

## **A histological study on the development of the digestive tract of Caspian salmon, *Salmo trutta caspius* (Kessleri), from hatching to parr stage**

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**Abstract:** Histological development of digestive tract of the Caspian salmon, *Salmo trutta caspius*, from hatching to 6 month post-hatching was studied using light microscope. The digestive tract of newly hatched larvae was a simple, undifferentiated tube which continued from mouth to anus. In 10 days post hatching larvae, the alimentary canal became more differentiated and secretion was started activity, with appearance of goblet cells in epithelium of the mouth, pharynx and esophagus. A thin layer of neutral mucopolysaccharid components covered the digestive tract's epithelium in this stage. At the onset of exogenous feeding (25 days post hatch, dph, at 7°C), the digestive tract became completely differentiated into mouth, pharynx, esophagus, glandular and non-glandular stomach, primary pyloric caeca, anterior and posterior parts of the intestine and rectum, similar to those of juveniles and adults. The alimentary canal was structurally completed and lined by a stratified squamous epithelium in the mouth, pharynx and rudimentary part of the

esophagus at 25dph, while the terminal part of esophagus, the stomach and the intestine were lined by a columnar epithelium. During this period, striated muscle layer became distinct from mouth to esophagus, while smooth muscle layer was appeared at the stomach and intestine. This pattern did not changed up to six months post hatch, except in development of the digestive organs. Histological analysis of the present study prepare some basic scientific knowledge on the Caspian salmon's digestive histology which may be used in further studies on digestive system, such as histochemical studies.

**Keywords:** Histology, Parr, Digestive tract, Caspian salmon

## Introduction

The Caspian salmon, *Salmo trutta caspius* (Kessleri, 1877), is a vulnerable and endangered species, living mainly in the southern part of the Caspian Sea. Artificial reproduction, of upstream migrating broodfish, and rearing of this fish upto smolt size, was considered for restocking purposes by the Iranian Fisheries organization since 1985 (Bahramian, 2001). In fact, Caspian salmon larvae passes three stages from hatching to releasing; fry, fingerling and smolt stages. When fish passed the first summer of growing, is called parr stage, and is known by appearance of vertical lines on the body sides (Vilaki, 1994). In larval rearing of this fish, as many other species, exogenous feeding is marked by a lion share of larval mortality, probably due to some nutritional problems associated with the absence of suitable starter diets. It is evident that a better knowledge of the digestive system and its functional capabilities in relation to age is of great interest for progress in larval rearing techniques (Vilaki, 1994).

Although the morphology of the digestive system of adult salmonids are been studied intensely (Verigina *et al*, 1974; Korovina, 1989; Bullock, 1993) and the histological characteristics of the digestive tract of some salmonids have been studied to some extent (Burnstock, 1963; Voronina, 1997; Korovina *et al*, 1992), only limited research on the Caspian salmon histochemistry of digestive tract is available (Bahrekazemi, *et al*, 2004).

Unlike histological studies comparative studies on salmonids are very rare.

Greene (1912) described digestive system of *Oncorhynchus tshawytscha* and concluded that there are close similarities to salmon and trout. The similarities of histological and histochemical traits of the intestine in three species of Salmonid fishes (*Salmo salar*, *Salmo trutta* and *Oncorhynchus mykiss*) were noted by Bullock (1993).

The aim of the present study was to describe, in details the development of digestive system of the Caspian salmon in order to achieve a better understanding and knowledge of digestive system abilities, especially during larval period.

## **Materials and Methods**

### **Supply and maintenance of fish**

Wild Caspian salmon brood stocks, caught during their spawning migration from the Caspian Sea to Cheshmeh Killeh river (Tonekabon) in October of 2002, were used for artificial reproduction. Eggs were incubated at the 6-8°C, using California incubators (Sticknery, 1991), at the Shahid Bahonar Cold Water Fishes Center, at the north part of Iran.

Larvae hatched at 60-64 days of incubation and started their exogenous feeding 20-25 days later, when approximately 2/3 of yolk sac reserves being absorbed. At first, larvae were fed with wet diet. Subsequently (when larvae weighted 110-120 mg), about one thousand larvae were transferred to two indoor rectangular concret tanks (100 liter capacity, 500 larvae per tank) and reared upto parr stage (appearance of parr marks on their sides). During the rearing period, water temperature ( $11.5 \pm 0.5^\circ\text{C}$ ) and dissolved oxygen ( $9 \pm 0.3\text{mg l}^{-1}$ ) were measured daily.

### **Sampling and histological procedures**

Samples for histological studies were taken from hatching to parr stage (6 months post hatching). The following stages were sampled: larvae at hatching, at 10, 25, 30 (days post hatching) during yolk sac resorption, and then monthly to 6 months post hatching. In each sampling, 20 specimens were sampled randomly and their total length and weight were measured (Table 1). Then specimens fixed in Bouin's fluid and transferred to the fishery laboratory of Natural Resources

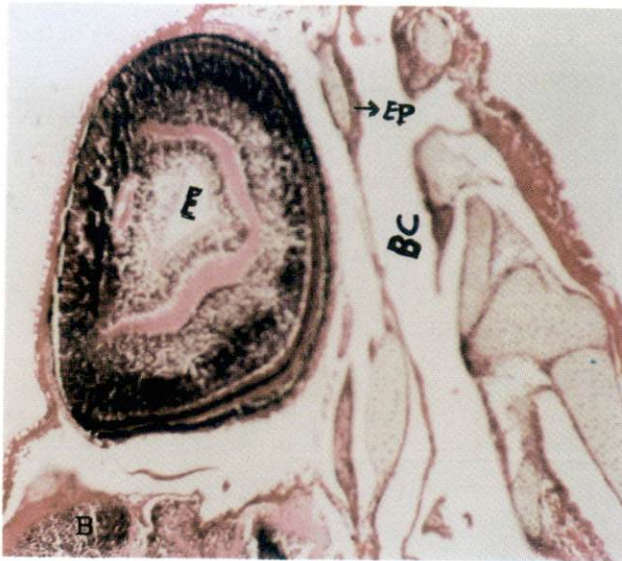
Collage, University of Tehran. In the next stage, samples were dehydrated, in graded ethanol and embedded in paraffin (Drury & Wallington, 1980). Twenty sagittal serial sections, 6  $\mu\text{m}$  thick, were made from each block, mounted on glass slides (5-6 serial per slide), air dried, and stained with either Hematoxilin-Eosin (H&E) or Periodic Acid Schiff (PAS) (Drury & Wallington, 1980).

**Table 1: Sampling stages and their characteristics**

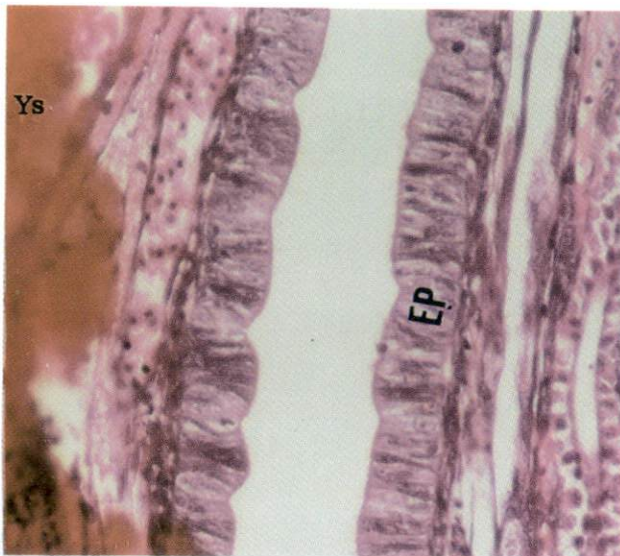
Sampling stages	Number of samples	Temperature (°C)	Total length (mm)	Weight (g)
1 day post hatch	20	8	17	0.92
10 day post hatch	20	8	20	1.1
25 day post hatch	20	7	23	1.3
1 month post hatch	20	7	24	1.4
2 month post hatch	20	8	32	1.8
3 month post hatch	20	9	35	2.2
4 month post hatch	20	13	50	3.2
5 month post hatch	20	12.5	63	4.3
6 month post hatch	20	12	73	5.1

## Results

When the Caspian salmon larvae emerge from the egg membranes, it poses a large yolk sac, making up the greatest part of the body. The alimentary canal is a simple, undifferentiated tube, being closed at the anal end, by a thin layer of tissue, and opened to some extent at the mouth end, being, covered with thin layer of stratified squamous epithelium (Fig.1). Other parts of the alimentary canal consisted of one layer of columnar epithelium (Fig. 2). At the terminal part of this tube, the posterior part of the intestine is distinguished. During the endogenous feeding phase, the digestive tract experienced a gradual anatomical differentiation, and when the first exogenous feeding took placed (25 dph), the alimentary canal consisted of a well developed and organized buccopharynx, esophagus, stomach and intestine. After the onset of the exogenous feeding, the organization and differentiation of the digestive tract did not undergo any noticeable modification upto the end of study (Table 2).



**Figure 1:** Longitudinal section of the head of the Caspian salmon, at hatching. Note to the Buccal Cavity (BC) with mouth opened to some extent and covered by Epithelial layer (EP), Eye (E), Brain (B). H&E (x400).



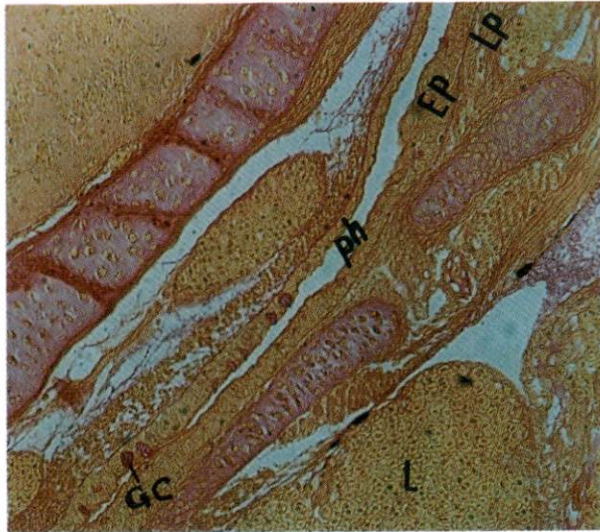
**Figure 2:** Longitudinal section of the primary digestive tract of the Caspian salmon at hatching. Note the columnar cells of Epithelium layer (EP) and Yolk Sac (Ys). H&E (x1000).

**Table 2: Summary of the main developmental events occurring in the digestive tract of the Caspian salmon (see text for details)**

Event	Age									
	dph			mph						
	1	10	25	1	2	3	4	5	6	
<b>Buccopharynx</b>										
Buccopharynx opening and development	↔									
Goblet cells appearance	↔									
Epithelial folding development	↔									
Taste buds appearance	↔									
Teeth development	↔									
<b>Esophagus</b>										
Separation of esophagus	↔									
Goblet cells appearance	↔									
Differentiation of secretory and transport regions	↔									
<b>Stomach</b>										
Separation of stomach	↔									
Glandular stomach development	↔									
Non-glandular stomach development	↔									
<b>Intestine</b>										
Posterior intestine appearance	↔									
Separation of three part of intestine	↔									
Intestine villies appearance	↔									
Goblet cells appearance	↔									
Spiral valve development	↔									
Pyloric caeca development	↔									
<b>Energy sources</b>										
Endogenous nutrition	↔									
Mixed nutrition	↔									
Exogenous nutrition	↔									

## Buccopharynx

At hatching (17mm TL), the mouth was opened to some extent, but the pharynx was not differentiated. Mouth was covered with a stratified squamous epithelium and primary cartilage tissue was partially seen. Stratification of the oral mucosa became more pronounced at about ten days after hatching (20mm TL). The pharyngeal region was distinguished from the buccal cavity by development of the gill structure. The buccopharynx was lined with squamous epithelium, interdispersed with goblet cells, and surrounded by a thin lamina propria in 10 dph larvae (Fig. 3). In larvae at the beginning of exogenous feeding (23mm TL), the buccopharynx was structurally completed and a thick stratified squamous epithelium, lamina propria and striated muscle sections became distinct. Also, epithelial folding was defined by dorsal and ventral parts of the buccopharynx. Taste buds appeared in the epithelium layer and teeth developed in the connective tissue (Fig. 4). From the onset of exogenous feeding to parr stage (73mm TL), the buccopharynx has developed substantially and stratified more with age. Taste buds became more numerous as specimens grew and teeth penetrated the buccopharynx epithelium (Fig. 5). Goblet cells increased in numbers posteriorly, toward the esophagus and as development proceeded (Fig. 6).



**Figure 3:** Longitudinal section of the pharynx at 10dph. (GC) Goblet Cells, (L) Liver, (ph) Pharynx, (EP) Epithelial layer, (LP) Lamina Propria. PAS (x400).



Figure 4: Longitudinal section of the buccopharyngeal at 25 dph. Epithelium layer (EP), interdispersed with Goblet Cells (GC), and primary Taste Buds (TB). Lamina Propria (LP) with Fat tissue (F) and Cartilaginous tissue (C), note to the primary teeth (DP) in this layer. H&E (x400).

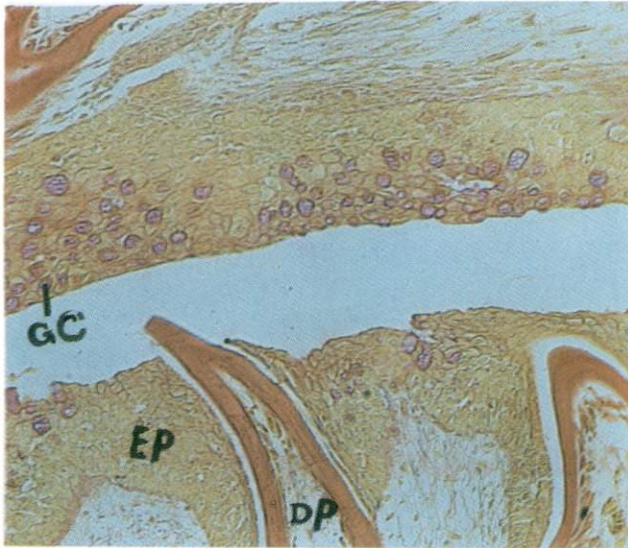
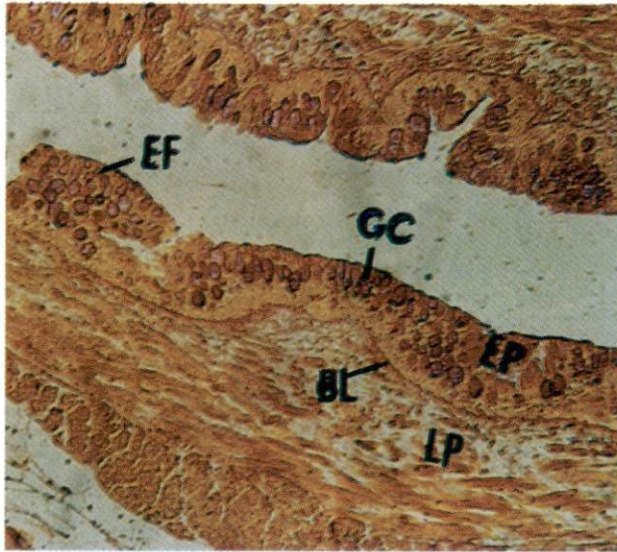


Figure 5: Longitudinal section of the buccal cavity at 3 mph. Note to the Epithelial layer (EP), interdispersed with Goblet Cells (GC) and the teeth Dental Particle (DP) which completed. PAS (x1000).





**Figure 6:** Longitudinal section of the pharynx at 3 mph. Note to the epithelial layer (EP) and epithelial fold (EF), interdispersed with many goblet cells (GC), lamina propria (LP), basal lamina (BL). PAS (x1000).

## Esophagus

One-day old larvae did not have a differentiated esophagus. In 10 dph larvae, esophagus appeared after the last gill arch, as a stratified squamous epithelium. A few goblet cells were observed by this age. From 25 dph to parr stage (6 mph), the esophagus was differentiated into two morphologically distinct zones. Zone I (anterior) consisted of a stratified squamous epithelium with many goblet cells, called secretion part (Fig. 7). Zone II (posterior) consisted of a columnar epithelium with a few goblet cells and the large mucosal folding, named food transport part (Fig.8). Goblet cells and the brush border of esophagus were strongly positive to PAS staining. In various stages of development, the striated muscle layer, being thicker at the terminal part of the esophagus, was surrounded with the serosa layer which remained thin and uniform throughout various stages (Fig 9).

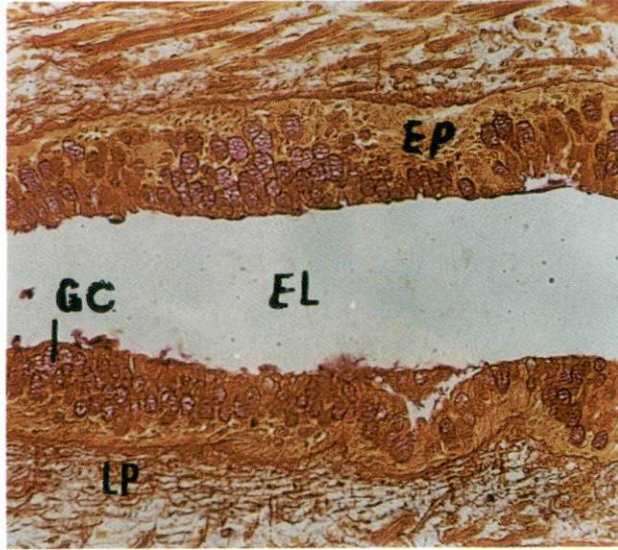


Figure 7: Longitudinal section of the anterior part of esophagus at 3 mph. Esophagus Lumen (EL), Epithelium layer (EP) with many Goblet Cells (GC), and Lamina Propria (LP), PAS (x1000).

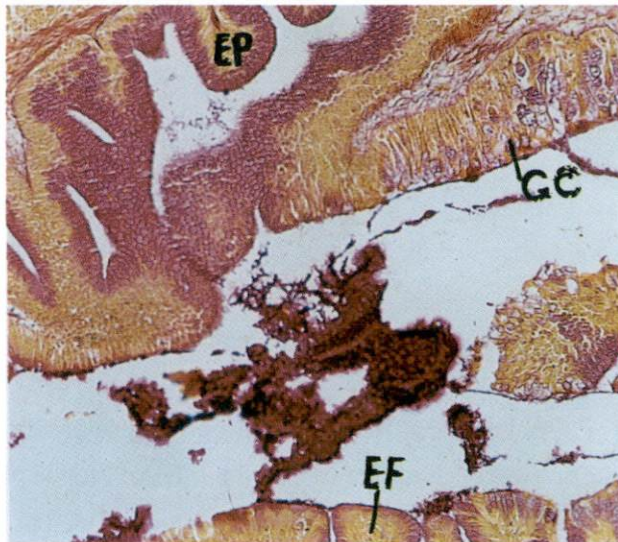
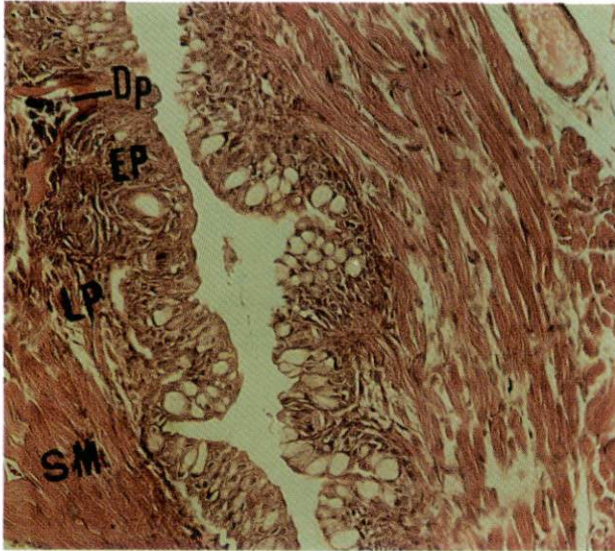


Figure 8: Longitudinal section of the posterior part of esophagus at 3 mph. Note to Epithelial Fold (EF), in the Epithelium layer (EP) of this part and many Goblet Cell (GC) in the anterior part. PAS (x1000).

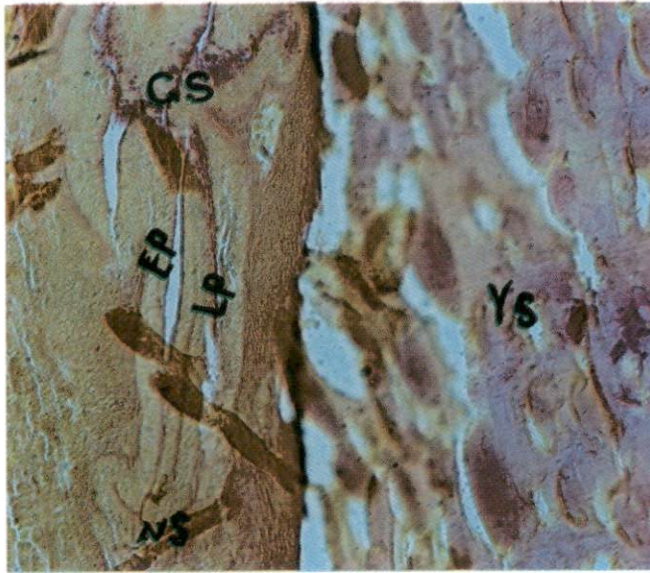


**Figure 9: Longitudinal section of the anterior part of the esophagus at 4 mph. Stratification of the esophagus wall becomes pronounced completely. Epithelium (EP), Lamina Propria (LP), Stripped Muscle Layer (SM). H&E (x1000).**

### **Stomach**

Ten days after hatching, the stomach was distinguished from the esophagus and the intestine by presence of two groups of folds with low columnar cells (Fig. 10). From 25dph larvae up to parr stage (6 mph), two different parts of the stomach could be recognized. A glandular stomach (cardiac region), lined with a simple columnar epithelium with some mucosal folding and devoid of the brush border and goblet cells. Several gastric glands, constituted of one kind of cuboidal cells, were visible in lamina propria in which cells' height increased by age. Smooth muscle layer and a serosa layer completed the glandular stomach wall (Fig. 11). The second recognizable part of the stomach at 6mph was a non-glandular stomach (pyloric region) which was connected to the anterior part of intestine, consisted of columnar cells with basal nuclei and several long mucosal folds (Fig. 12). In comparison, the mucosal fold of pyloric region became deeper relative to the

cardiac region, and the smooth muscle layer was thicker in non-glandular stomach. At the onset of exogenous feeding (25dph), food particles were observed in the stomach, although the yolk sac still remained. The glandular and non-glandular parts of stomach did not show any further noticeable modification until the parr stage. The circular and longitudinal muscle layer was observed at parr stage. The columnar epithelial cells of the stomach contained neutral mucosubstances which were also observed also in the glands' lumen (Fig. 13).



**Figure 10: Longitudinal section of the primary stomach at 10 dph. Glandular Stomach (GS), Non-glandular Stomach (NS), Yolk Sac (YS), Epithelial layer (EP), and Lamina Propria (LP). PAS (x1000).**

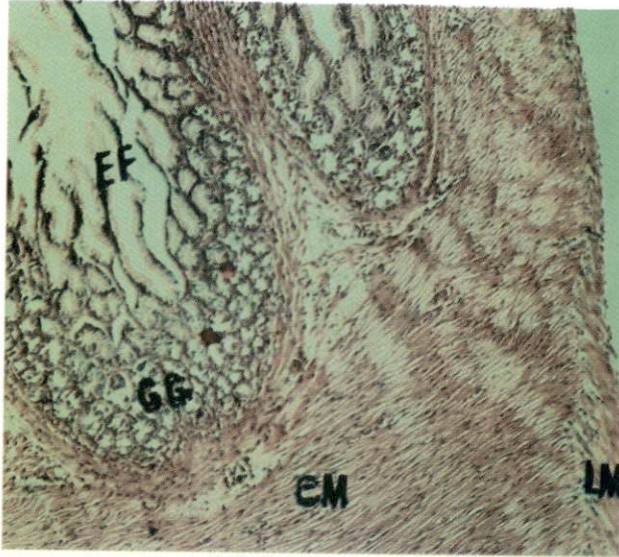


Figure 11: Longitudinal section of the glandular stomach at 6 mph. Gastric Gland (GC), Epithelial Fold (EF), the Circular layer of smooth Muscular fibers (CM), and the Longitudinal layer of smooth Muscular fibers (LM). H&E (x1000).

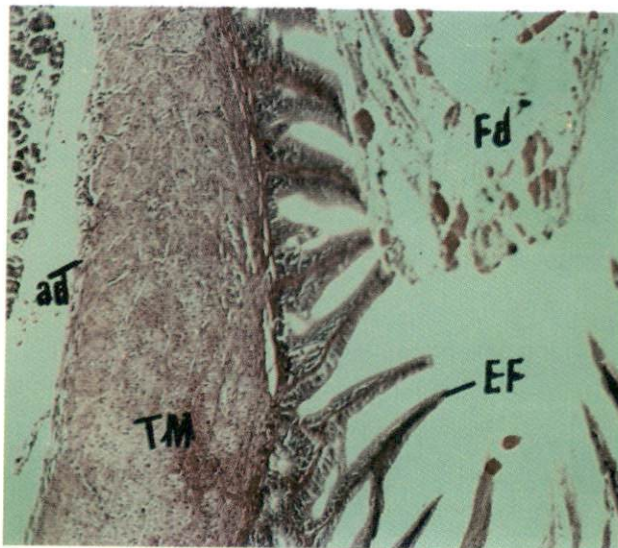
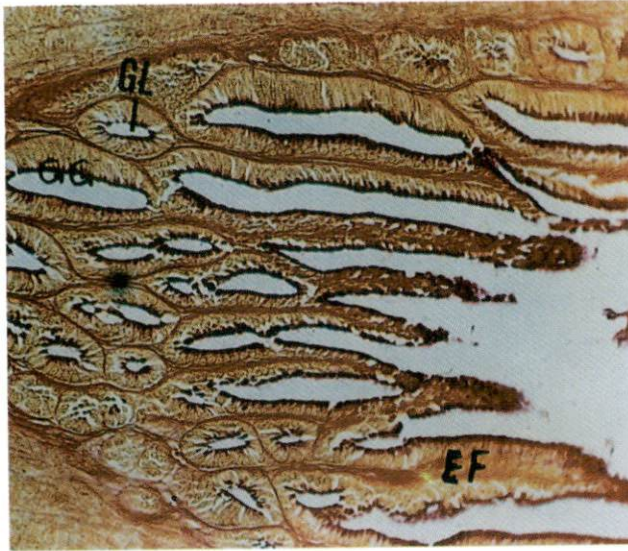


Figure 12: Longitudinal section of the non-glandular stomach at 6 mph. Note to Epithelial Folds (EF), which their shape is affected by Food Particles (Fd), smooth muscle layer (Tm), and adventitia (serosa) (ad). H&E (x1000).

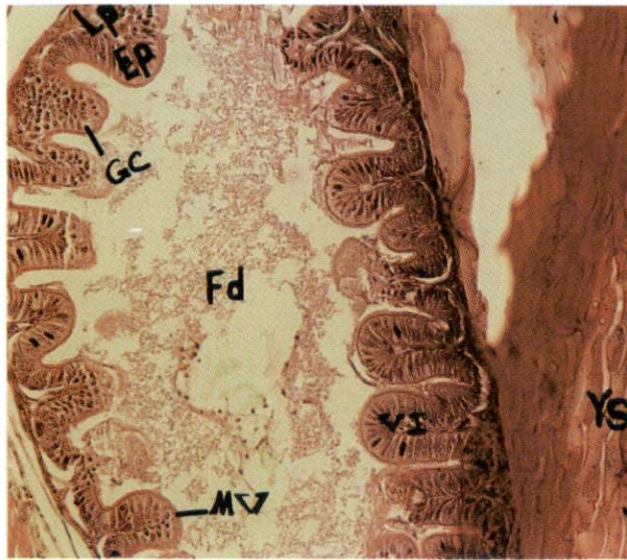


**Figure 13:** Longitudinal section of the glandular stomach at 3 mph. Note to neutral mucopolysaccharid components on the surface of Epithelium Fold (EF) and Gland's Lumen (GL) of Gastric Glands (GG). PAS (x1000).

### Intestine

One-day old larvae (17mm TL), possessed a primordial intestine, lined by a simple columnar epithelium, which only the posterior part of the intestine being evident. By 10dph, the anterior and intermediate part of the intestine was formed to some extent, but no folding was not evident. The intestine became more elongated and differentiated in 25dph larvae. The mucosal epithelial layer was composed of columnar cells with a distinct microvillus brush border and a few goblet cells (Fig. 14). At this age, a large number of low epithelial villies was distinguished in the anterior and posterior parts of the intestine, but in the middle gut, a series of large asymmetric folds, in the mucous membrane which form the spiral valves, was recognized. The spiral valves were lined by a simple columnar, ciliated epithelium, with their coils increasing by age (Fig. 15). By 25dph, the intestinal mucosa (anterior part), immediately posterior to the pyloric stomach, showed a pronounced

folding, indicating the beginning of caecal development. The length of pyloric caeca increased by age and was structurally similar to other parts of the intestine (Fig 16). No histological differences were observed among the various regions of the intestine, and a thin layer of lamina propria, the smooth muscularis and serosa layer surrounded the intestine's villies. In rectum, the only difference was seen in the epithelial layer, being composed of stratified squamous cells (Fig. 17). Goblet cells increased by age in all developmental stages, stained red with PAS.



**Figure 14: Longitudinal section of the anterior part of intestine at 25dph. The Yolk Sac (Ys) which exist to some extent and the Food Particle (Fd). Intestine Villies Formed (VI) and Microvillies (MV) are distinguished, Epithelium (EP), Lamina Propria (LP) and a few goblet cells (GC). H&E (x1000).**

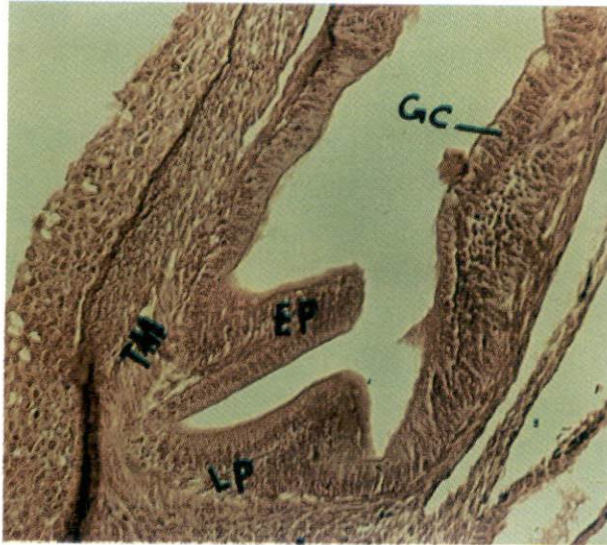


**Figure 15:** Longitudinal section of the intermediate intestine (spiral valve) at 3 mph. The Spiral Valve (SV) is distinguished with Columnar Epithelium (EP) and a few Goblet Cell (GS). PAS (x1000).



**Figure 16:** Transverse section of the pyloric caeca at 3 mph. Pyloric Caeca (PC), Goblet Cell (GC), Anterior part of Intestine (AI). PAS (x1000).





**Figure 17: Longitudinal section of the rectum at 1 mhp. Note to the stratified squamous Epithelium (EP), Lamina Propria (LP), Goblet Cell (GC), and Smooth Muscle Layer (TM). H&E (x1000).**

## Discussion

When hatched, the digestive tract of the Caspian salmon was an undifferentiated canal similar to that of other salmonid species (Voronina, 1997; Korovina *et al*, 1992), except for the mouth which opened in one dph larvae. Goblet cells were fully developed and functional 15 days before the onset of exogenous feeding. It shows the high digestive ability of this fish (Bahrekazemi *et al*, 2004). At the onset of exogenous feeding the buccopharynx was structurally completed, and taste buds and teeth could be seen in mucosal layer. The appearance of taste buds in teleost species such as *Pleuronectes ferruginea* (Baglolle *et al*, 1997) and *Solea senegalensis* (Sarasquete, 1996) take places at about 46 and 16dph, while in *Acipenser baeri* (Gisbert *et al*, 1999), *Acipenser naccarii* (Boglione, 1999) and *Acipenser persicus* (Pahlavan *et al*. 2001), occur at 3, 3 and 5 days after hatching, respectively. It seems that, the appearance of taste buds, which are related to taste sense for food finding, occurs earlier in sturgeon species.

Secretion of neutral mucopolysaccharids by goblet cells, which increased by age, might indicate their protective activities, because they can help to food transposition and protect the mucosal layer from physical and mechanical damages

(Pousti & Marvasti, 2000). The esophagus was recognized as a narrow short canal, in 10dph larvae. The anterior and posterior parts of the esophagus were different on the epithelium structure, distribution of goblet cells and mucosal foldings, appearing by 25 days post hatch. At the histological level, the results revealed structural similarities between esophagus of the Caspian salmon and that of the other salmonids' genus such as *Oncorhynchus* and *Salvelinus* (Voronina, 1997). The epithelium of the anterior part of esophagus was more similar to that of the pharynx's epithelium, but in posterior part, it changed to columnar cells. Appearance of goblet cells in the anterior part of esophagus of the Caspian salmon and their secretions, carry the mammalian salivary glands functions in protecting the mucosa of the alimentary canal, although they cause food transition easy (Pahlavan *et al.*, 2001).

Another characteristic of the structure of salmonids' esophagus is the development of the adiposa layer, between the proper lamella and the muscular membrane. This layer, which is important in spawning migration and during the feeding is discontinued, was noted for the first time by Verigina and Savvaitova (1974) in *Salvelinus sp.* Adiposa layer was not appear in the esophagus of the Caspian salmon until parr stage and this is similar to that in *Onchorhynchus sp.* and *Hucho sp.* (Voronina, 1997). The primary stomach, as two groups of folds, were recognized in 10dph larvae. Development of the cardiac and pyloric parts, however, occurred in the onset of exogenous feeding. The simple and tubular gastric glands, apparently comprising of only one cell type, probably secreted both hydrochloric acid and enzymes. Absence of glands in the pylorus stomach suggested that the pylorus might not contribute enzymes or hydrochloric acid to further chemical digestions, but may only serve to facilitate such digestion by mechanical means (Ferraris *et al.*, 1987). Presence of mucopolysaccharid secretions, as our results revealed, may serve to protect epithelial cells from auto-digestion by the hydrochloric acid and enzymes produced by the gastric glands (Ferraris *et al.*, 1987). The folded structure of the mucous membrane of the stomach wall especially in the cardiac side is important at stomach dilation. Also, the findings revealed that the length of cardiac branch of stomach is longer than pylorus, confirmed that the predatory fishes posse a longer cardiac stomach, but the length of pyloric part of stomach does not change significantly (Verigina *et al.*, 1974).

The results revealed that stomach formation in the Caspian salmon is similar to that in other Salmonid species, from both morphological and histological point of views (Voronina, 1997). It has been hypothesized that stomach formation is important because that improved mechanical and enzymatic digestion of food, so development of the gastric glands and two parts of the stomach, in the onset of exogenous feeding, showed that the Caspian salmon larvae can digest dry diets at that time. Thus, because of beginning of secretion of digestive enzymes wet diets can be substituted by commercial foods (Bahrekazemi *et al.*, 2004). Although in 10dph larvae, we could recognize three parts of the intestine in the Caspian salmon but it became more differentiated by 25dph and the mucosal folds developed in the onset of active feeding. These folds, increase absorptive area without necessitating any increase in length of the gut and may aid in mixing the food with hepatic and pancreatic enzymes as well as mucous secreted by goblet cells (Baglolle *et al.*, 1997). Furthermore, the Caspian salmon has intestinal mucosal cells displaying cilia projecting into the lumen interior, which may function to aid in food movement. At 25dph larvae, the primary pyloric caeca were observed in the anterior part of intestine which increased in the number and length by age. It is believed that the pyloric caeca are involved in nutrient absorption (lipid) and digestion (proteinaceous compounds), primarily by an increase in surface area without increasing the length or thickness of the intestine itself (Baglolle *et al.*, 1997). They may also neutralize the acid entering the intestine from the stomach which is supported by the absence of pyloric caeca in stomachless fish (Gawlicka *et al.*, 1995). Another important morphological structure of the Caspian salmon's intestine, was series of large asymmetrical folds in the mucous membrane. It has been shown that they form the spiral valves, characteristic of all investigated representatives of the most recent bony fishes. The function of the spiral valves is to increase the absorption surface and to regulate food transportation along the intestine (Voronina, 1997). Voronina (1997) investigation revealed the presence of such folds in the middle gut of *Oncorhynchus sp.*, *Salvelinus sp.* and *Coregonus sp.* Such structure also was reported in the intestine of sturgeon fishes (Baglione, 1999; Gisbert *et al.*, 1998). It seems that in Salmonid fishes, pyloric caeca has more influence in food digestion than spiral valves, because its number surpass that of the spiral valve's coils.

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