
The morphology of the post-gastric alimentary canal in teleost fishes: a brief review

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Abstract: The rapid expansion of aquaculture in many parts of the world has supported vigorous research programmes on nutrition and the feeding of cultivated aquatic organisms. Teleosts, as an important source of food supply for human, have successfully adapted themselves to every type of aquatic habitat. This versatility is reflected in their mode of feeding. The digestive tract of fishes shows a remarkable diversity of morphological and functional characteristics. This is related to different feeding habits and to taxonomy, as well as to body shape and weight, size and sex. The morphology of post-gastric alimentary canal has also been studied from many species of fish because knowledge of fish's alimentary canal morphology is becoming increasingly important in fish digestive physiology and improvement of nutrition protocols. Identification of digestive tract structure is essential for understanding the related histophysiological mechanisms and nutritional functions. This knowledge may help identify differences in microscopic anatomy of alimentary canal among various teleost species. Fish intestine plays a vital role in digestion and absorption of dietary nutrients. The anatomical and histological characteristics of fish intestine are expected to be helpful for understanding the related functional mechanisms and feeding habits, which can further be helpful for diagnosing some intestinal diseases and formulating suitable feeds. The histological characteristics of fish intestine can be affected by abiotic and biotic factors. In present review, the morphological features of teleostean fish's intestine have been discussed in many species to provide the best available information on intestinal structure and morphology.

Key Words: morphology, post-gastric, alimentary canal, teleosts, review

Introduction

Aquaculture continues to be the fastest-growing animal-food-producing sector and to

outpace population growth, with per capita supply from aquaculture increasing from 0.7 kg

in 1970 to 7.8 kg in 2008, an average annual growth rate of 6.6 percent. World aquaculture is heavily dominated by Asia-Pacific region, which accounts for 89 percent of production in terms of quantity and 79 percent in terms of value (FAO Fisheries and Aquaculture Department 2010).

The fish sector is a source of income and livelihood for millions of people around the world. Employment in fisheries and aquaculture has grown substantially in the last three decades. In the past two decades, considerable progress has been made in addressing aquaculture governance issues through national and international corporate efforts with the common goal of sustainability of the sector. According to the report of Food and Agricultural Organization of the United Nations (FAO) in its most recently released State of World Fisheries and Aquaculture (2010), Fish accounted for 15.7 percent of the global population's intake of animal protein and 6.1 percent of all protein consumed in 2007. Globally, fish provides more than 1.5 billion people with almost 20 percent of their average per capita intake of animal protein, and 3.0 billion people with at least 15 percent of such protein. In 2007, the average annual per capita apparent fish supply in developing countries was 15.7 kg, and 14.4 kg in low-income food-deficit countries (FAO Fisheries and Aquaculture Department 2010).

Teleosts, as an important source of food supply for human, have successfully adapted

themselves to every type of aquatic habitat (Banan Khojasteh and Abdullahi, 2008). This versatility is reflected in their mode of feeding. Fishes inhabiting the same habitat resort to different types of feeding to avoid competition for food and also to utilize every available source of food. They can be broadly classified into carnivores, herbivores and omnivores. It is only natural that depending on the kind of food the alimentary canal should undergo suitable modifications for maximum utilization of the food taken (Anna Mercy and Pillai, 1985).

Understanding the biology of the innumerable number of aquatic species in our planet is the focus of sustained research efforts. Environmental degradation, management or rehabilitation of wild stocks, and the forecasted climatic changes are fueling interest in study of the ecology, feeding behavior and nutrition of aquatic animals in their natural habitat. In parallel, the rapid expansion of aquaculture in many parts of the world has supported vigorous research programmes on nutrition and the feeding of cultivated aquatic organism. More than 250 aquatic species are cultivated on a commercial scale using a wide variety of production systems. This great diversity results in great opportunities and tremendous challenges (Cyrino *et al.*, 2008).

The structure of the digestive tract of teleosts varies with different factors. Its functions include digestion, nutrients absorption, hormone secretion, immune

protection and water and salt transfers for hydro mineral homeostasis. It regulates energy and material exchange between the environment and the internal medium. Its structure is also variable according to the nature of the diet. Rather short in carnivorous species (20% of body length), the digestive tract is long (20 times the body length) in herbivorous fish. It comprises distinct portions: the mouth cavity, the esophagus, the stomach (some fishes are stomachless), the anterior and posterior intestine, and the rectum. With regard to its particular cytological characteristics, the intestinal epithelium, in addition to nutriment absorption, serves also osmoregulatory functions (Giffard-Mena *et al.*, 2006).

Correspondingly, of all vertebrate organ systems, the gastrointestinal tract and respiratory system are structurally the most variable (Rios *et al.*, 2004; Domeneghini *et al.*, 1999).

The digestive tract of fishes shows a remarkable diversity of morphological and functional characteristics. This is related to different feeding habits and to taxonomy, as well as to body shape and weight, size and sex (Kapoor *et al.*, 1975; Banan Khojasteh *et al.*, 2009a; Diaz *et al.*, 2008). However, regions in the intestine are not differentiated macroscopically (Scocco *et al.*, 1997; Gargiulo *et al.*, 1998). There have been many contributions, mainly morphological, to the knowledge of the structure of the alimentary tract of fishes

(Murray *et al.*, 1996; Voronina, 1997; Calzada *et al.*, 1998; Park and Kim, 2001, Diaz *et al.*, 2008; Al Abdulhadi, 2005; Cinar and Senol, 2006; Carrason *et al.*, 2006; Marchetti *et al.*, 2006; Dai *et al.*, 2007; Banan Khojasteh *et al.*, 2009a and 2009, b; Delashoub *et al.*, 2010; Banan Khojasteh *et al.*, 2011).

The morphology of post-gastric alimentary canal has also been studied from many species of fish (Murray *et al.*, 1996) and is of primary importance in the digestion and absorption of dietary nutrients. Each respective region has mucosal specializations that maximize the efficiency of the secretion, absorption and digestive functions (Buddington and Diamond, 1987; Stinson and Calhoun, 1993).

Knowledge of fish's alimentary canal morphology is becoming increasingly important in fish digestive physiology and improvement of nutrition protocols. Identification of digestive tract structure is essential for understanding the related histophysiological mechanisms and nutritional functions. This knowledge may help identify differences in microscopic anatomy of alimentary canal among various teleost species. On the other hand, study of the variation of the structure of the digestive system of fish species is useful for the nutritional development researches, preparation of diets and the handling of the feeding.

The interest to approach the histological study of these structures resides in the application of the knowledge more about

pathology of fishes, as contribution to the development of the fish farming and a rational use of the natural resources (Hernandez *et al.*, 2009).

The purpose of this review article is to provide the best available information on intestinal morphology of teleosts.

1. Ontogeny of the fish digestive system

The ontogeny of the digestive system of teleost fishes accompanies a significant number of changes at morphological and functional levels and has been studied in various species,

including sea bream (*Sparus aurata*), rainbow trout (*Oncorhynchus mykiss*), pike-perch (*Sander lucioperca*), *Solea senegalensis*, marble goby (*Oxyeleotris marmoratus*) and yellowtail kingfish (*Seriola lalandi*) (Calzada *et al.*, 1998; Sariyyupoglu *et al.*, 2000; Teresa, 2005; Riebeiro *et al.*, 1999; Abol- Munafi *et al.*, 2006; Chen *et al.*, 2006). While few fishes develop directly into juvenile with a complete functional digestive tract at hatch (Wolffish, *Anarhichas lupus*). The vast majority undergo a larval period before entering into the juvenile stage (Falk- Peterson and Hansen, 2001) (Fig. 1).

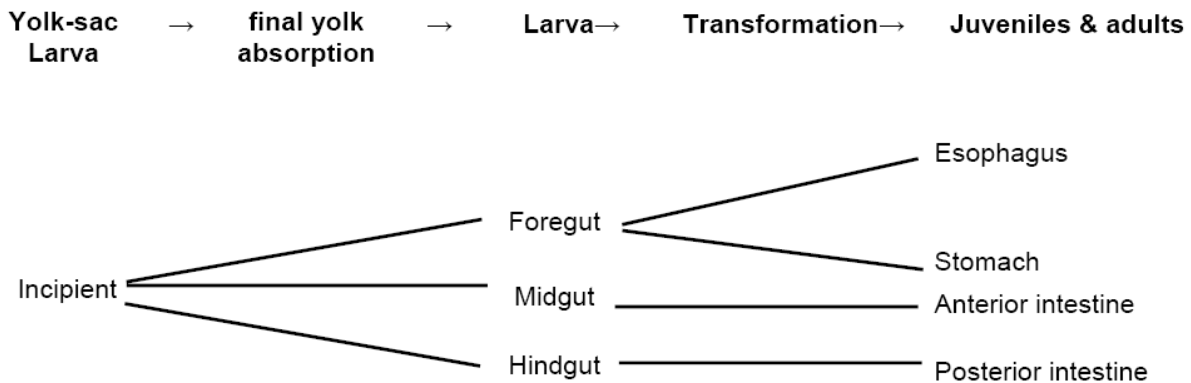


Fig. 1: The derivation, sequence and timing of alimentary canal organs in typical larval fishes (Govoni *et al.*, 1986)

From the time of hatching, teleost larvae must develop efficient structures and mechanisms for searching, capturing, absorbing and digesting food. Major morphological and functional changes must occur for the larva to survive one of the most critical stages of its life span, when these yolk reserves are almost exhausted (Calzada *et al.*, 1998).

The alimentary canal of fish larvae is morphologically, histologically and physiologically less elaborates than the alimentary canal of adult fishes. Unlike the gradual development of some other organ systems, e.g., the integument, visual, musculature, and acoustico-lateralis systems, the development of the alimentary canal from the simple, undifferentiated, straight incipient gut of the yolk-sac larva to the complex segmented alimentary canal of the adult proceeds by periodically rapid changes rather than continuous graduation (Govoni *et al.*, 1986).

Ontogenetic development of the digestive system in most teleost fish is generally divided into three major phases (Buddington, 1985; Boulhic and Gabaudan 1992; Bisbal and Bengtson, 1995). The first phase starts from hatching and ends at the completion of endogenous feeding. During this period, larvae depend on energy reserves in the yolk sac and oil globules. Toward the end of the first phase, fish experience a transition of endogenous to exogenous feeding before exclusively feeding on external food. The second phase starts from the

onset of exogenous feeding and ends before the formation of gastric glands in the stomach, characterized by the lack of sufficient digestive capabilities. During this phase, larval fish mainly depend on pinocytosis and intracellular digestion and absorption. As a result, fish larvae usually feed on live food such as rotifers that can be easily ingested and digested. The third phase starts from the presence of gastric glands and pyloric caeca to metamorphosis onward, indicating the functional maturation of the digestive system (Tanaka 1971; Bisbal and Bengtson 1995). The third developmental phase coincides with metamorphosis, when the digestive system anatomically and physiologically is ready to accept artificial pellets. Despite the overall similarity of the developmental pattern, the duration of each developmental phase varies among fish species. The understanding of ontogenetic development of the digestive system is crucial for larval fish rearing in any economically important aquaculture species (Chen *et al.*, 2006).

2. Gut organization

2.1. Topographical regions

The gastrointestinal tract of fishes can be subdivided into four topographical regions: The headgut, foregut, midgut and hindgut. Further morphofunctional subdivisions can be superimposed on this basic plan. The headgut is composed of the mouth and pharynx and its function is to acquire food and mechanically

process it. The foregut follows and is comprised of the esophagus and stomach, where chemical digestion of food begins (Fig. 1). In some fishes, the mechanical breakdown of food may also occur partially or fully in the stomach. The midgut accounts for the greatest proportion of the gut length and is where chemical digestion is continued and absorption mainly occurs. The hindgut is the final section of the gut, which includes the rectum; although in some cases there is no clear morphological distinction between midgut and hindgut. The foregut epithelium is of ectodermic and the hindgut of

endodermic origin (Grosell *et al.*, 2011).

2.2. The gross anatomical peculiarities of intestine

The intestine follows the pylorus or esophagus in gastric and agastric fishes, respectively. In some stomachless fishes, the anterior intestine may bulge to form an intestinal bulb or pseudogaster (Cyprinidae) and functions in temporary food storage (Fig. 2). Some parrotfish have a spherically shaped caecal chamber extending from the anterior intestine just after the esophagus to serve a similar function (Al- Hussaini, 1946).

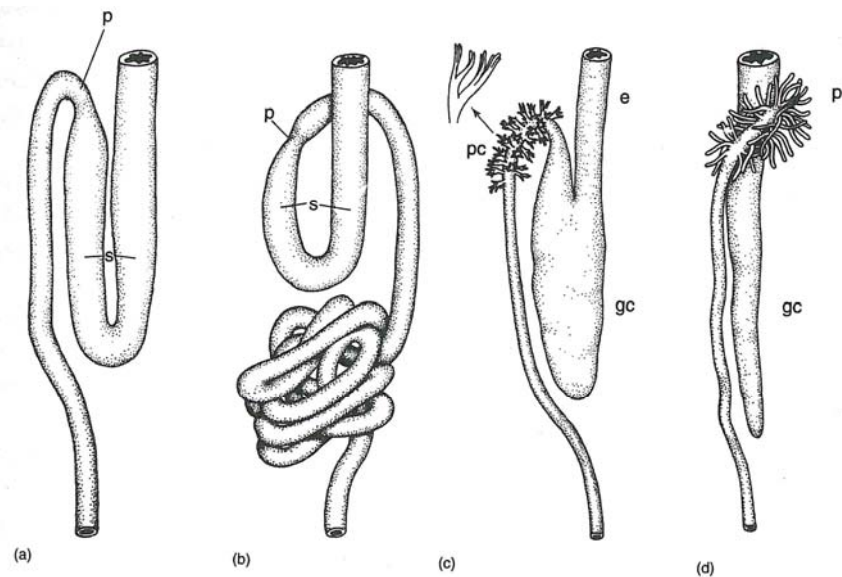


Fig. 2: Alimentary canals of four teleost fishes. (a) Fundulus, (b) Cyprinodon, (c) Elops and (d) Trichiurus. e: esophagus, gc: caecumlike stomach, p: pylorus, pc: pyloric caeca, s: intestinal bulb (or stomach) (Kent and Miller, 1997)

In contrast to mammals, there is no marked distinction between small and large intestine in fishes. Intestinal length is variable and is

generally correlated with feeding habits; carnivorous species often have shorter intestines than herbivorous fishes, and in these

latter extensive coiling takes place (Genten *et al.*, 2009).

The primary function of the intestine is the completion of the digestive processes started in the stomach and the absorption of nutrients. Central to this is optimizing intestinal surface area within the constraints of the coelomic cavity, which has a marked impact on intestinal morphology (Al- Hussaini, 1946).

Some species of bony fishes have an intestine with a relatively smooth surface. Other have longitudinal folds or folds forming a rather complex pattern or network and still others have villi, very similar to those found in higher vertebrates. A villus is a finger- like process of the mucosa which consists of an epithelial covering and a core of connective tissue containing blood and lymph capillaries. In fishes which possess villi, there may be considerable variation in their form between different species (Genten *et al.*, 2009).

A wide range of looping and coiled arrangements can be seen within the teleosts with long intestines (e.g. Cyprinidae; Loricariidae). However, some fish just have short, straight intestines with no looping or spiral valves (e.g. Cobitidae; Salmonidae) (Fig. 2). The intestine in some Scarides is constricted at short intervals giving a sacculated structure forming irregular internal pouches. Blind ended appendages (pyloric caeca) are found in osteichthyes (Buddington and Diamond, 1987). The blind diverticula termed pyloric caeca are

along the proximal intestine of many fish (Fig. 2 and 3). Over 2000 years ago, Aristotle described them in detail, recognized their distinction from the distally placed intestinal caeca of birds and mammals, and speculated that their function was "to store up the food as it might be in additional cellars and there putrefy it up and concoct it." Modern speculations about function have also focused on food storage, fermentation and digestion (Buddington and Diamond, 1986). On the other hand, the development of pyloric caeca in a variety of unrelated actinopterygians is an evolutionary strategy for effectively increasing intestinal surface area without increasing the length or thickness of the intestine. Caeca contribute significantly to total post-gastric surface area in some species (Perciformes) and experiments indicate that they are capable of enzymatic digestion and nutrient uptake similar to the proximal intestine (Eastman and Devries, 1997).

Hossain and Dutta (1996) estimated that 60% of known fish species possess pyloric caeca, which vary greatly in number (0-1000s), length and diameter. For example, in the flounder (Platichthyes) the caeca only appear as a few bumps on the intestinal wall, where as in the Salmonidae the caeca are long and numerous (Harder, 1975).

There is a strong positive correlation between the presence of pyloric caeca and the presence of a stomach (Genten *et al.*, 2009).

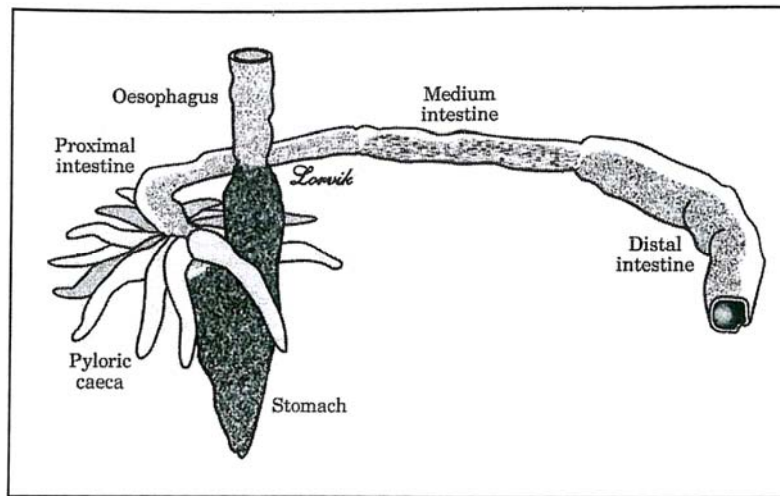


Fig 3: The Shi drum digestive tract (Pedini *et al.*, 2002)

Notably, intestinal villi (finger-like projections), characteristic of the mammalian intestine, are rare in fishes (Harder 1975; Kapoor *et al.*, 1975). The central villus lacteal (lymphatic vessel) is also absent in fishes. Mucosal glands are lacking in the intestine of almost all fishes with the exception of the Gadidae (cods), which have glands that are similar in appearance to the crypts of Lieberkuhn (Genten *et al.*, 2009).

Intestinal length is used as a morphological indicator of trophic level in nutritional ecology. However, intestinal length is influenced by a number of other factors apart from diet, which include fish size (mass and length) and body shape, recent feeding history (starved versus fed), ontogeny and phylogeny (Horn 1989).

2.2.1. Rectum

The ileorectal valve is only found in some teleost fishes. The rectum ends in a muscular sphincter that empties into the vent. Histologically the rectum is quite similar to the midgut in the teleosts. In trout, the rectal epithelial cells have vacuolated cells similar to the posterior intestine with their characteristic apical tubulovesicular system representing a differentiation of the intermicrovillous plasma membrane and large irregular vacuoles (Ezeasor and Stokoe, 1981).

2.3. Fine structure of intestinal wall

Compared to mammals, the teleost gastrointestinal tract is histologically simple and some fundamental points in the architecture of this tube, are remarkably constant (Genten *et al.*, 2009).

The intestine of fishes consists of structures similar to those found in terrestrial vertebrates. The histological patterns are also similar, and the same nomenclature can be applied in most cases (Banan Khojasteh *et al.*, 2009b).

Radially, the gut wall from foregut to hindgut consists of four concentric layers:

(1) The tunica mucosa usually consists of a mucosal epithelium overlying a layer of loose connective tissue or lamina propria that is vascularized and contains nerves and leukocytes (Stoskopf, 1993) (Fig. 4 and 5). The lamina propria may have a stratum compactum of dense connective tissue, such as is found in the intestine of rainbow trout (Banan Khojasteh *et al.*, 2009a) (Fig. 6). It is believed that the stratum compactum containing dense collagen layers function to strengthen and preserve the entirety of the gut wall (Banan Khojasteh *et al.*, 2009a). The lamina propria may also have a stratum granulosum consisting of granular eosinophilic cells found in the intestines of many fish (Stoskopf, 1993) (Fig. 6). Eosinophilic granule cells (EGCs) are considered to be analogous to mammalian mast cells and have been extensively described in various mucosal tissues including intestine, gills and skin. The function of the EGCs remains obscure although they have been implicated in physiological and pathological reactions. Involvement in such

reactions has led to the suggestion that they are analogous to the mammalian mast cells. It have described a potential association between EGCs and local nerves by inducing degranulation with the neurotoxin and tachykinin releasers capsaicin, and the neurotransmitter, substance P.A reduction in the number of observable EGCs within the intestinal stratum granulosum was seen within 1h following systemic administration of the drugs and recovery was observed by 4h. So, it has characterized a series of rapid morphological EGCs responses to bacterial pathogens which may be involved in mediating inflammatory reactions in fish (Powell *et al.*, 1993).

Underneath the lamina propria is usually a muscularis mucosae, for example in common carp (*Cyprinus carpio*), silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Hypophthalmichthys nobilis*) (Banan Khojasteh *et al.*, 2009b; Banan Khojasteh *et al.*, 2011; Delashoub *et al.*, 2010). However, some species like rainbow trout, lack muscularis mucosae (Banan Khojasteh *et al.*, 2009a).

(2) The three layers of the tunica mucosa are supported on a connective tissue tunica submucosa. Tunica submucosa is less cellular and contains blood vessels, lymphatic tissue and nerve plexi. Submucosal glands are usually lacking in fishes (Stoskopf, 1993).

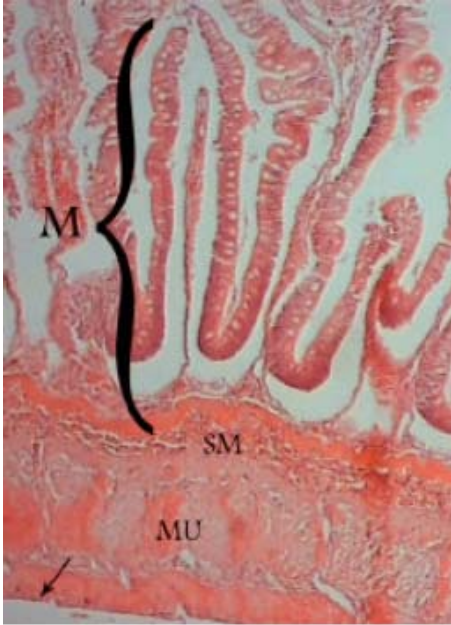


Fig. 4: Photomicrograph of mucosa of the intestinal wall of rainbow trout formed by tunica mucosa (M), tunica submucosa (SM), tunica muscularis (MU) and tunica serosa (arrow) (H&E, × 40) (Banan Khojasteh *et al.*, 2009a)

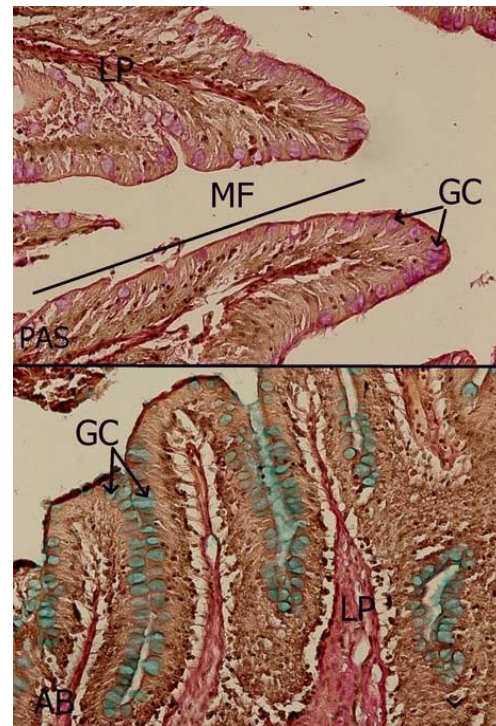


Fig. 5: Photomicrograph of transverse section of the proximal intestine in walking catfish with PAS and AB staining. Mucosal folds (MF) and goblet cells (GC) are shown (Raji and Norouzi, 2010)

(3) The tunica muscularis usually consists of inner circular and outer longitudinal layers of either striated or smooth muscle, although the relationship between these layers can be quite variable. Between these two layers, there are

Auerbach's plexi (Stoskopf, 1993).

(4) The tunica serosa is only present within the coelomic cavity and corresponds to mesothelial cells and loose connective tissue containing blood vessels (Genten *et al.*, 2009).

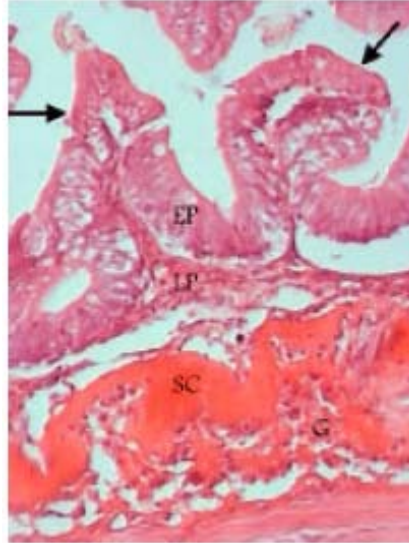


Fig. 6: Photomicrograph of intestinal wall of rainbow trout. Mucosal villi (arrows), epithelium (EP), lamina propria (LP), stratum compactum (SC) and stratum granulosum (G) (H&E, ×100) (Banan Khojasteh *et al.*, 2009a)

2.3.1. The intestinal epithelial cells

The intestine epithelium function primarily in lipid absorption and transport and that the rectum is important at least partially for protein degradation (Murray *et al.*, 1996).

The intestinal epithelium of the simple or pseudostratified columnar type, is made up of cells named enterocytes (columnar absorptive cells) possessing a well-marked striated border (apical brush border or microvilli). Goblet-type mucous cells, lymphocytes and enteroendocrine cells are scattered throught the epithelium and rodlet cells are also found in some species of teleost fishes (Kapoor *et al.*, 1975).

The columnar epithelial cells that dominate the intestinal epithelium are relatively homogenous in appearance but show regional

differentiation (Yamamoto, 1966).

2.3.1. a. Enterocytes

Enterocytes (or columnar absorptive cells) in many fish species are generally similar to those in other vertebrates (Marchetti *et al.*, 2006). These cells are both absorptive and secretory in function (Cyrino *et al.*, 2008). Enterocytes are generally tall and narrow, with elongated nuclei located just below the middle of the cell, mitochondria located in both apical and basal regions, a well developed brush border and lamellar structures running parallel to the lateral plasma membrane. It should be noted that fish generally lack the lateral interdigitations characteristic of mammalian enterocytes (Banan Khojasteh *et al.*, 2009 a).

Enterocytes show strong basolateral expression of $Na^+ / K^+ - ATPase$ which is essential in driving a number of transepithelial transport processes important for nutrient uptake and ion regulation (Genten *et al.*, 2009).

The brush border contributes greater than 90% to total intestinal surface area (*Tilapia aurea* and *T. zilli*; Frierson and Foltz, 1992) and forms the critical digestive/ absorptive interface, a functional microenvironment where enzymes involved in further food breakdown are located and where absorption and transport will occur (Kuzmina and Gelman, 1997). A number of enzymes like alkaline phosphatase, disaccharidases, leucine- aminopeptidase, and tri- and di-peptidases are localized to the brush border membrane in vertebrates including fishes (Kuzmina and Gelman, 1997).

The presence of these enzymes in the brush border has been demonstrated by enzyme histochemistry and immunohistochemistry. It has been demonstrated that the condition of the brush border, in particular the size of enterocyte microvilli in fish of different species can vary significantly. There is probably a link between feeding habits and the structure of the enterocyte brush border. The quantitative characteristic of the brush border is certainly dependent on the localization of the enterocyte in different parts of the fish intestine. Totally, there is fundamental similarity between the ultra structure of the intestinal epithelium in fish and other vertebrates (Kuperman and Kuzmina,

1994).

The general appearance of the enterocyte indicates an absorptive function. In the trout, lipid absorption in the anterior intestine and pyloric caeca has been demonstrated (Sire *et al.*, 1981).

In the posterior intestine, columnar epithelial cell, with large vacuoles have been identified as the site of macromolecular protein uptake (Genten *et al.*, 2009). However, it is important to keep in mind that the majority of protein uptake (80%) takes place in the anterior intestine (Fange and Grove, 1979).

3.3.1. b. Goblet cells

Goblet cells are common components of the post- gastric mucosa in fish (Buke, 1971; Groman, 1982). They first can be determined early during the differentiation of the intestinal mucosa of fish (Petrinec *et al.*, 2005).

Goblet cells are the dominant mucous cell type in the intestine of fishes. They derive their name from challis- like shape. The nucleus is located in the tapered stem, which widens and then constricts to form an apical pore through which mucus is discharged. When viewed by TEM (Transmission Electron Microscopy), the mucin granules that fill the greater part of the cells, have variable sizes and electron densities and occupy almost the whole cytoplasm of the cells (Banan Khojasteh *et al.*, 2009a; Reifel and Travill, 1979) (Fig. 7).

The intestinal goblet cells of many fish

species, synthesize neutral and sulphate mucins, and sialomucins containing sialic acid. The acid mucosubstances are made by carboxylated and sulfated mucocoujugates. The mucus secreted by goblet cells in the intestine has many functions. It lubricates undigested materials for onward progression into the rectum. Intestinal mucins may have a possible role in osmoregulation. Some studies have shown that the quality of gut mucosubstances is directly related to environmental conditions,

which in turn may directly affect the function of the alimentary tract. The presence of mucosubstances, especially those sulfated in the intestine; possibly regulate the transfer of proteins, or a fragment of them, as well as of ions and fluids. The possible role of mucosubstances in intestinal absorption processes is supported by the findings of Bozic *et al.*, (2001) who observed that starvation induced an increase in the number of intestinal goblet cells in carp (Petrinec *et al.*, 2005).

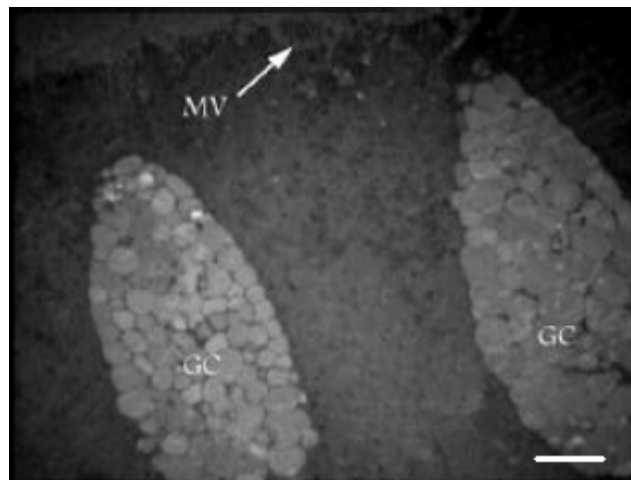


Fig. 7: Electron micrograph of goblet cells in intestine of rainbow trout that have mucus granules with different sizes and densities. MV: microvilli, GC: goblet cell (scale bar: 5 μ) (Banan Khojasteh *et al.*, 2009a)

Carbohydrate compounds are the main component of intestinal mucus in vertebrates. Grau *et al.*, (1992) reported that neutral mucous compounds of the intestine participate in enzymatic food digestion, formation of food

mass and absorption (Teresa, 2005).

In many species, it has observed that their number increased from the pyloric caeca to the rectum. The increased number of goblet cells in the rectum may imply the need for increased

mucosa protection and lubrication for fecal expulsion (Murray *et al.*, 1996).

It has known that the mucus Produced by the fish goblet cells protects the mucosa of digestive tract. Sialic acid in fish mucus disturbs receptor detection by the viruses, and protects the mucosa against the bacterial sialidase (Teresa, 2005).

2.3.1. c. Rodlet cells

The rodlet cells are associated with many epithelial tissues, including gut lining of teleostean fishes. They have been observed in a large number of species, although expression is not always consistent between individuals of a given species (Reite, 1998). The cells have remained an enigma in fish biology. The mature cells are ovoid, have a basally located nucleus and characterized by a wide fibrous layer beneath the plasma membrane and the presence of large rod-shaped cytoplasmic granules from which they get their name. They have typical cellular organelles. These cells have been hypothesized to be of either an exogenous (parasitic) or endogenous origin, with recent data supporting the latter (Manera and Dezfuli 2004).

Some researchers suggested that rodlet cells may be involved in water or electrolyte transport or have functions similar to those of mucous cells, e.g. pH control, lubrication, antibiotic effects and reaction to the presence of ectoparasites on epithelial surfaces and that an

antibiotic substance secreted by these cells helps dampen the parasitic infections. Some observations suggested that rodlet cells play a role in host defense mechanism in fish (Reite, 1998).

2.3.1. d. Enteroendocrine cells

Gastrointestinal endocrine cells are distributed in the mucosa of the gastrointestinal tract and they synthesize various kinds of gastrointestinal hormones. They play important functions in the regulation of the physiological functions of the digestive tract. The existence of endocrine cells has been immunohistochemically demonstrated in the gastrointestinal tract mucosa of different fish species (Diler *et al.*, 2011). These cells have found throughout the epithelium of the digestive system (Holmgren and Olsson, 2009) and with the pancreas constitute the gastroenteropancreatic (GEP) endocrine system.

Many reports have dealt with the identification of regulatory peptides of the alimentary tract in fish species using silver-staining techniques and either radioimmunochemical methods. Secretions of many endocrine cells act in digestion processes together in fishes. The secretions, located in the gastrointestinal tract, are the chemicals regulating tracts structure and functions. These chemicals in gastrointestinal tract, accepted as the largest endocrine organ, are mainly secreted by endocrine cells. These secretions,

which are called peptide and/ or amine, are detected in lamina epithelialis, glands, several connective tissues, mucosal nerve ganglions and intermuscular nerve plexus. These secretions assure the mobility as well as the proper functioning of the nervous system, regulation of secretion through the cellular interaction, cellular proliferation, and regulation of the intestinal epithelium and the contraction of the smooth muscles (Kuru *et al.*, 2010).

They can be readily identified by the presence in the cytoplasm of very characteristic secretory vesicles, the so-called dense core vesicles, which have a halo between the electron- dense core and the surrounding membrane. Subtypes of enteroendocrine cells are classified by their relative position within the epithelium with the open type extending to the apical membrane while the closed type does not, as well as on the basis of difference in secretory granule morphology (size, shape and the electron density) and the expression of neuroendocrine substances by immunohistochemistry (e.g. gastrin/cholecystokinin, ghrelin, somatostatin, serotonin) (Holmgren and Olsson, 2009; Genten *et al.*, 2009).

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