

ANATOMY AND HISTOLOGY OF THE ALIMENTARY TRACT OF THE ANTARCTIC TOOTHFISH *DISSOSTICHUS MAWSONI* NORMAN (PISCES: NOTOTHENIIDAE)

By V. M. KOROVINA ¹, A. V. NEYELOV ¹ & E. P. VORONINA ¹

With 5 figures

ABSTRACT. Anatomohistological characteristics of the alimentary tract of Antarctic toothfish *Dissostichus mawsoni* Norman, 1937, have been described. Total length of the alimentary tract and relative lengths of its different parts, in this species, are close to average values noted for the family Nototheniidae; the number of *pyloric caeca* of these fishes is close to maximal values known for the suborder Notothenioidei. The wide esophagus and sack-like stomach of the Antarctic toothfish have an histological structure similar to that described in a number of predatory bony fishes. Mesenchymatous derivatives (primarily muscle coat) in intestine wall and *valvae praerectalis*, situated on the boundary of midgut and hindgut, are weaker in the Antarctic toothfish than in the Patagonian toothfish, *Dissostichus eleginoides* Smitt, 1898. This is apparently determined by its specialization in feeding on relatively small and easily digestible food items.

RESUMO. No presente trabalho são descritas as características anatómo-histológicas do tracto alimentar do peixe *Dissostichus mawsoni* Norman, 1937, do Antártico. O comprimento total do tracto alimentar e os comprimentos relativos das suas diferentes partes, nesta espécie, estão próximas dos valores médios encontrados para a família Nototheniidae e o número de apêndices pilóricos é próximo do número máximo encontrado na sub-ordem Notothenioidei. O largo esófago e o estômago de tipo saco de *D. mawsoni* têm uma estrutura histológica

¹ Zoological Institute, Russian Academy of Sciences, Universitetskaya nab., 1, 199034 S. Petersburg, Russia. E-mail: voron@zin.ru

semelhante à descrita para um certo número de teleósteos predadores. Derivados do mesênquima (primariamente a cobertura muscular) na parede do intestino e a *valvae praerectalis*, situada na fronteira entre o intestino médio e o intestino posterior, são mais fracos do que no seu congénere patagónico, *D. eleginoides* Smitt, 1898. Este facto é aparentemente determinado pela sua especialização no consumo de itens alimentares relativamente pequenos e de fácil digestão.

Until now numerous works have been published on Antarctic fishes, including toothfishes, the largest fishes of Antarctica. Distribution of these fishes has been studied; species characteristics of their morphology and ecology described. Many researchers have studied feeding of toothfishes in different regions of their distribution range (TARVERDIEVA, 1972; CHECHUN, 1984; PERMITIN, 1987; McKENNA, 1991 and others). The monograph by YUKHOV (1982) is devoted to the study of life history of Antarctic toothfish, *D. mawsoni*, which is placed in the group of secondary pelagic species (ANDRIASHEV, 1987). Much less information is known on the structure of viscera in fishes of the genus *Dissostichus*. Histological features of the intestine of Patagonian toothfish, *D. eleginoides* Smitt, were described by KOROVINA and co-authors (1991a). Data on anatomy of the alimentary tract of antarctic tooth fish were published by EASTMAN & DeVRIES, (1997). The object of this research was to study anatomical-histological features of alimentary tract of Antarctic toothfish and compare them with those in the earlier studies of the notothenioid fishes.

MATERIAL AND METHODS

Material for the study of structure of alimentary tract of Antarctic toothfish was collected during a voyage of FRV “Evrika” in 1987 near the Orkney Islands. A whole alimentary tract of a toothfish female (SL 62 cm) was fixed in formalin (10%); pieces of different parts of a much larger female (SL 98 cm) were fixed in Bouin’s solution. Tissue samples were embedded in paraffin wax, sectioned at 7, 10 and 15 μm and stained with M. Heidenhain’s azan method or van Gieson’s method.

RESULTS

General view of the spread alimentary tract of the Antarctic toothfish is represented in Fig. 1. It shows distinct differentiation into following parts: short esophagus, large sacklike stomach, midgut and hindgut. Length of alimentary tract is 83% of fish body length (SL), length of esophagus - 8%, stomach - 18%, midgut - 62% and hindgut - 11% of alimentary tract total length.

Five relatively thick *pyloric caeca* of about equal length (approximately 8% of the SL) surround pyloric part of the stomach in fish of SL 62 cm. In fish of SL 98 cm there were 6 *pyloric caeca*. The intestine forms three abrupt curves in body cavity. Melanophores are absent in visceral and parietal part of the peritoneum, as well as in the wall of the compartments throughout the entire length of the alimentary tract (Fig. 2A). Shown for comparison (Fig. 2B) is a photograph of an unstained section of esophagus of another inhabitant of benthopelagial, *Gvozdarus svetovidovi* Balushkin, whose tunica propria of the mucous coat contains melanophores and therefore is much darker than surrounding tissues.

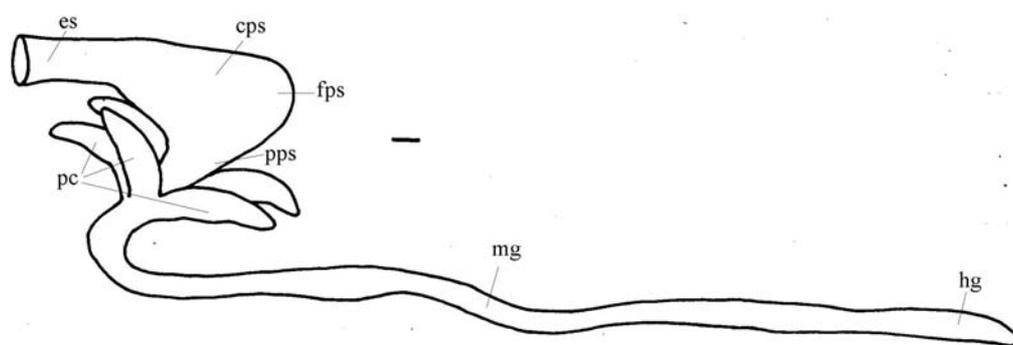


Fig. 1 - Gross morphology of spread alimentary tract of *D. mawsoni* (SL 62 cm). Abbreviations: cps - cardial part of stomach; es - esophagus; fps - fundal part of stomach; hg - hindgut; mg - midgut; pc - *pyloric caecum*; pps - pyloric part of stomach. Scale bar: 1 cm.

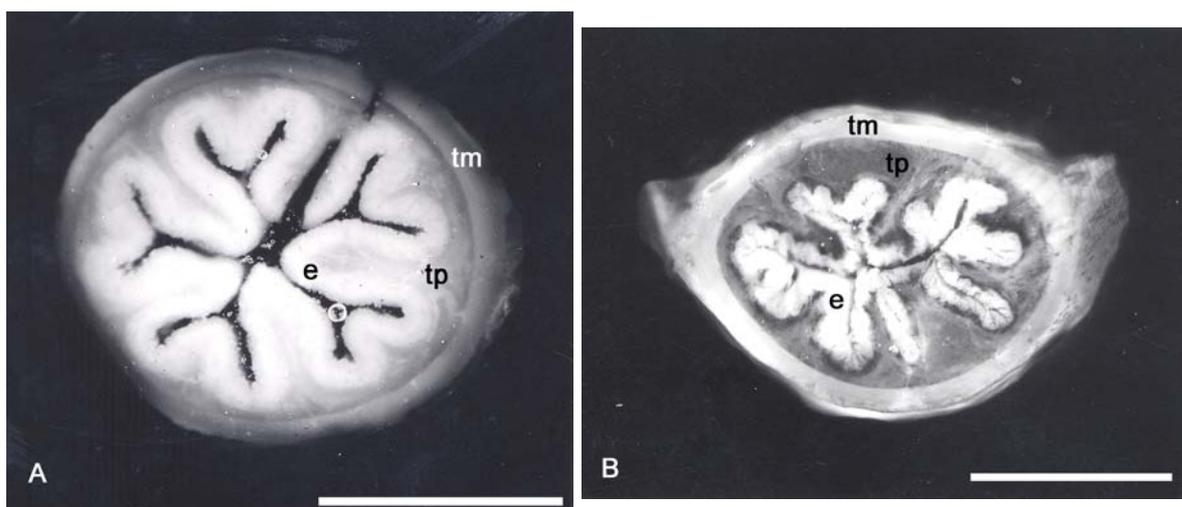


Fig. 2 - Unstained cross section of esophagus: A - *D. mawsoni* (SL 62 cm); B - *Gvozdarus svetovidovi* (SL 52 cm). Abbreviations: e - *epithelium*; tm - *tunica muscularis*; tp - *tunica propria*. Scale bars: 1 cm.

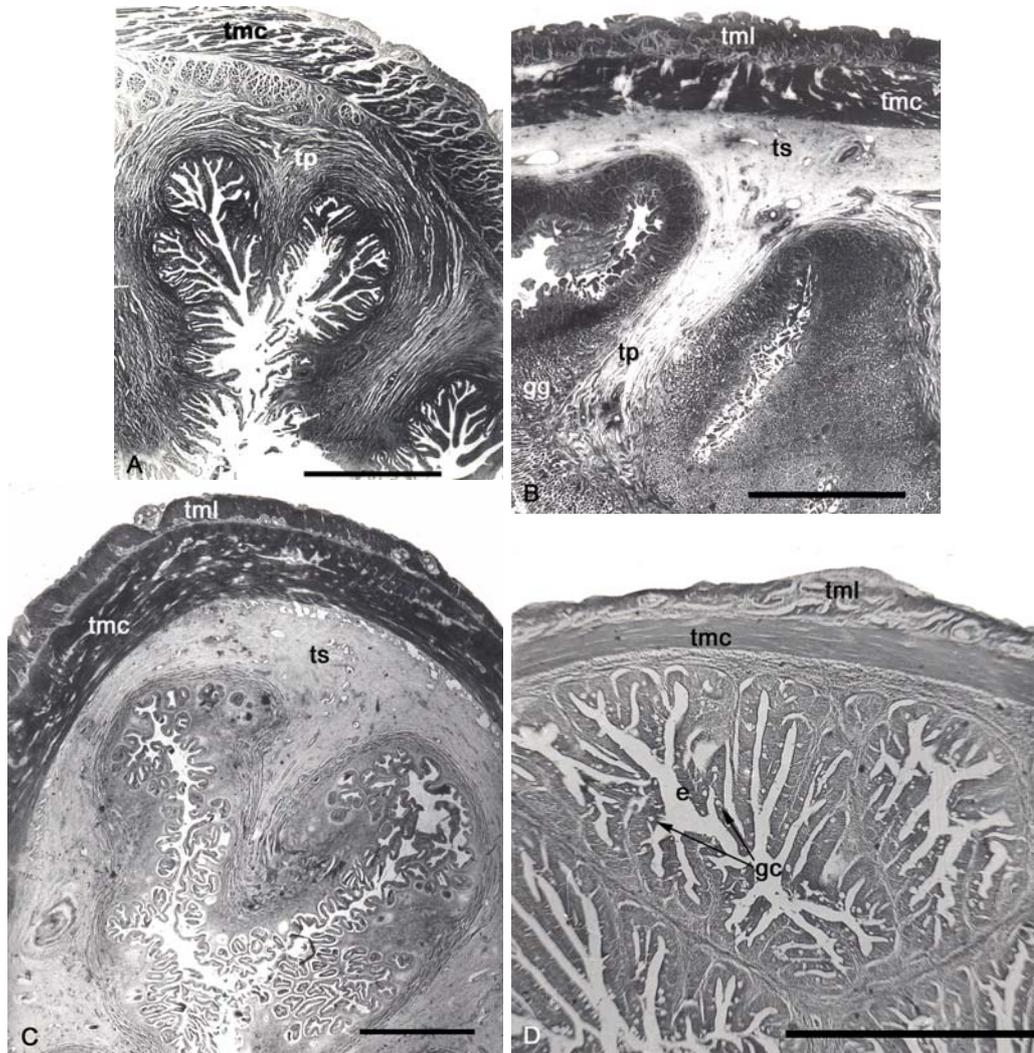


Fig. 3 - Portions of the cross sections of the different parts of the alimentary tract in *D. mawsoni* (SL 98 cm), Van Gieson's stain: A - esophagus; B - cardiac part of stomach; C - pyloric part of stomach; D - pyloric caecum. Abbreviations: e - epithelium; gc - goblet cells; gg - gastric glands; tmc - tunica muscularis circularis; tml - tunica muscularis longitudinalis; tp - tunica propria; ts - tunica submucosa. Scale bars: 250 μ m.

Esophagus

The mucous coat of the esophagus has 10 large longitudinal folds, the basis of which is formed by thick projections of *tunica propria*, consisting of a simple type of areolar connective tissue and rich in collagen fibers (Fig. 3A). Broad and thick *tunica propria* reaches also in the numerous small secondary foldings, covered by stratified epithelium. The apical part of the epithelial layer is completely covered by mucous cells. There are no glands in the esophagus. A thick circular layer of interweaving striated muscle fibres forms muscle coat.

Stomach

In the cardiac part of the stomach the folds of mucous coat are also only longitudinal, wide, but more complex than in the esophagus (Fig. 3B). Epithelial lining is represented in the columnar epithelium. Tubular gastric glands with branching distal parts form a wide layer, particularly strongly developed in the fundal part of the stomach. Thickness of the loose *tunica propria*, providing for a large elasticity of stomach, in that part constitutes approximately 25% of thickness of the entire wall, its numerous thin collagen membranes reach far into the folds of the mucous coat. Situated beneath *t. propria* is the *t. submucosa*, which also provides for strong elasticity of stomach, but is somewhat different in its structure from *t. propria*. Whereas *t. propria* appears to be loose mesh connective tissue with collagen forming stratified membranes, *t. submucosa* has the appearance of homogeneous and dense connective tissue with somewhat larger amount of cell elements. Muscular coat is formed by circular and longitudinal layers of smooth muscular fibers and its thickness is equal to a half one of the entire wall.

The pyloric part of the stomach is short and narrow. Folds of mucous coat here are also longitudinal bearing numerous strongly anastomosing secondary foldings (Fig. 3C). Epithelium here is also columnar, mucous and goblet cells are lacking as in the cardiac part. At the base of folds of the mucous coat structures reminiscent of glands can be seen; however the nature of epithelium on those is the same as at the apex of folds, therefore it can be assumed that this is rather the result of folds anastomoses. Relatively loose *tunica propria* consists mainly of collagen fibers and contains few cell elements. As in the cardiac part it is underlain by denser *t. submucosa*. Thickness of muscular coat exceeds one half of the entire wall thickness. The circular layer of smooth muscular fibers constituting two thirds that of the muscular coat is most developed. In the pyloric part of the stomach serose is thicker as compared to other parts of the alimentary tract.

Intestine

The wall of the midgut of Antarctic toothfish is much thinner than in other parts of its alimentary tract. The height of folds of mucosa exceed the thickness of the intestine wall more than 1.5 times. Folds are split, anastomosing with many secondary folds. Thickness of the epithelial layer constitutes approximately 14% of intestine wall. In addition to epithelial cells, of cylindrical type, there are many goblet cells. A thin layer of *tunica propria* reaches into the folds; mostly in its periphery there are numerous cell elements as well as intercellular substance - collagen fibers. The latter form a durable network, which substitutes in these fishes a layer of specialized collagen - *Stratum compactum*; *S. granulosum* is not developed. Between the circular and slightly thinner longitudinal strata of smooth muscular fibers, forming muscular coat, there is a layer of connective tissue with a large number of blood vessels. Blood vessels in the intestinal wall of the Antarctic toothfish do not have thickened collagen coat increasing its

durability, as described in large predators of other fish groups (KOROVINA & VASIL'EVA, 1976).

Fine structure of *pyloric caecum* (Fig. 3D), similar in general with the structure of midgut, differs only in the ratio of histological layers. Walls of *pyloric caeca* are thinner and more dense because of collagen membranes of *tunica propria*. The circular layer of muscular coat is 2.5 times thicker than the longitudinal one. Between the layers there is no connective tissue layer.

As in many notothenioid fishes *valvae praerectalis* is present on the boundary of midgut and hindgut of the Antarctic toothfish. According to the data of EASTMAN & DeVRIES (1997) it is situated at a distance of 70-80 mm (3-6% of SL) from the anus. It can be seen in the transversal sections of the intestine (in our material) that the valve begins asymmetrically, closes as a ring and retains connection with the wall of the intestine by means of thin anastomoses. As a result, a section of intestine in this part has a "lacy" pattern (Fig. 4). Length of the valve is not large, it constitutes 53 mm in an individual with a body length of 98 cm. Muscular coat of intestinal wall in the region of *valvae praerectalis*, as well as muscle sphincter of the valve itself, is thin and constitutes approximately 40% of intestine wall thickness. A large number of goblet cells is noted in the epithelium particularly in that lining inner surface of the valve.

Behind this *valvae* the diameter of the hindgut increases considerably, whereas the height of longitudinal folds of mucosa and the ratio of histological layers of the intestinal wall change little.

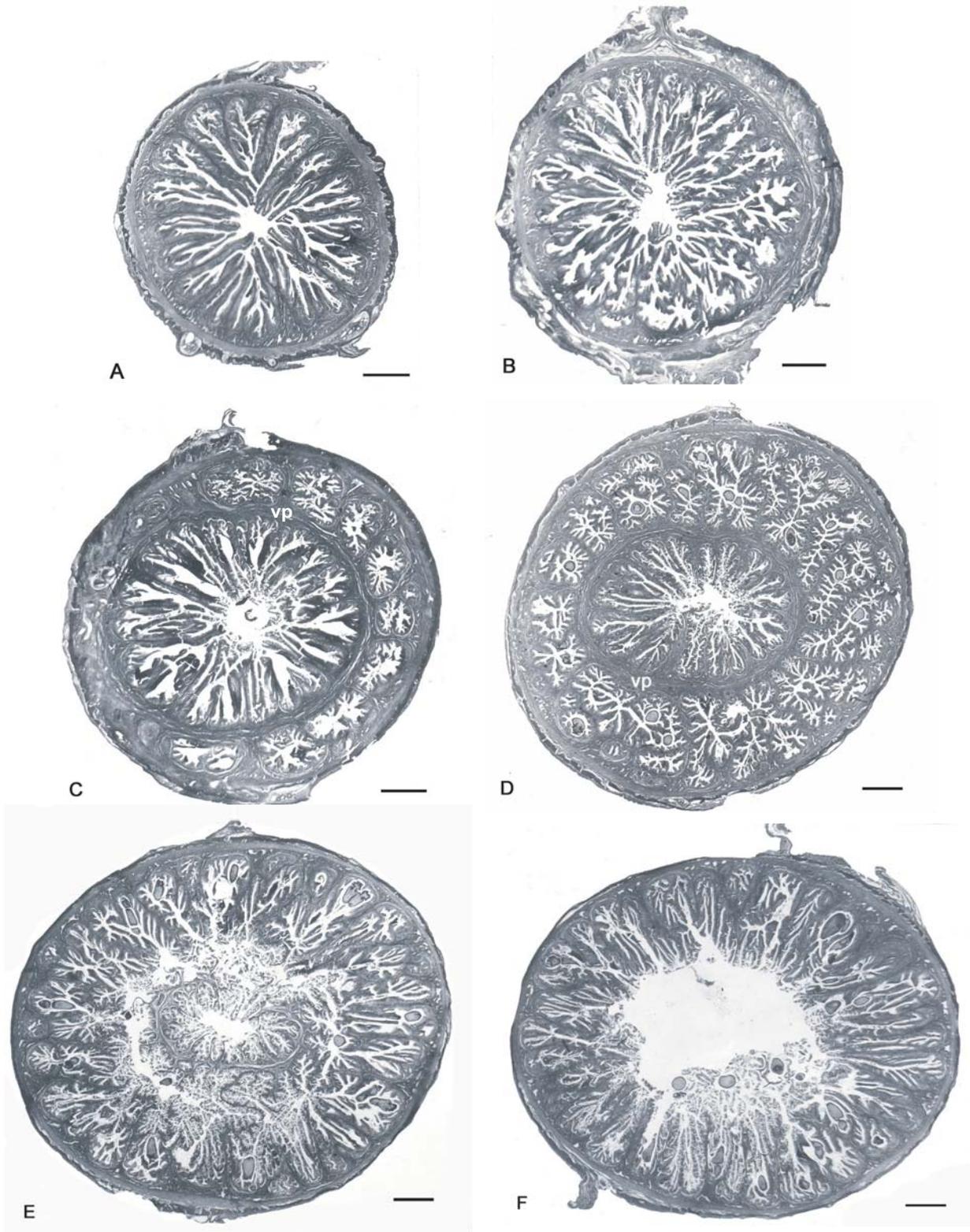


Fig. 4 - Cross sections of *valvae praerectalis* in *D. mawsoni* (SL 98 cm), arranged consecutively in caudal direction, M. Heidenhain's azan stain. Abbreviations: vp - *valvae praerectalis*. Scale bar: 1 mm.

DISCUSSION

There is an opinion that differences in the external morphology of nototheniids as a whole is not accompanied by notable interspecific differences in the structure of the digestive system (EASTMAN & De VRIES, 1997). In fact the general structural plan of the alimentary tract of the Antarctic toothfish completely corresponds to that in other fishes of the order Notothenioidei studied in this respect (KOROVINA *et al.*, 1986, 1991a, b; EASTMAN & De VRIES, 1997). It was assumed that elongation of the entire alimentary tract or its parts is typical of fishes feeding on food objects of low nutrition value or indigestible objects (KOROVINA & PRIRODINA, 1986; OJEDA, 1986; EASTMAN & De VRIES, 1997; VORONINA & BALUSHKIN, 1998). According to our data total length and relative length of different parts of alimentary tract of Antarctic and Patagonian toothfishes are within the limits of average values known for the family Nototheniidae. Therefore in anatomy of the alimentary tract toothfishes cannot be regarded as specialized forms. The number of *pyloric caeca* of these fishes is close to the maximal for the Order Notothenioidei and suggests, with the generalized state of the genus, that their number reduced in evolution (NEYELOV & VORONINA, 1996; EASTMAN & De VRIES, 1997). Neither in the Antarctic nor in the Patagonian toothfishes were melanophores found in the peritoneum or in the wall of alimentary tract, as was noted before. It was emphasized that except *D. mawsoni*, extensive melanism of the alimentary tract accompanies pelagization in different nototheniid groups (EASTMAN & De VRIES, 1997). Therefore a generalized state of the genus *Dissostichus* is suggested also by the absence of melanism of viscera and body cavity with pelagization, a convergent feature of nototheniids living in the water column. This conforms to the opinion, based on other morphological criteria, of the generalized state of the subfamily of Elegendopsinae to which this genus belongs (BALUSHKIN, 1984).

Unfortunately data on histological structure of the anterior part of the alimentary tract (esophagus and stomach) of nototheniid fishes are absent. It can be only noted that structure of the esophagus and stomach of the Antarctic toothfish is, in general, similar to that described in many carnivorous bony fishes. Elasticity of stomach, as cardinal to the pyloric part, is provided by thick loose *tunica propria* with collagen membranes, and denser *tunica submucosa*. Gastric glands form a layer in the cardinal part, are especially wide in the fundal part, and the glands are absent in the pyloric part of stomach. Thick muscle coat ensures durability of the walls in case of extension of the esophagus and stomach. As in other nototheniid fishes studied by us, nuclei of epithelial cells are very weakly stained by stains used.

Comparing structure of intestines of Patagonian and Antarctic toothfishes we revealed features in common, as well as notable differences. Relief of mucosa of the midgut of both fishes is similar: a high anastomosing of folds, bearing folds of the

second order. *Strata compactum et granulosum* are absent. There are numerous thin-walled blood vessels in the wide thick *tunica propria* and between layers of muscle coat. On the boundary of midgut and hindgut there is a short *valvae praerectalis*. The lumen of the hindgut is much wider than that of the midgut. The difference to be noted in the first turn is that in the Patagonian toothfish 70 cm (SL) ratio of intestine wall thickness and diameter is 1: 8.6, whereas in Antarctic toothfish with even considerably larger body length (SL 89 cm) it is 1: 2.5. The difference in ratios is determined by much thicker muscular coat in the intestine wall of Patagonian toothfish. In this species the epithelial layer is only 5-6% of the thickness of intestine wall, whereas in Antarctic toothfish it is approximately 15%. The sphincter of the *valvae praerectalis* of Patagonian toothfish is also much thicker (Figs. 4, 5).



Fig. 5 - Cross section of *valvae praerectalis* in *D. eleginoides* (SL 70 cm), M. Heidenhain's azan stain. Abbreviations same as Fig. 4. Scale bar: 1 mm.

The diet is undoubtedly the main biological factor of morphogenesis in the digestive system. Patagonian toothfish with body length of 40 cm feeds almost exclusively on fish, bottom species included (CHECHUN, 1983). Cases are noted when sizes of prey of Patagonian toothfish attain 20-40% of its body length (TARVERDIEVA,

1972), although in Kerguelen region it prefers fishes of moderate sizes (CHECHUN, 1984). At the same time squids form the major part of diet of Antarctic toothfish. Cases when stomachs of toothfishes contain remains of small mesopelagic fishes are extremely rare (YUKHOV, 1982).

Morphological adaptations to ingestion of large amounts of food or indigestible objects shown for other fish groups included development of additional membranes of specialized collagen (*stratum compactum*) at the periphery of *tunica propria* in intestine with the stomach of many fishes. These membranes are a kind of shock absorber, providing durable support to the intestine wall, and ensuring smooth passing of food through the intestine. The piscivorous Patagonian toothfish whose intestine is devoid of such mechanical structure has particularly strongly developed muscle coat serving as shock absorber. It has been assumed that in fishes with stomachs, the midgut where mostly digested food mass enters (unlike the anterior part of alimentary tract), is not subject to strong impact of food ingested. At the same time, insufficient development of the muscle coat of the intestine wall was shown for salmonid fishes feeding on artificial foods devoid of indigestible material (KOROVINA & VASIL'EVA, 1976). A much smaller amount of indigestible material enters intestine of the adult Antarctic toothfish, as it feeds mainly on squids. Even though the structural plan of thin intestine wall is similar in both species of toothfishes, apparently specialization of the Antarctic toothfish in feeding on relatively small easily assimilated prey - squids, determines the essential difference in the thickness of muscle coat.

To trace possible evolutionary changes of the alimentary tract (of its anterior and posterior parts) of notothenioid fishes it is necessary to analyze and summarize its structure in representatives of the entire suborder, Notothenioidae, particularly in connection with different food specialization. This is proposed in the future.

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