Linton, 1977; Mattei *et al.*, 1982; Cruz-Hofling & Cruz-Landim, 1984; Dimovska *et al.*, 1990; Russell & Griswold, 1993).

However, literature data about the changes in the testes in the postspawning period in different species of Teleostei, i. e. changes which occur immediately affter the spawning, and even later, are less (Billard, 1970; Billard *et al.*, 1972; Hurk *et al.*, 1975; Dimovska *et al.*, 1986, 1987;

Tavciovska-Vasileva, 1992, 1993, 1994; Dimovska & Tavciovska-Vasileva, 1996; Tavciovska-Vasileva & Dimovska, 1996).

The studies about the annual reproductive cycle in natural and experimental conditions in trouts (Salmonidae), are also relatively few (Henderson, 1962; Hurk *et al.*, 1978; Billard, 1983; Nakamura *et al.*, 1993; Russell & Griswold, 1993; Loir, 1994). The Sertoli cells were analysed in the postspawning period when their phagocytotic role was remarkable (Hurk *et al.* 1978).

The lack of literature data concerning the testes of Ohrid trout - *Salmo letnica* (Karaman) (Tavciovska-Vasileva & Dimovska, 1996; Dimovska & Tavciovska-Vasileva, 1996) has motivated this research.

On the other hand, the Ohrid trout was chosen as an object of research because of its big economic significance for the Ohrid Lake and due to the fact that it represents a relic and endemic species of this lake.

MATERIALS AND METHODS

Testes of sexually mature male Ohrid trout caught in the Ohrid Lake within a period of 3 years (1993/1996) were analysed by electronic microscopy. Small parts of testes (1–2 mm) were used. The material was prepared using the following procedure: Immediately after obtaining tissue specimens, they were fixed in 3% glutaraldehyde and then conserved in 0.1 M phosphate buffer for 12 hours. After adequate fixation, the material was submitted to postfixation in 1% osmium tetraoxide (OsO_4). Further, the material was washed in phosphate buffer, dehydrated in series of acetone and uranyl acetate, and then dehydrated in dry acetone. The tissue sections were infiltrated with Durcopan ACM mixture, mixture of acetone – Durcopan, Durcopan № 1, Durcopan № 2, fit in Durcopan № 2 and polymerized.

For the ultrastructural analysis, ultrathin section of 40–60 ηm were prepared using glass knives, on Reichert–Yung "Ultracut" ultramicrotom, installed on copper nets and contrasted with uranyl acetate and lead citrate.

The sections were observed on Tesla BS 500 and OPTON (Zeis) EM 109 electronic microscope. The microphotographs for electronic microscopy were obtained on Agfa Scientia EM Film 23056/6.5×9 cm, ORWO NP 20 panchromatic 120, Kodak 120 and made on Agfa Papirtone Paper P1–3.

RESULTS

Prespawning period

In the prespawning period, the Sertoli cells which covered completely the seminiferous lobules, were maximally extended are characterised with endotheliomorphic (squamous) appearance.

It is difficult to distinguish the cytoplasmic territory of Sertoli cells in Ohrid trouts in this period. Sertoli cells could be however easily noticed on the level of lobules because of their characteristic nuclei, which were of euchromatic type in the prespawning period, and had a well visible nucleolus, which was in contact with the nuclear membrane and a bright cytoplasm. This showed their activity.

With their basal part, Sertoli cells lied on a smooth basal plate. On the level of the Sertoli cells, an initial vacuolisation was observed (presence of vacuoles with small dimensions, but in some species vacuoles with bigger dimensions could be noticed).

Postspawning period

In the postspawning period the most important changes in testes of Ohrid trouts occured on the level of Sertoli cells, being in the structure of lobules, as somatic component.

Compared to the prespawning period in which Sertoli cells were characterised with an endotheliomorphic appearance, as the process of involution of seminiferous lobules continued, in the postspawning period, they gradualy lost the endotheliomorphic form, increased their dimensions and acquired polymorphic nuclei. The presence of lipid vacuoles of different sizes was evident in their cytoplasm.

At an ultrastructural level, a nucleus with prominent nucleolus could be seen in the Sertoli cells' cytoplasm (Fig. 1). On the surface of the nucleus there was a nuclear cover (Fig. 2). Mitochondria with lamelar crysts, lysosomes, as well as lipid droplets of different sizes could also be observed (Fig. 3).

Also, at an ultrastructural level, the cell membrane between the adjacent Sertoli cells (Fig. 4), the basal lamina of the seminiferous lobules themselves (Fig. 5), as well as interdigitations between the Sertoli cells were clearly noticed (Fig. 6).

One of the functions of Sertoli cells is phagocytosis of the sperm residues. The presence of transversal cut fragments of flagellumes of sperm residues in the cytoplasm of Sertoli cells (Fig. 7) or phagolysosomes with already digested material of sperm origin (Fig. 8) supported this fact.

In the later phase of the life cycle of Sertoli cells, a more distinct vacuolisation of their cytoplasm could be observed, which caused a degeneration of these somatic cells, characterised by karyopyknosis. The final phases of Sertoli cells' life cycle were followed by delamination (exfoliation, desquamation) from the wall of the lobules, desintegration and complete destruction of the cells, presence of residues (detritus) in the lumen of the seminiferous lobules, as well as lysis. Desintegration and destruction of some Sertoli cells (torn cell borders, presence of

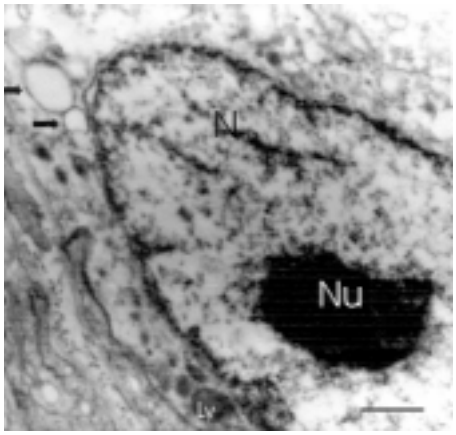

Fig. 1. A part of cytoplasm of Sertoli cell with well visible nucleus (N), prominent nucleolus (Nu), vesicles of smooth endoplasmatic reticulum (black arrows) and lysosomes (Ly). Ultrathin section, bar = 1 μm.

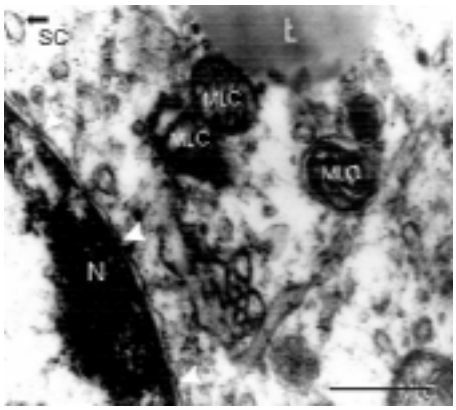

Fig. 2. Cytoplasm of Sertoli cell (SC) with motochondria with lamelar crysts (MLC), vesicles of smooth endoplasmatic reticulum (black arrow), lipid droplets (L) and nucleus (N) with nuclear memebrane on its surface (white arrow). Ultrathin cection, bar = 1 μm.

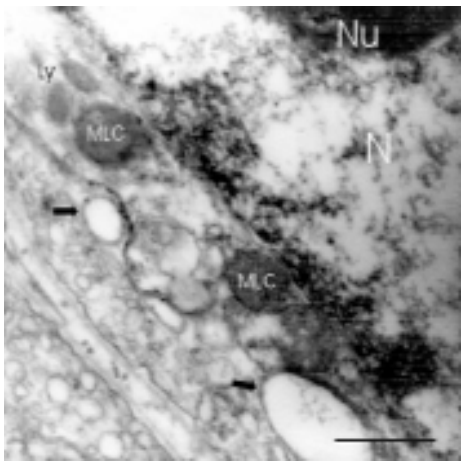

Fig. 3. A part of Sertoli cell with well visible nucleus (N), prominent nucleolus (Nu), mitochondria with lamelar crysts (MLC), vesicles of smooth endoplasmic reticulum (black arrows) and lysosomes (Ly). Ultrathin section, bar = 1 μm.

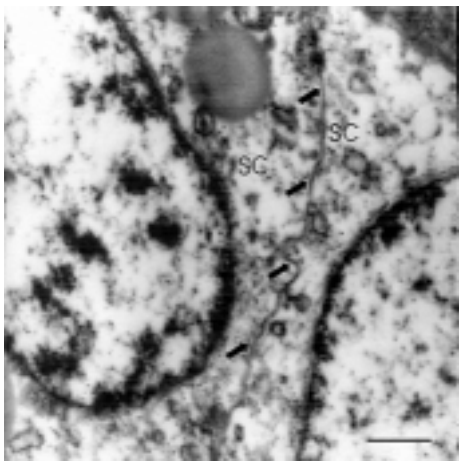

Fig. 4. Clearly visible cell membrane (black arrows) between two adjacent Sertoli cells (SC). Ultrathin section, bar = 1 μm.

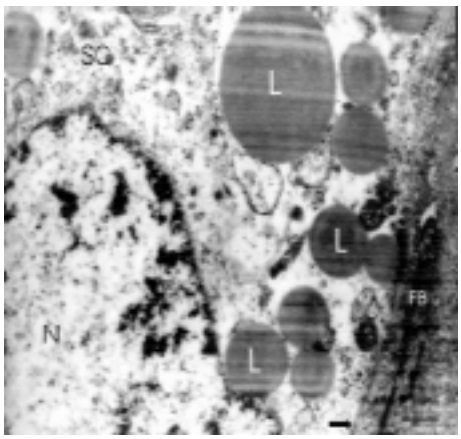

Fig. 5. A part of Sertoli cell (SC). Presence of lipid droplets (L) with different size and well visible nucleus (N). The basal lamina of the lobule (black arrow) and presence of one fibroblast (FB) near the basal lamina are visible. Ultrathin cestion, bar = 1 μm.

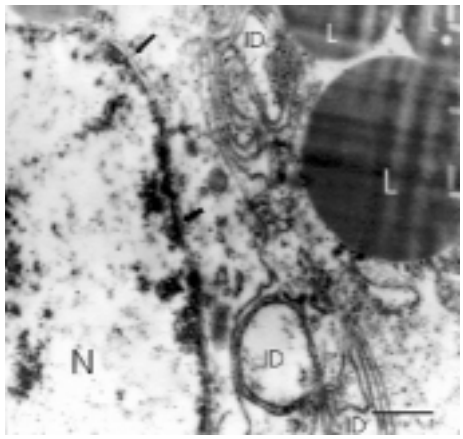

Fig. 6. Interdigitations (ID) between two adjacent Sertoli cells, lipids (L) in the cytoplasm and prominent nucleus (N) with well seen nuclear membrane (black arrows). Ultrathin section, bar = 1 μm.

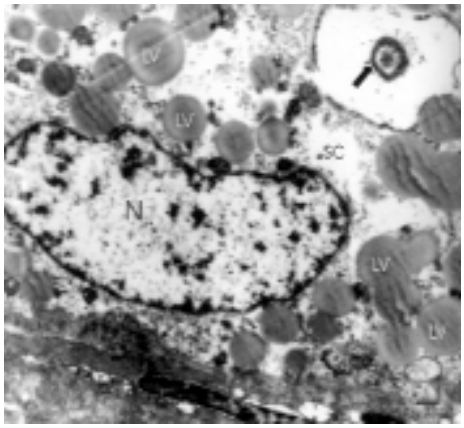

Fig. 7. A part of cytoplasm of Sertoli cell (SC) with well seen nucleus (N) and lipid vacuoles (LV) of different size. Presence of transfersally cut fragments of flagellumes of sperm residues (black arrow). Ultrathin section, bar = 1 μm.

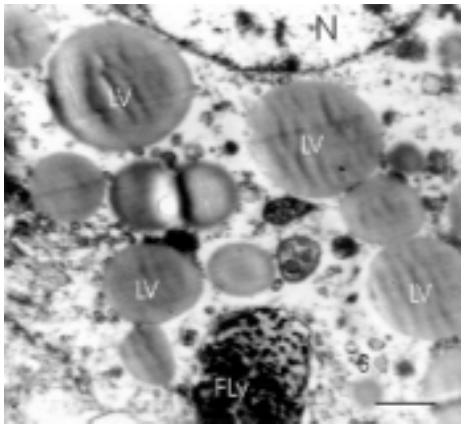

Fig. 8. A part of Sertoli cell cytoplasm with phagolysosomes (FLy) with sperm residual material. Presence of lipid vacuoles (LV) of different size and a part of nucleus (N) of the Sertoli cell are also visible. Ultrathin section, bar = 1 μm.

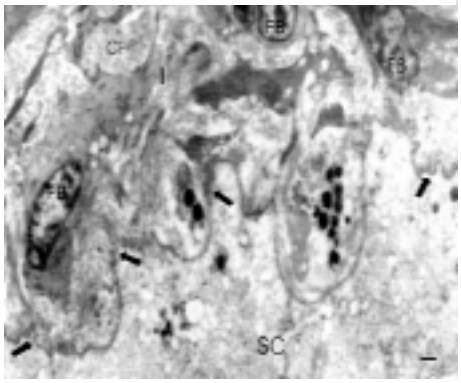

Fig. 9. Well distingushed interstitium (I) with fibroblast (FB) and collagenous fibers (CF). A part of Sertoli cell (SC) cytoplasm in degeneration is seen, as well as the basal lamina (black arrow) of the lobule. Ultrathin section, bar = 1 um.

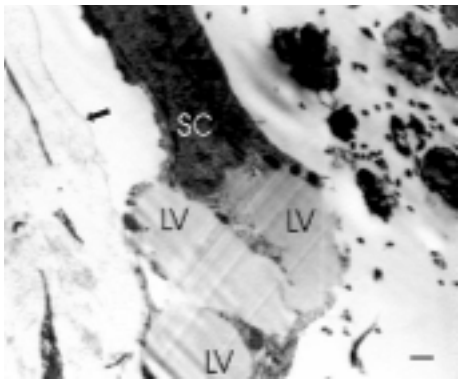

Fig. 10. Sertoli cell (SC) in degeneration. Presence of lipid vacuoles (LV) in the cytoplasm and separation of cytoplasm from basal membrane (black arrow) are visible. Ultrathin section, bar = 1 μm.

vesicular nucleus, or nucleus in pyknosis with emphasized hyperchromatic characteristics, undifferentiated nucleolus) were evident on ultrathin sections (Fig. 9).

The degeneration of the cells was followed by detachment of the nuclear membrane, a process which was well distinguished at an ultrastructural level (Fig. 10).

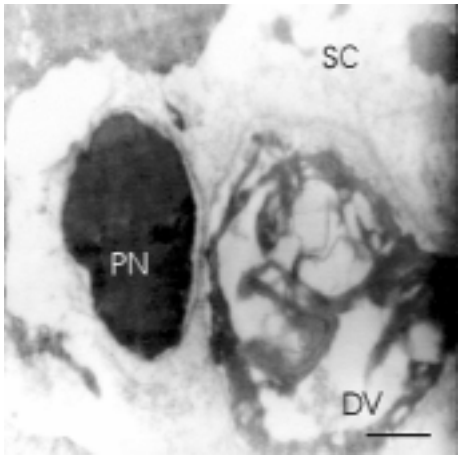

Fig. 11. A part of cytoplasm of Sertoli cell (SC) in degeneration with a pyknotic nucleus (PN) and a digestive vacuole (DV). Ultrathin section, bar = 1 μm.

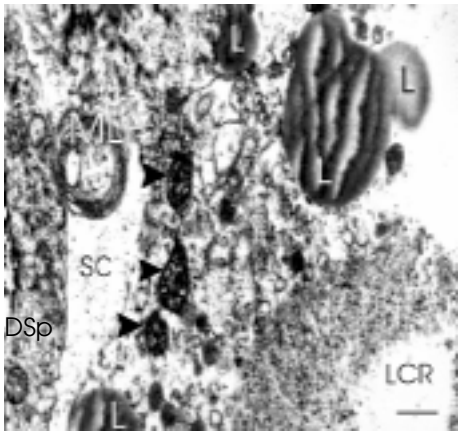

Fig. 12. A part of cytoplasm of Sertoli cell (SC) in degeneration, with lysosomes with "myeline-like" figures (MLF), lysed cytoplasmic regions (LCR), mitochondria in degeneration (black arrows), lipid droplets (L) with different size. A part of one spermatogonium in degeneration (DSp) is shown. Ultrathin section, bar = 1 μm.

In the cytoplasm of Sertoli cells in degeneration, excluding the presence of pyknotic nucleus, digestive vacuoles (autophagosomes) were noticed, indicative for autophagia occuring on the level of these cells (Fig. 11).

On ultrathin sections the degeneration of Sertoli cells was demonstrated by a presence of lysosomes with "myeline-like" figures in their cytoplasm, endoplasmic reticulum in desorganisation, mitochondria with initial signs of degeneration (with widened crysts and thickened matrix), hyaloplasm with granular structure, and lysed cytoplasmic regions (Fig. 12). All these changes, occuring on the level of Sertoli cells showed their degeneration in the postspawning period.

DISCUSSION

The ultrastructural analysis of testes of Ohrid trouts during the prespawning and postspawning periods showed certain features which provided a characteristic histological picture of testes in these periods.

In postspawning period visible changes on the level of the seminiferous lobules, especially in the Sertoli cells were observed. All these changes occured successively. In the initial phase of the postspawning period that followed directly after the spawning, sperm residues were still present in the lumen of seminiferous lobules. As changes progressed, degeneration of Sertoli cells took place. The mentioned changes, especially those which happened in the final phase of the postspawning period (at a sufficient extent) changed the histoarchitectonics of testes, in comparison with the prespawning period. On the basis of consequent characteristic changes which happened on the level of the testes in the postspawning period in Ohrid trouts, we concluded that this was a period of reorganisation of the testes.

The seminiferous lobules underwent important transformations in the post-

spawning period. As a somatic component of the seminiferous lobules Sertoli cells suffered significant degenerative changes which caused their involution, i. e. involution of seminiferous lobules themselves. This process in Salmonidae is repeating every year. The seminiferous lobules and the Sertoli cells themselves, in Salmonidae, are not constant elements of testes, but temporary formations which are formed every year after the spawning.The findings of this study confirmed our preliminary investigations (Tavciovska-Vasileva & Dimovska, 1996; Dimovska & Tavciovska-Vasileva, 1996) on changes which happen on the level of testes of Ohrid trouts – collapsing and desintegration of the lobules, degeneration, i. e. involution of the Sertoli cells, etc.

This process was also noted in other Teleostei (Turner, 1919; Van Oordt, 1925; Hann, 1927; Weisel, 1943; Dimovska *et al.*, 1986, 1987; Tavciovska-Vasileva, 1992; Russell & Griswold, 1993). Therefore, our results support the difference between mentioned species and mammals, where seminiferous lobules or tubules are constant elements of the testes. There are literature data for different Teleostei species which point out the presence of degenerative changes of Sertoli cells during the postspawning period. After phagocytosis of the residual bodies by Sertoli cells, the latter suffer lipid degeneration, i. e. involution. So, in *Perca flavescens* Mitch. an involution of the seminiferous tubules in the postspawning period was described, which in an indirect way points to involution of Sertoli cells (as a unique somatic component of the tubules in this period) (Turner, 1919). Also, similar statements were given about the fate of the Sertoli cells after the finished sexual cycle with *Perca fluviatilis macedonica* K a r. by Dimovska *et al.* (1986, 1987, 1990) and Tavciovska-Vasileva (1992).

After the expulsion of sperm cells in the lumen of the tubules, in several species of Teleostei, Sertoli cells suffer lipid degeneration, and probably, finaly are resorbed (Lofts & Marshall, 1957; Stanley *et al.*, 1965; Chan & Philips, 1967; Billard *et al.*, 1972; Belsare, 1973; Nagahama *et al.*, 1978; Yeung *et al.*, 1985). Similarly, it was also pointed out that in *Cymatogaster aggregata,* many Sertoli cells suffer degeneration (Wiebe, 1968, 1969; Gardnier, 1978). The degeneration of Sertoli cells in some species of Atheriniformes, as *Poecilia reticulata* was also described (De Felice & Rasch, 1969; Billard, 1970).

According to Turner (1919) the genesis of seminiferous tubules in Teleostei during their embrionic development is similar to that in mammals.

Recently the phenomenon of the life cycle of Sertoli cells has been noted by other authors, not only with Teleostei, but in other low Vertebrata as well (Lofts, 1972). However, the fact is that a small number of authors have dealt with this problem. Relatively few authors have treated the postspawning period, (the changes which happen immediately after the spawning, and later) (Billard, 1970, Billard *et al.*, 1972; Hurk *et al.*, 1975; Dimovska *et al.*, 1986, 1987; Tavciovska-Vasileva, 1992, 1993, 1994; Dimovska & Tavciovska-Vasileva, 1996; Tavciovska-Vasileva & Dimovska, 1996).

Our investigations in Ohrid trouts pointed out that directly after the spawning, similarly to other examined Teleostei, an intensive phagocytosis of sperm residues by Sertoli cells took place. The phagocytic activity of these somatic elements of seminiferous lobules was accompanied at the same time by numerous

changes which reflected upon their cytomorphological appearance. In the prespawning period, Sertoli cells are characterized with endotheliomorphic (squamous) appearance, whereas in the postspawning period, they gradually lost the endotheliomorphic form, and increased their dimensions. The presence of increased number of vacuoles of different sizes was evident in their cytoplasm. Close to or in contact with these Sertoli cells, and their cytoplasm numerous sperm residues were evident. In favour of this fact was the presence of transversally and longitudinally cut fragments of flagellumes of sperm residues in the cytoplasm of these cells and the lysis, which indicated the phagocytic role of these seminiferous lobules' somatic elements during this period of the year.

In Salmonidae the phagocytic activity of Sertoli cells in the postspawning period was reported in *Salmo salar* by Jones (1940), in *Salvelinus fontinalis* by Henderson (1962), in *Salmo gairdneri* by Hurk *et al.* (1978). The phagocytic activity of Sertoli cells was demonstrated also by the ultrastructural findings of Grier (1976, 1981) and Grier & Linton (1977).

Gresik *et al.* (1973) noticed presence of philopodia and residual bodies on the level of Sertoli cells in the postspawning period in *Oryzias latipes*. The presence of philopodia and residual bodies of Sertoli cells has been also pointed out in Poecilidae, *Lebistes reticulatus* (Vaupel, 1929), *Poecilia latipina* (Grier, 1975; Pudney & Callard, 1984), *Mollinesia latipina* (Hurk *et al.*, 1975). The presence of philopodia in Sertoli cells of different species of Teleostei in the postspawning period was reported in *Esox lucius* (Lofts & Marshall, 1957), *Gobius paganelus* (Stanley *et al.*, 1965), *Cyclostoma nigrofaciatum* (Wiebe, 1968, 1969; Nicholls & Graham, 1972); in *Salmo trutta fario* and *Salmo gairdneri* by Billard *et al.* (1972), in *Oncorhynchus kisutch* and *Oncorhynchus gorbuscha* by Nagahama *et al.* (1978), in *Cymatogaster aggregata* (Gardiner, 1978).

The phagocytic activity of Sertoli cells in Ohrid trouts – *Salmo letnica* (Karaman) is characterized by subsequent considerable cytological changes, manifested by intensive vacuolisation of the cytoplasm, lipid degeneration, karyopyknosis, total destruction and delamination, lysis and presence of their residues in the lumen of the seminiferous lobules, mitochondria with desintegrated crysts, autophagosomes, "myeline-like" structures.

In Salmonidae similar statements concerning the definitive fate of Sertoli cells in the postspawning period were given by Weisel (1943) and Hurk *et al.* (1978). In their study on testes of *Salmo gairdneri* Hurk *et al.* (1978) pointed out that in the period of intensive phagocytic activity some Sertoli cells separating from the wall of tubules and undergoing degeneration could be observed.

CONCLUSIONS

The cytological analysis based on ultrastructural findings in some regions of testes of Ohrid trouts – *Salmo letnica* (Karaman) in the prespawning and postspawning period, with a special emphasis of Sertoli cells allowed us to conclude that:

1. Sertoli cells, as an integral part of the seminiferous lobules suffered considerable changes, changing their cytomorphological aspect. The cells with endotheliomorphic appearance, characteristic for the prespawning period, gradually increased their dimensions. Lipid vacuoles of different size were present in their cytoplasm while the nuclei acquired a polymorphic appearance.

2. The close contact of Sertoli cells with the sperm residues, as well as the presence of fragments of their flagellumes in cytoplasm of Sertoli cells, showed their phagocytic activity.

3. In seminiferous lobules with rare sperm residues, Sertoli cells suffered further changes which caused their involution.

4. The degenerative changes of Sertoli cells were manifested by extreme vacuolisation, mitochondria with desintegrated crysts or mitochondria in degeneration (with widened crysts and thickened matrix), with desorganised endoplasmic reticulum, digestive vacuoles (autophagosomes), "myeline-like" structures and lysed cytoplasmic regions. The above mentioned changes were followed by karyopyknosis, complete degeneration and delamination of the cells from the wall of the seminiferous lobules, lysis and formation of detritus (Sertoli cell necrotic material) in the lumen of the lobules.

5. The degeneration of Sertoli cells was followed by destruction of the basal membrane of the lobules.

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