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Histology and Cytology of Testes of the Catfish *Parasilurus aristotelis* (Siluridae, Teleostei) from Greece

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Abstract The morphology and histology of the catfish (*Parasilurus aristotelis*) testes were studied during the spawning period (March to August). Unlike other typical catfish, the testes of *P. aristotelis* are devoid of seminal vesicles. Both the cranial and caudal regions have a similar structure, with spermatogenic rather than secretory function. The main sperm duct of each unpaired testes is unusual in being divided into two parts: an upper one lined with germinal epithelium; and a short lower section lined with cuboidal epithelium. The seasonal reproductivity in this catfish is less pronounced than in other species. Its breeding season is protracted with continuous, asynchronous spermiogenesis. The testes histological structure resembles that of other teleosts. Observations revealed highly significant correlations ($p<0.01$; $p<0.001$) between: male body length and quantity of seminiferous tubules in a unit area of sectional surface; diameter of seminiferous tubules and their quantity; weight of testes and diameter of seminiferous tubules; and total number of seminiferous tubules vs. sperm-laden tubules.

The catfish *Parasilurus aristotelis* (Siluridae) is an endemic species found only in the freshwaters of west-central Greece, where it populates the Acheloos River as well as the lakes of the Etoloacarnania region (Berg, 1949; Ladiges and Vogt, 1979; Economidis, 1972-1973, 1991).

The species is commercial important not only in the above area but also in central and west Macedonia (North Greece), where catches are sent to the local fish cooperatives. For this reasons studies on the general biology of this species (Iliadou and Ondrias, 1986), and especially studies on its reproduction and gonads, are important for the understanding and preservation of population dynamics.

The gonads of teleost fish have been the subject of numerous histological investigations, although only a few such studies have been made of catfishes (Ghosh and Kar, 1952; Sathyanesan, 1959; Sneed and Clemens, 1963; Lehri, 1967; Nayyar and Sundararaj, 1970; Jaspers et al., 1978; Burke and Leatherland, 1984). Regarding gonad histology of the species *Silurus glanis* and *P. aristotelis*, representing the siluroid catfishes, only two works have been published: one of which (Shihshabekov, 1978) provides a brief report on the gonad histology of some freshwater species including *S. glanis*, from natural reservoirs in Dagestan, North Caucasus, USSR; the second work (Krasznai and Marian, 1986) offers some histological comments on the female gonads of *S. glanis* from Hungary.

Special interest in some reports (Sundararaj, 1958; Nawar, 1960; Rastogi, 1969; Sundararaj and Nayyar, 1969; Yoakim, 1976; Schoonen and Lambert, 1986; Van den Hurk et al., 1987; Fishelson et al., 1994) has been focused on the so-called seminal vesicles-accessory sexual glands attached to the testes in the male catfish. The function of these glands has not yet been entirely elucidated. Some authors (Sundararaj, 1958; Schoonen and Lambert, 1986; Resink et al., 1987; Fishelson et al., 1994) argue that the primary function of these vesicles is the production of a fluid that activates female responsiveness and thus improves fertilization.

The present paper provides a light microscopic description of *P. aristotelis* testes, together with observations on monthly changes in this organ throughout the spawning period.

Materials and Methods

During the spawning season (March to August) of 1992, samples of 15 to 20 specimens of *Parasilurus aristotelis* were collected from Lake Trichonis,

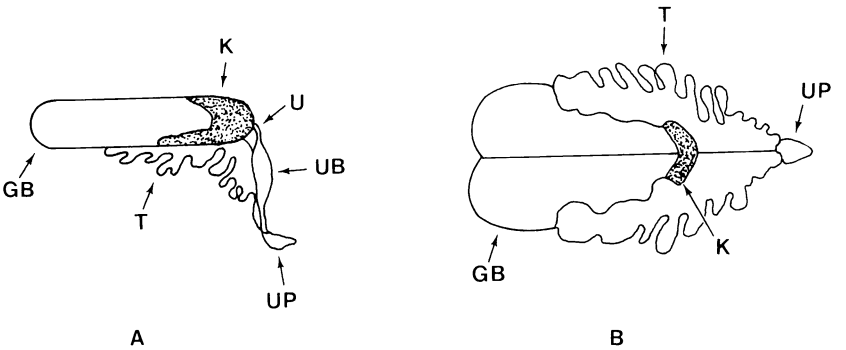

Fig. 1. Sketch of testes of *Parasilurus aristotelis* (natural size). A) Lateral and B) ventral view in abdominal cavity. *T*—testes; *UB*—urinary bladder; *U*—ureter; *K*—kidney; *GB*—gas bladder; *UP*—urinogenital papilla.

Greece. The fish were immediately sacrificed and male body and testes length and weight were measured. For histological studies, pieces were taken from anterior (cranial) and posterior (caudal) parts of each testis, fixed in Bouin's, then dehydrated separately, embedded in paraffin and sectioned at 10 μm. Cross- and longitudinal serial sections were stained with Ehrlich's haematoxylin and eosin and photographed with Leitz Ultramicroscope.

For statistical analysis, six microsections were taken from the anterior part of the testes of each of 24 specimens with monthly low and high gonosomatic index, and analysed using the s.c. point counting method (Weibel, 1979) as follows: a transparent sheet with only horizontal broken lines forming a net-square with 10 cm sides was placed over the screen of a videoscan microscope. From the screen it was possible to determine the total number of free points of broken lines that fell on the seminiferous tubules in the net-square; the number of free points located on the lumen and wall separately; as well as the number of total, full and empty seminiferous tubules in the net-square.

Using the above method, data were obtained for dimensions and density in relation to the fullness or emptiness of the seminiferous tubules in a unit area of sectional surface. The percentage of the total number of seminiferous tubules in the unit area and the mean diameter of one seminiferous tubule were also noted and used to determine testes activity. Simple statistics e.g. mean ($\bar{x}$), standard error (SE), standard deviation (D) and the correlation coefficient (r) were calculated to establish possible relations between these parameters and the standard male body length, testes weight and diameter of seminiferous tubule.

Results

Macromorphology of the testes.—The testes of *Parasilurus aristotelis* are paired organs, situated dorso-laterally to the alimentary canal and ventro-laterally to the kidney and gas bladder, occupying the posterior region of the abdominal cavity. They are suspended on the mesorchium which runs along the entire length of the testes.

Both testes possess a solid appearance. They are elongated and flattened structures, only slightly folded in young sexually mature males and strongly folded in adult fish, and are of almost equal size. They are separated from each other for almost two thirds of their length and becoming contiguous for the final one third, with the inner margins running adjacent to the median line (Fig. 1). At the hindmost region, just posterior to the urinary bladder, they form a common sperm duct leading immediately into the urinogenital papilla (Fig. 2A), which also encloses the urinary canal. A main testicular artery and vein run parallel to the median line with several branches leading to and from the testes.

Histology.—The testes are covered on the exterior with a vascular tunica of connective tissue and the interior is composed of a highly convoluted body of seminiferous tubules which anastomose to form a dense network (Fig. 2C). The tubules are separated from each other by wall of smooth muscle and collagenous fibres, blood capillaries and clusters of interstitial cells, the latter being mainly found where the intertubular space widens (Fig. 2B).

Histological examination of the anterior and posterior regions of the testes reveals a similarity in structure, with both regions possessing a network of seminiferous tubules, lined with germinal epithelium

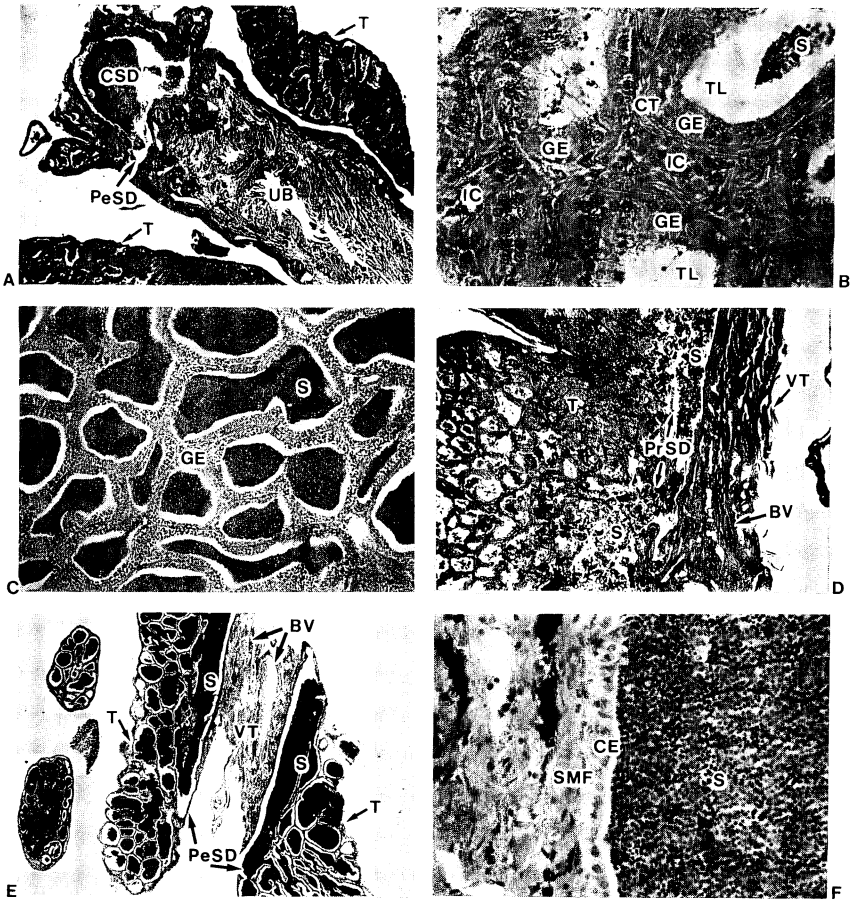

Fig. 2. Cytology of sperm duct and testes of *Parasilurus aristotelis.* A) Common sperm duct (CSD) posterior to urinary bladder (UB) (×30); B) simple layer of germinal epithelium (GE) on tubule wall and clusters of interstitial cells (IC) between contiguous tubules (×320); C) cranial (caudal) parts of testes (×80); D) provisional sperm duct (PrSD) in cranial region of unpaired testis during reproduction (×30); E) permanent sperm duct (PeSD) in caudal region of each of connected testes with sperm (×30); F) wall of common sperm duct (×320). *T*—testis; *TL*—tubule lumen; *S*—sperm; *CT*—connective tissue; *VT*—vascular tunica of connective tissue; *BV*—blood vessel; *SMF*—smooth muscle fibers; *CE*—cuboidal epithelium.

and a central lumen, empty or packed with sperm during the spawning period (Fig. 2C). There are no secretory regions in the testes, signifying that they are devoid of seminal vesicles.

The main sperm duct of each unpaired testis extends along the entire inner margin. On the anterior two thirds, where the two testes are not attached, the duct is formed from the interconnected, sperm-filled lumen of neighbouring tubules during the breeding season (Fig. 2D). In the final one third, where the testes are closely connected, the duct is formed from a specialized evagination of the tunica, which surrounds the testis and opens towards the gonad (Fig. 2E). The walls of these two parts of the main sperm duct—provisional and permanent—is histologically similar to that of the seminiferous tubules, being lined with germinal epithelium, lacking in the main testicular ducts of teleosts. In contrast, inside the urinogenital papilla, the wall of the short common sperm duct comprises smooth muscle fibres and is lined with a cuboidal epithelium (Fig. 2F).

The testes of *P. aristotelis* are of the unrestricted type, according to Grier et al. (1980), in which spermatogenesis occurs along the entire length of the tubules, beginning immediately beneath the tubular basement membrane (Fig. 3A). The testes exhibited

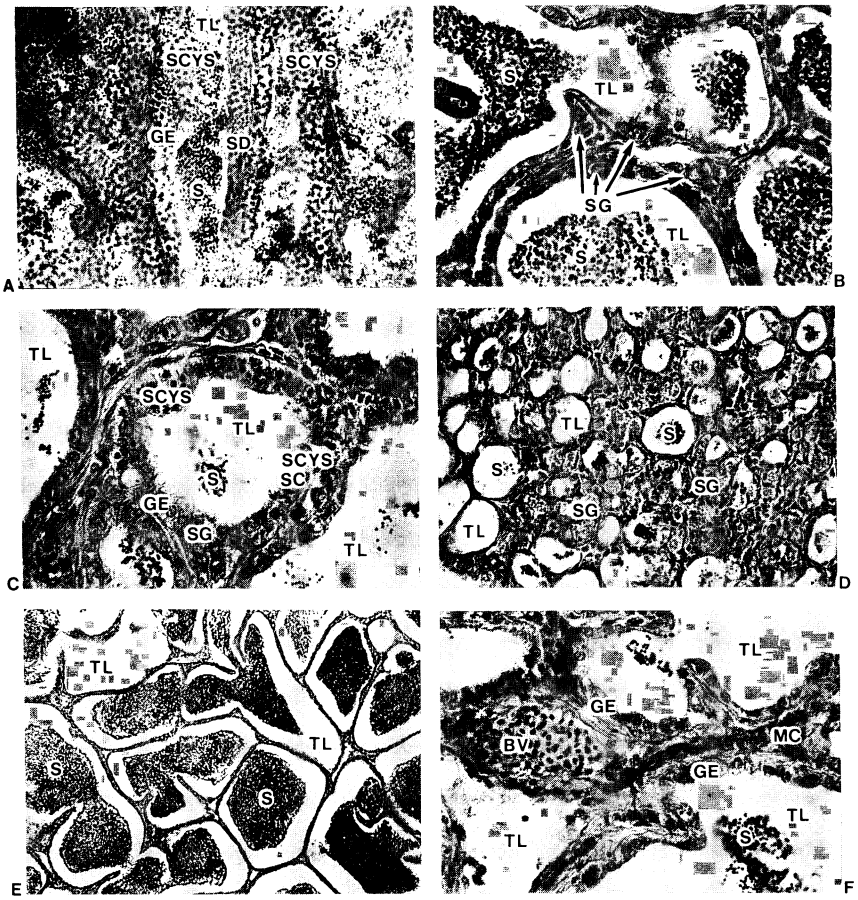

Fig. 3. Spermiogenesis in testes of *Parasilurus aristotelis.* A) Multilayer germinal epithelium (GE) with spermatocysts (SCYS) along tubules (×200); B) naked wall of tubules with single spermatogonia (SG) (×320); C) germ cells mitosis and sperm expulsion (×320); D) early stage of sexual maturation (×200); E) general view of cranial part of testes (×80) where communication between sperm-filled lumen of neighbouring tubules is seen; F) large blood vessel (BV) in regression and dark-stained melanocentres (MC) in interstitial cells (×320). *SC*—spermatocytes; *SD*—spermatids; *S*—sperm; *TL*—tubule lumen.

a definite seasonal cycle (Iliadou and Ondrias, 1986) but as revealed by histological sections, no sharp changes occurred during the spawning period and from March to August spermiogenesis was continuous. During this period some of the testes sampled from the fish were packed with ripe sperm and had very few or no cysts of germinal cells (Fig. 3B), whereas others had very little sperm in the tubules lumen but their walls were filled with cysts of maturing germ-cells (Fig. 3A). Spermatogenesis in this species is asynchronous as the testes revealed high numbers of spermatocysts at various stages of development, situated in close proximity (Fig. 3A, C). However, within the same cyst, germ-cells are found at approximately the same developmental stage, maturing in unison (Fig. 3C).

With the onset of ripening in each individual the tubule germ-cells become activated, completing the stages of maturation from single spermatogonia and a simple germinal layer of epithelium on the tubule wall (Fig. 2B) to a multilayer germinal epithelium of spermatocytes and spermatids (Fig. 3A). Juvenile males lack a well-defined tubular system and primary and secondary spermatogonia are the only germ-cells present, totally displacing the tubular lumen. At an early stage of maturation (two-year old fish), numerous tubular lumen, either empty or containing only a few sperm, increase in number as spermatogenic

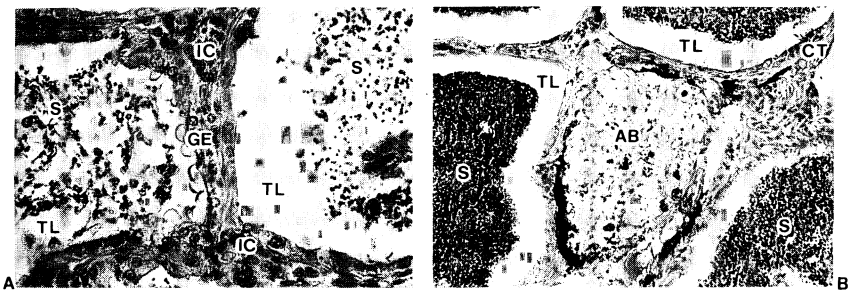

Fig. 4. Final stages of spermiogenesis in testes of *Parasilurus aristotelis.* A) Increase in interstitial cells (IC) (×320) and degradation of germinal (gametogenic) epithelium (GE) on tubule wall mucotic covering (×320); B) "atretic body" (AB) (×200). *TL*—tubule lumen; *S*—sperm; *CT*—connective tissue of tubule.

activity progresses (Fig. 3D). Following spermiogenesis a marked reduction is noted in the thickness of the germinal epithelium and of the number of single spermatogonia (Fig. 3B). The massed sperm in the tubular lumen causes the tubular wall to thin and finally burst, establishing lacunar spaces between the sperm-filled lumen of the neighbouring tubules (Fig. 3E). At this stage, the provisional sperm duct at the inner region of the testes is formed (Fig. 2D). Regression of blood vessels and an increase in interstitial cells within the intertubular stroma tissues is detectable (Figs. 3F, 4A). Dark stained melanocentres are sometimes formed in the interstitial cells as well as degradation of the gametogenic epithelium mucotic covering (Figs. 3F, 4A). Such degraded tubules finally form the s.c. atretic bodies (Fig. 4B).

Data analysis.—The following Tables (1–4) provide data on biometrical analyses that compare relationships between dimensions and number of various compounds in the testes.

The data demonstrate a negative correlation between body length of the male fish and the total number of seminiferous tubules in the measured unit area ($r=-0.640$; $p<0.01$), which is higher in young males than in older ones (Table 1). The cause is probably that the tubules enlarge with ripening of the growing fish. Therefore, as expected, the total number of seminiferous tubules per section is negatively correlated with their diameter ($r=-0.847$; $p<0.001$) (Table 2). It can also be seen that concomitant with the increased weight of the testes towards the breeding season, the diameter of the seminiferous tubules also become significantly enlarged ($r=0.544$; $p<0.01$), possibly due to the active spermiogenesis (Table 3). However, the percentage of the total number of seminiferous tubules in the unit area of sectional surface does not vary ($r=-0.166$; $p>0.05$) throughout the season (Table 3). There is a notable positive correlation between total number of seminiferous tubules and number of full seminiferous tubules (i.e. packed with sperm) in the unit area of sectional surface ($r=0.978$; $p<0.001$) during

Table 1. Relationship between the number of seminiferous tubules and the body length of *Parasilurus aristotelis* (mean $\bar{x}$; standard error SE; standard deviation D)

Body length (S.L.) of fish (cm)	Parameters								
	Total number of seminiferous tubules			Number of full seminiferous tubules			Number of empty seminiferous tubules		
	Range	$\bar{x}\pm$SE	D	Range	$\bar{x}\pm$SE	D	Range	$\bar{x}\pm$SE	D
13.0–17.0 $n=4$	152–1179	672.25±209.68	419.36	38–1158	486.75±259.05	448.67	6–192	68.25±42.45	73.53
17.1–21.0 $n=10$	62– 975	200.8 ± 86.73	274.25	0– 975	147.0 ± 93.93	281.8	0–101	26.0 ± 9.84	29.52
21.0–25.0 $n=7$	60– 158	86.57± 12.84	33.98	0– 157	55.43± 21.01	51.46	0– 82	20.29±11.8	28.9
25.1–29.0 $n=3$	64– 117	98.67± 17.34	30.04	9– 115	58.0 ± 30.95	43.64	0– 10	3.67± 3.19	4.5

the spawning period with the increased weight of the testes (Table 4), demonstrating that during this period of high sperm production tubules branch and immediately enter into gametogenesis.

Discussion

Several studies of the male reproductive system of various species of catfish (Sundararaj, 1958; Nawar, 1960; Lehri, 1967; Rastogi, 1969; Sundararaj and Nayyar, 1969; Nayyar and Sundararaj, 1970; Yoakim, 1976; Schoonen and Lambert, 1986; Van den Hurk et al., 1987; Fishelson et al., 1994) report the existence of morphologically different seminal vesicles-accessory sexual glands. Their exact function has not yet been precisely elucidated. Other works (Sathyanesan, 1959; Sneed and Clemens, 1963; Jaspers et al., 1978; Burke and Leatherland, 1984), do not refer to accessory glands, but to different structure between the anterior and posterior parts within the testes itself. According to these authors, the posterior (caudal) part of the testes in catfishes is not spermatogenic, unlike the anterior (cranial) part: its intratubular lining comprises a single layer of epithelium, with numerous glandular

Table 2. Relationship between the number of seminiferous tubules and the mean diameter of one tubule of the testes of *Parasilurus aristotelis* (mean $\bar{x}$; standard error SE; standard deviation D)

Mean diameter of one seminiferous tubule (μ.)	Parameters								
	Total number of seminiferous tubules			Number of full seminiferous tubules			Number of empty seminiferous tubules		
	Range	$\bar{x}\pm$SE	D	Range	$\bar{x}\pm$SE	D	Range	$\bar{x}\pm$SE	D
10.0– 50.0 $n=4$	675–1179	878.0 ±122.22	211.69	38–1158	700.0 ±246.43	426.81	0–192	66.75±43.2	74.83
50.1– 90.0 $n=11$	71– 158	128.55± 8.68	27.46	0– 157	88.36± 17.45	55.19	0–101	18.73± 9.35	29.56
90.1–130.0 $n=9$	60– 117	74.78± 6.01	17.0	0– 67	23.0 ± 9.25	26.16	0– 82	23.67± 9.0	25.44

Table 3. Relationship between the mean diameter of one seminiferous tubule and the weight of the testes of *Parasilurus aristotelis* (mean $\bar{x}$; standard error SE; standard deviation D)

Weight of the testes (gr)	Parameters					
	Percentage of total number of seminiferous tubules in the unit area of sectional surface (mm^2)			Mean diameter of one seminiferous tubule (μ.)		
	Range	$\bar{x}\pm$SE	D	Range	$\bar{x}\pm$SE	D
0.10–1.00 $n=15$	0.38–0.80	0.65±0.04	0.13	27.92–128.63	83.89±6.39	23.9
1.01–2.00 $n=6$	0.43–0.75	0.65±0.05	0.12	90.25–118.29	102.91±4.41	9.87

Table 4. Relationship between the number of seminiferous tubules and the weight of the testes of *Parasilurus aristotelis* (mean $\bar{x}$; standard error SE; standard deviation D)

Weight of the testes (gr)	Parameters								
	Total number of seminiferous tubules			Number of full seminiferous tubules			Number of empty seminiferous tubules		
	Range	$\bar{x}\pm$SE	D	Range	$\bar{x}\pm$SE	D	Range	$\bar{x}\pm$SE	D
0.10–1.00 $n=15$	60–975	172.6±58.04	217.16	0–975	133.73±61.92	231.68	0–101	18.07± 7.11	26.61
1.01–2.00 $n=6$	64–117	78.83± 8.38	18.75	0– 67	24.67±11.41	25.51	0– 82	24.67±13.12	29.35

cells, and the function of this secretory portion of the testes may be also to store and conduct sperm. The present study shows that *Parasilurus aristotelis* possesses no seminal vesicles or glandular structures as the anterior (cranial) and posterior (caudal) regions of the gonads produce germ cells. The absence of seminal vesicles in *P. aristotelis* may have two different explanations. The first—an evolutionary one—is that this species represents a branch of cat-fishes marked by this character. In this case, if more species will be studied, close-related forms will be then described. It is remarkable, for example, that in *Clarias gariepinus* larvae, the onset of formation of the vesicles is marked by an increase of interstitial aggregation of Leidig-like cells in the primordial testes (Fishelson et al., 1994). It may speculate that this stage of cell accumulation remains permanent in *P. aristotelis*, as a functional but rudimentary organ. The second possibility could be the specific reproductive strategy of this species.

In catfishes, the common sperm duct comprises a long tube arising from fusion of both distinct testicular ducts. It extends from the posterior part of the testes to the urinogenital papilla, channelling and receiving seminal vesicles (Sundararaj, 1958; Sathyanesan, 1959; Nawar, 1960; Lehri, 1967; Rastogi, 1969; Nayyar and Sundararaj, 1970; Yoakim, 1976; Burke and Leatherland, 1984; Van den Hurk et al., 1987). In *P. aristotelis*, however, the structure is radically different: the sperm duct of each unpaired testis is located within the testis itself and formed histologically through the continuation of the adjacent testicular tubules, thereby forming provisional ducts, distinctly lined with germinal epithelium. Their post-testis extension, the common sperm duct, is formed by the joining of both unpaired sections and is very short, located entirely within the urinogenital papilla and lined with a cuboidal epithelium.

Similar to some other catfishes (Sathyanesan, 1959; Lehri, 1967; Nayyar and Sundararaj, 1970; Shihshabekov, 1978; Burke and Leatherland, 1984) the testes of *P. aristotelis* undergo regular seasonal changes, although less pronounced (Iliadou and Ondrias, 1986). In *P. aristotelis* the testes start to develop at two years of age, although individual variation is encountered. The gonosomatic index reaches its maximum in April, gradually decreasing towards August, from which time the GSI remains almost stable with a gradual increase occurring throughout the winter. During the spawning season (March to August), the value fluctuates between 0.3 to 1.3% (Iliadou and Ondrias, 1986). Although most individuals of *P. aristotelis* breed during spring, numerous summer spawners are also encountered. Spermiogenesis is accordingly continuous and asynchronous, as the cysts at different stages of development are found to be in close proximity. The histological structure of the testes basically resembles that of other teleosts.

The interstitial cells occur between contiguous seminiferous tubules, distinctly aggregated at sites where the intertubular space widens. An increase in these cells was observed at the end of the reproductive season together with the final stages of gamete production, particularly between tubules lined with residual germinal epithelium. Phagocytic activity of darkly staining macrophages was also evident at this time, in both the interstitial cells and in the gametogenic epithelium. According to Grier et al. (1980) phagocytosis is regarded as a criterion for establishing Sertoli-cell homology.

Analysis of the data has shown that statistically significant correlations exist between some pairs of parameters, such as negative correlation between body length and quantity of seminiferous tubules in the unit area; and between diameter of seminiferous tubules and their quantity. A positive correlation exists between weight of testes and diameter of seminiferous tubules; and between the total number of seminiferous tubules and those packed with sperm.

Acknowledgments

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ギリシャ産ナマズ *Parasilurus aristotelis* の精巣の細胞・組織学的観察

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産卵期におけるナマズ *Parasilurus aristotelis* の精巣について，形態学的ならびに組織学的研究を行った．本種は，他のナマズと異なり，貯精嚢を欠く．精巣の前部と後部は同じ構造で，分泌機能よりも精子形成能を持っている．精管は二部に分かれ，上方部の管壁には生殖上皮により，下方部の短い管は立方上皮により裏打ちされている．生殖力の季節的変動は明確でない．産卵期は，連続的で非同時性の精子形成により長い．精巣の組織構造は，他の魚種とあまり変わらない．雄の体長と切片における単位面積当りの細精管の量，細精管径と細精管量，精巣重量と細精管径，全細精管数と精子含有細精管数との間には，有意な相関 ($p<0.01$; $p<0.001$) がみられた．