

Histological structure of the Altai Osman digestive tract, *Oreoleuciscus potanini* (Cypriniformes: Leuciscidae)

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Abstract

This study focuses on the histomorphological analysis of the digestive tract of the omnivorous ecological form of Altai Osman (*Oreoleuciscus potanini* Kessler, 1879), an endemic carp species of Central Asia that lacks a morphologically distinct stomach. Four distinguishable sections were identified: esophagus, foregut, midgut, and posterior intestine. The esophagus was characterized by the presence of a multilayered squamous epithelium, an abundance of goblet cells (average 15.6 cells/100 μm), and a thick muscle layer (263.1 μm) consisting of transverse striated muscle. The foregut exhibited the maximum height of the mucosa fold (811.6 μm), the height (811.6 μm), columnar epithelium (77.5 μm), and enterocyte nuclei (27.4 μm^2), indicating its leading role in digestion and nutrient absorption. The midgut was characterized by a decrease in the fold height (581.7 μm) and an increase in the number of goblet cells (2.9 cells/100 μm) compared to the foregut. The posterior intestine exhibited the lowest fold height but the highest number of goblet cells (5.6 cells/100 μm) and intraepithelial leukocytes (16.4 cells/100 μm). Supranuclear vacuoles were also found in the posterior epithelium. Elements of gut-associated lymphoid tissue (GALT), including intraepithelial leukocytes and eosinophil-like cells, were detected in all parts of the digestive tract. The study revealed histomorphological characteristics of the Altai Osman digestive tract attributable to its omnivorous diet.

Keywords

Histology, intestine, esophagus, stomachless fish, goblet cells, histomorphometry, nutrition

Introduction

Fishes are the most numerous groups, comprising more than half of the total number of vertebrate species. Their ubiquity contributes to a wide range of functional adaptations to diverse habitats and considerable morphological diversification (Wilson and Castro 2010). The digestive system of fishes is characterized by exceptional variability, exhibiting many specific adaptations, including: jaw morphology and topography (Adamek-Urbaska et al. 2023), gastric shape (Wilson and Castro 2010; Alonso et al. 2015), position, shape, and number of pyloric appendages (Genten et al. 2009), length of the intestinal tract (Rincón et al. 2023), and shape, position, and tissue organization of the pancreas and liver (Akiyoshi and Inoue 2004). The relationship between digestive morphology and trophic status in fish is well documented in the literature (Okuthe and Bhomela 2021; Qu et al. 2012; Pewhom and Vanikasampanna 2024). Predatory species tend to have a well-developed stomach and a relatively short intestine, while herbivorous species are characterized by a smaller stomach and an elongated intestine. Omnivorous fish, whose diets include both plant and animal components, typically have large stomachs and moderately long intestinal tracts (Grosell et al. 2011). It is important to note that the structure of the gastrointestinal tract is not only determined by the type of diet, but is also closely related to the phylogeny and ontogeny of a particular species (Ahsan-ul-Islam 1951; Wilson and Casto 2010).

Of considerable interest to researchers are agastric fish, characterized by the absence of a morphologically differentiated stomach and the presence of intestines without clear anatomical boundaries. The clade Atherinomorpha, which includes the orders Atheriniformes, Beloniformes, and Cyprinodontiformes, is the most representative group of gastricless fishes (Domínguez-Castanedo et al. 2024). The absence of the stomach is also observed in members of carp, finfish, sucker, goby, and several other families (Wilson and Castro 2010). The presence of the stomach is a key evolutionary innovation in vertebrates that significantly increases digestion efficiency through acid-peptic cleavage. The absence or secondary loss of the stomach in many species of fish is considered an adaptation that optimizes digestion and metabolism in response to a specific diet characterized by low-calorie components and to certain feeding strategies (Grosell et al. 2011).

Altai Potanin Osman (*Oreoleuciscus potanini* Kessler, 1879) belongs to the carp family and is an endemic species widely distributed in water bodies of Central Asia (Popov 2013; Dgebuadze et al. 2017). This species is characterized by several morphoecological forms (dwarf – planktonophage, herbivorous, predatory, and sharp-nosed), whose morphological adaptations are determined by habitat conditions and diet (Kottelat et al. 2006). The ecology and peculiarities of the Osman diet have been

investigated in detail in a number of works (Mironovsky et al. 2019; Golovanova et al. 2007), which indicate that its diet mainly consists of plant components and invertebrates, while large individuals consume fish. However, to our knowledge, the histological structure of the Osman digestive system has not been previously investigated. The different feeding habits of Osman ecological groups may be reflected in the unique digestive system adaptations of fish, which can be identified at the histological level.

Histological methods are an important tool for studying the morphofunctional diversity of organs (Peterson et al. 2015). The study of the organization of the digestive system is of great importance for understanding the mechanisms of morphological diversification and the formation of the trophic structure of aquatic ecosystems (Jeamah et al. 2023). Additionally, histological data allow for a more detailed investigation of digestive physiology and feeding patterns (Lampang et al. 2021). Extensive data from the literature on the structure of the digestive system of fish from different taxonomic groups provide valuable information to clarify the phylogenetic position of species (Alonso et al. 2015). For farmed species, these data can also contribute to the optimization of feed formulations (Buddington et al. 1997).

The aim of the study was to investigate the histological structure of the Altai Osman digestive tract (*Oreoleuciscus potanini*) and to characterize its parts on the basis of the histomorphometric parameters of the tissues.

Materials and methods

Specimens of Altai Potanin's Osman were caught from Lake Kidelyu (50°29'50.881"N, 87°39'03.416"E), located in Ulagan District, Altai Republic, Russian Federation. The fish were captured in September 2021 using gill nets (mesh size 18–40 mm) set at various locations within the lake for 12 h. The identification of Osman was performed using data from Dgebuadze et al. (2020). Standard length (SL) and body weight were measured following established protocols (Froese 2006), age was determined from otoliths or scales (Panfili et al. 2002), and gut contents were evaluated using standard dissection methods (Amundsen, Sánchez-Hernández 2019). The digestive tract of Osman predominantly contained various algae and chironomid larvae; some individuals also contained gastropod mollusks.

For histological preparation, digestive tract sections were sampled from 10 Altai Osman, aged 3+, with an average length of 9.2 ± 0.5 cm and a weight of 9.8 ± 1.5 g. Tissue samples (3–7 g) were fixed for 24 h in Davidson's solution and then transferred to 70% ethanol for further processing. The samples were processed through a series of increasing concentrations of ethanol: 80% for 1 hour, 95% for 1 hour, and 99% for two changes of 1 hour each, using a Citadel 2000 automated tissue processor (Thermo FS, USA). Subsequently, the samples were clarified in xylene for 1.5 hours and embedded in paraffin. Using a Minux S700A microtome (RWD Life Science, China) microtome, 4- μ m-thick serial sections of 4 m thick were cut from

the samples and stained with hematoxylin-eosin (HandE) and periodic acid–Schiff (PAS). Histological section preparation and staining followed standard methodology (Suvarna et al. 2018). The preparations were examined using an Olympus BX53 light microscope (Olympus Corp., Japan) equipped with Carl Zeiss ERc 5s (Zeiss, Germany) and ToupCam 16.0 MP cameras (ToupTek Photonics, China). Image acquisition and analysis were performed using ZEN lite software (Zeiss, Germany) and ToupCam view 16.0 (ToupTek Photonics, China).

Using the Fiji ImageJ2 v2.15.0 program (Schindelin et al. 2012), the following histomorphometric parameters were measured and calculated from tissues of different parts of the digestive tract: height of mucosal folds and epithelium; area of epithelial nuclei and goblet cells; thickness of intrinsic lamina (lamina propria), submucosa, muscularis, and serosa; and the number of intraepithelial leukocytes and cells per 100 μm of mucosa (cell/100 μm). For each gut region, a minimum of 30 independent measurements per parameter were taken per individual fish ($n = 10$). A detailed description of the measured morphometric parameters is provided in earlier studies (Kochetkov et al. 2023; Kochetkov et al. 2024).

Data comparing the variables analyzed are presented as mean \pm SD. Statistical significance was determined using a non-parametric Kruskal–Wallis test with Dunn's post-hoc test for pairwise comparisons. This was preceded by an assessment of data distribution and homogeneity of variances using Shapiro–Wilk and Levene tests. A value of $p < 0.05$ was accepted as statistically significant. Statistical data were processed using GraphPad Prism v 9.0 (GraphPad, San Diego, CA, USA) and RStudio v 3.6.0 (RStudio, PBC, Boston, MA) with R v 4.4.3 (R Core Team 2025).

Results

On histological sections, the Altai Osman digestive tract showed the following clearly distinguishable regions: esophagus (ES), anterior (AI), middle (MI) and posterior intestine (PI) (Fig. 1). Throughout its length, the digestive tract comprised the following layers: mucosa, submucosa, muscularis, and serosa. The mucosa formed folds, whose sizes varied between different regions of the digestive tract (Fig. 1a–d). Serosa in all regions consisted of the mesothelium and vascularized connective tissue.

The height of the esophageal folds varied considerably, averaging 370.9 μm (Table 1). The epithelium included a large number of goblet cells (mucoïd), which were located throughout the mucosal surface (Fig. 1i). Their occurrence averaged 15.6 cells per 100 μm of mucosa (cells/100 μm), significantly higher ($p < 0.05$) than those found in other sections (Table 1). The esophageal mucosal epithelium was predominantly represented by a stratified squamous epithelium (Fig. 2a, b), which transitioned to columnar in the posterior part of the esophagus. Clusters of intraepithelial leukocytes and eosinophil-like cells were observed near the basal membrane (Fig. 2a). The submucosa consisted of loose connective tissue and contained immuno-

competent cells (lymphocytes and eosinophil-like cells) (Fig. 2C). The esophageal muscle consisted of transverse striated muscle, exhibiting characteristic striation. The esophageal muscular layer was significantly the thickest ($p < 0.05$) among all parts of the digestive system, measuring 263.1 μm .

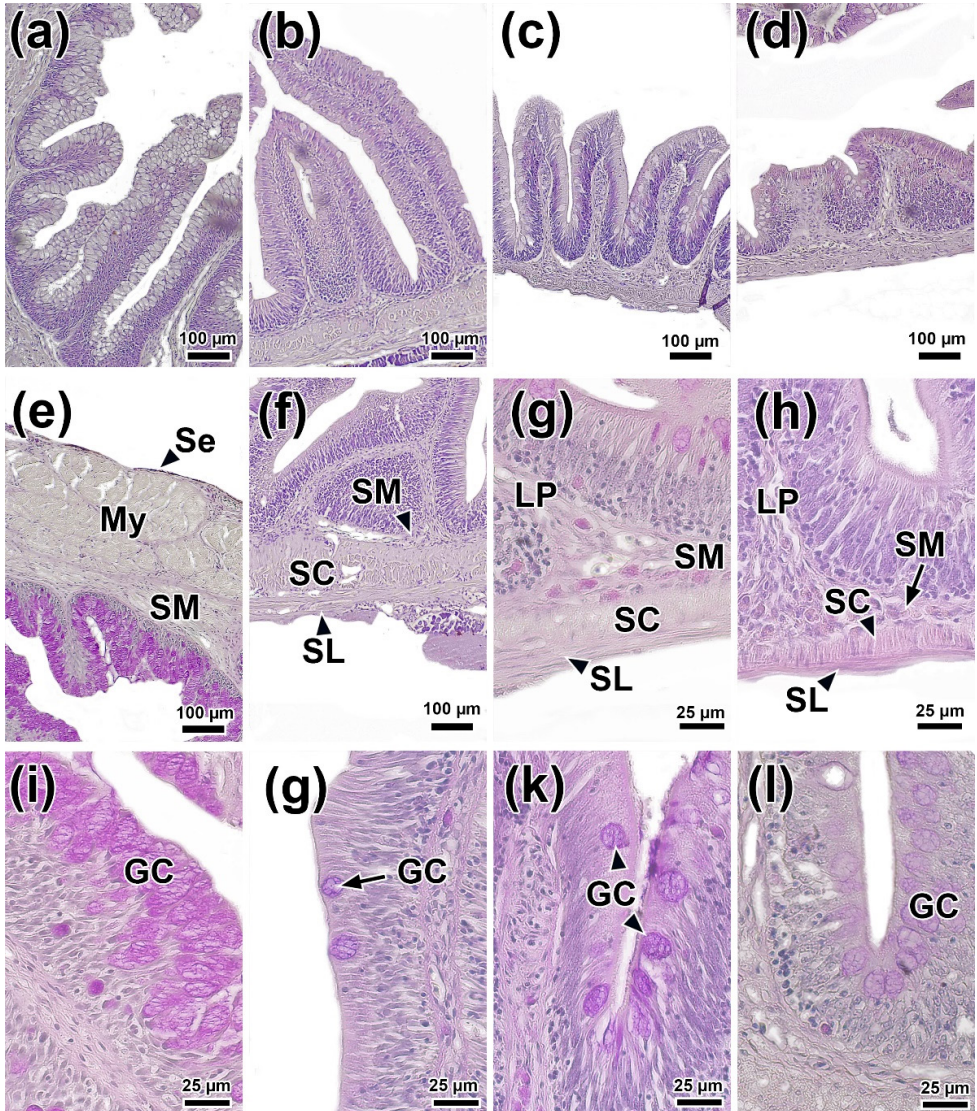


Figure 1. Histological sections of the esophagus (a, e, i), anterior (b, f, j), middle (c, g, k), and posterior (d, h, l) intestine of the Altai Osman. Abbreviations: Se – serosa, My – muscularis, SM – submucosa, SC – stratum circulare, SL – stratum longitudinale, LP – lamina propria, GC – goblet cell. Scale bars are 100 (a–f) and 25 μm (g–l). H&E (a–d, f, h) and PAS (e, g, i–l) staining.

At the transition from the esophagus to the intestine, an esophageal-intestinal sphincter, composed of smooth muscle, was observed. The mucosal folds in the anterior part of the intestine exhibited the significantly highest height ($p < 0.05$) compared to other sections (Fig. 1d). The anterior mucosa consisted of a columnar epithelium with dense cytoplasm and elongated basophilic nuclei positioned near the basal membrane (Fig. 2d). The height of the epithelium in this section was averaged 77.5 μm , significantly higher ($p < 0.05$) than that of the middle and hindgut. Microvilli were present on the apical side of enterocytes (Fig. 2e). The density of goblet cells was minimal in this section, averaging 1.0 cells/100 μm (Fig. 1g). Intraepithelial lymphocytes formed groups near the basal membrane of enterocytes (Fig. 2e). Eosinophil-like cells were found predominantly in the submucosa (2.3 cells/100 μm). The intestinal musculature was made up of smooth muscle, arranged in two layers: an inner circular layer (stratum circulare) and an outer longitudinal layer (stratum longitudinale) (Fig. 1f).

Table 1. Histomorphometric parameters of different parts of the digestive tract of the Altai Osman

Parameters	ES	AI	MI	PI
Fold height, μm	370.9 \pm 18.5 ^{bc}	811.6 \pm 20.6 ^a	581.7 \pm 38.5 ^{ab}	278.2 \pm 23.0 ^c
Epithelium height, μm	87.9 \pm 3.7 ^a	77.5 \pm 1.3 ^{ab}	45.2 \pm 0.7 ^b	40.3 \pm 1.3 ^b
Epithelium nuclei Area, μm^2	19.0 \pm 0.4 ^b	27.4 \pm 1.1 ^a	26.7 \pm 0.9 ^a	20.0 \pm 0.7 ^b
Number of goblet cells, cell/100 μm	15.6 \pm 0.2 ^a	1.0 \pm 0.1 ^c	2.9 \pm 0.1 ^{bc}	5.6 \pm 0.1 ^b
Area of goblet cells, μm^2	152.2 \pm 6.9 ^{ab}	187.3 \pm 3.8 ^a	130.1 \pm 4.5 ^{bc}	111.1 \pm 4.4 ^c
Lamina propria thickness, μm	19.9 \pm 1.8 ^a	15.5 \pm 0.6 ^{ab}	13.7 \pm 0.3 ^b	15.6 \pm 0.5 ^{ab}
Number of intraepithelial leukocytes, cell/100 μm	11.5 \pm 0.1 ^c	12.4 \pm 0.3 ^{bc}	13.8 \pm 0.3 ^{ab}	16.4 \pm 0.7 ^a
Number of eosinophil-like cells, cell/100 μm	1.7 \pm 0.1 ^b	2.3 \pm 0.2 ^{ab}	3.3 \pm 0.1 ^a	2.5 \pm 0.2 ^{ab}
Subucosa thickness, μm	52.6 \pm 3.1 ^a	27.9 \pm 1.4 ^{ab}	19.6 \pm 0.5 ^b	18.8 \pm 0.4 ^b
Muscularis thickness, μm	263.1 \pm 6.4 ^a	105.8 \pm 4.3 ^b	37.7 \pm 1 ^c	26.4 \pm 2.1 ^c
Serosa thickness, μm	13.1 \pm 0.4	13.0 \pm 0.5	12.1 \pm 0.6	11.9 \pm 0.5

Note: Superscript letters (a, b, c) indicate statistical significance ($p < 0.05$) between different groups from the Kraskell-Wallis test.

The middle intestine was characterized by a decrease in the height of the mucosal folds (581.7 μm) and the height of the columnar epithelium (45.2 μm) compared to the anterior intestine (Fig. 1c). Furthermore, the area of epithelial nuclei was not significantly different between the two sections, but was significantly higher than in the esophagus ($p < 0.05$). There were no morphological differences in enterocytes compared to the anterior section (Fig. 3a). The number of goblet cells in this section was 2.9 cells/100 μm , significantly different from other intestinal sections (Fig. 1k).

Individual rodlet cells were found in the mucosa, which had an oval shape, a round nucleus, thick capsule-like borders and rod-like cytoplasmic inclusions (Fig. 3b). Groups of intraepithelial leukocytes were observed throughout the mucosa, with a density of 13.8 cells/100 μm . Eosinophil-like cells were common in both the submucosa and epithelium, with a density of 3.3 cells/100 μm , significantly higher ($p < 0.05$) than in the esophagus and foregut. These cells had an eosinophilic cytoplasm and prominent granulation when stained with H&E, and were PAS positive, making them easier to count (Fig. 3c). The thickness of the submucosa and muscularis decreased significantly after the transition to the middle section (Fig. 1g).

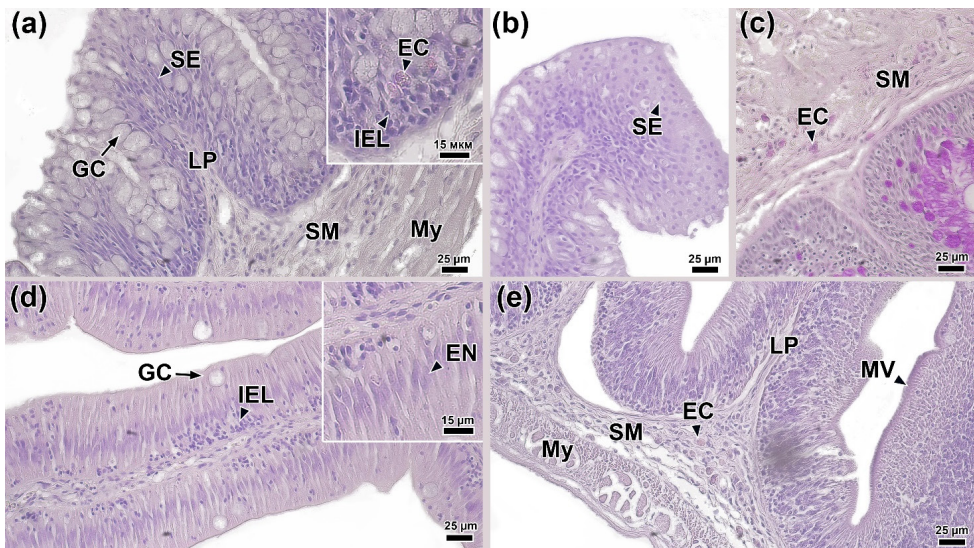


Figure 2. Histological sections of the esophagus (a–c) and anterior intestine (d, e) of Altai Osman. Abbreviations: GC – goblet cell (Mucoid), SE – squamous epithelium, LP – lamina propria, My – muscularis, SM – submucosa, IEL – intraepithelial leukocyte, EC – eosinophil-like cell, EN – enterocyte nuclei, MV – microvilli. The scale bars are 25 and 15 μm . H&E (a, b, d, e) and PAS (c) staining.

The posterior intestine of Altai Osman had the least developed mucosal folds; the average height of the folds was 278.2 μm (Fig. 1d). The epithelial nucleus area was the smallest among all intestinal sections. The columnar epithelium of the posterior section exhibited obvious granulation on the apical side (supranuclear vacuoles) (Fig. 3d). Enterocytes possessed well-developed microvilli. The number of goblet cells (Fig. 1l) and intraepithelial lymphocytes (Figs. 3d, f) was the highest in this section compared to the anterior and middle intestine. Individual rodlet cells were observed in the mucosa, predominantly located on its luminal surface (Fig. 3e). The thickness of the submucosa was not significantly different from the midgut, but was significantly lower ($p < 0.05$) than in the esophagus and anterior intestine

(Fig. 1h). Similar differences were also observed for the muscularis. The appearance of eosinophil-like cells was slightly lower than in the midgut. The distribution of these cells in the tissue was similar to that of the middle intestine.

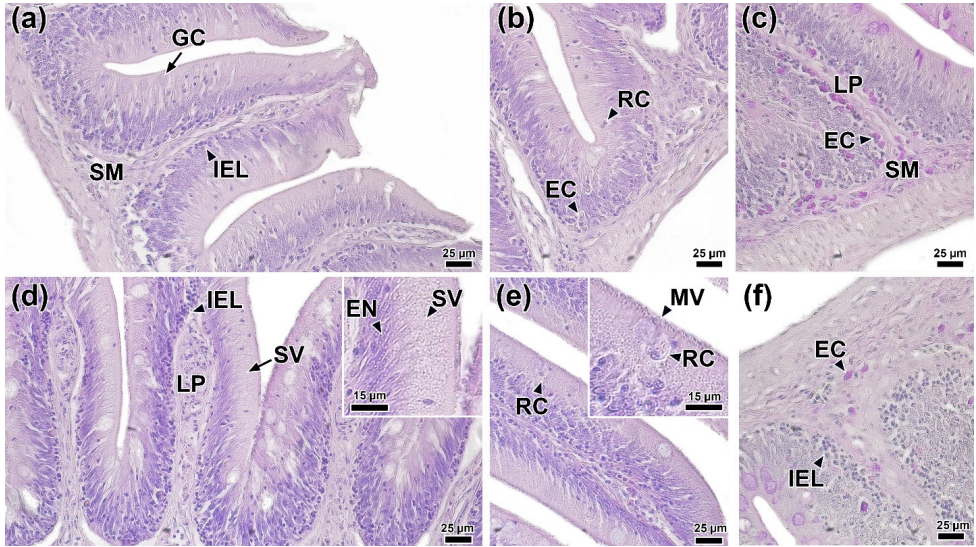


Figure 3. Histological sections of the middle (c–d) and posterior intestine (d–e) of the Altai Osman. Abbreviations: GC – goblet cell, LP – lamina propria, SM – submucosa, IEL – intraepithelial leukocyte, EC – eosinophil-like cell, SV – supranuclear vacuoles, EN – enterocyte nuclei, RC – Rodlet cell, MV – microvilli. The scale bars are 25 and 15 μm. H&E (a, b, d, e) and PAS (c, f) staining.

Discussion

Currently, the digestive system of fish is topographically divided into four parts: (1) headgut, consisting of the mouth and pharynx; (2) anterior, including the esophagus and stomach; (3) middle, comprising the greatest length of the gut; and (4) posterior, including the rectum (Grosell et al. 2011). Based on functional features, it has been proposed to supplement the division of the intestine into anterior, middle, and posterior compartments. This approach has been successfully applied in studies on the model organism *Danio rerio* (Hamilton, 1822), a representative of agastric fishes (da Cunha et al. 2020). In the present work, four parts of the Osman digestive tract were investigated: the esophagus, the anterior, middle, and posterior intestines. Histomorphometric analysis revealed distinct microanatomical differences between these sections. No significant morphological differences were found between the rectum and the hindgut in the studied Osman individuals, as previously reported for some fish species (Wilson and Castro 2010).

The key histological features of the esophagus were the presence of a squamous epithelium in the mucosa and a large thickness of the muscular layer represented by skeletal muscle. The presence of multilayered epithelium in the mucosa, together with mucin produced by mucoid cells, provides protection for the underlying tissues from the physical impact of food. The ability of the squamous epithelium to rapidly renew allows rapid repair of damage and ensures the integrity of the mucosa. The skeletal musculature, due to its ability to contract rapidly and forcefully, ensures the passage of food from the esophagus to the intestine (Kalhoró et al. 2018). A similar esophageal structure has been observed in fish with different feeding types: *Allenbatrachus grunniens* Linnaeus, 1758 (Mitparian et al. 2021), *Larimichthys crocea* Richardson, 1846 (Kalhoró et al. 2018) and *Stegastes fuscus* Cuvier, 1830 (Canan et al. 2012). The transition from squamous to columnar epithelium in the distal esophagus, as previously reported in the literature (Okuthe and Bhomela 2021; Mitparian et al. 2021), is presumably associated with the onset of chemical digestion. The thickness of the oesophageal muscular wall and the abundance of goblet cells may be adaptations that enable the Osman to feed on crustaceans with hard chitinous cuticle, as well as small gastropods.

Of all sections of the digestive tract, the Altai Osman exhibited the most developed mucosal folds, the highest epithelial layer height and the largest enterocyte nuclear area of enterocytes. These prominent folds significantly increase the area for nutrient absorption, and the substantial height of the columnar epithelium indicates increased tissue metabolic activity (Sun et al. 2019). This suggests that the anterior compartment plays an important role in digestion and nutrient absorption. Similar results have been previously reported in *Pristolepis fasciata* Bleeker, 1851 (Pewhom and Vanikasampanna 2024) and *Anablepsoides urophthalmus* Günther, 1866 (Nascimento et al. 2018). In agastric fishes, characterized by the absence of a stomach and compact digestive glands, the dominant types of digestion are cytosolic and membrane digestion. Microvillus enzymes and trypsin play a key role in this process (Olsson et al. 2009; Toledo-Cuevas et al. 2024). The pancreas and gallbladder ducts open into the foregut of agastric fish, confirming its crucial role in digestion (Rombout et al. 2011). For the omnivorous form of the Altai Osman, which consumes both algae and various invertebrates, this type of digestion allows adaptation to a low-calorie diet with frequent consumption of food in small portions. This once again demonstrates the significance of the foregut for the digestion of agastric fish.

The middle intestine of the Altai Osman had less developed mucosal folds and thinner muscularis, with a higher occurrence of goblet cells. Mucin produced by goblet cells not only provides protective and lubrication functions but also facilitates the emulsification and enzymatic breakdown of nutrients due to the presence of cofactors (Peterson, 2015; Grosell et al. 2011; Anderson, 1986). The key role of the middle intestine in nutrient absorption in fish has been demonstrated in studies on *Ctenopharyngodon idella* Valenciennes, 1844 (Stroband and Meer, 1979), as well as

Sparus aurata Linnaeus, 1758 and *Oncorhynchus mykiss* Walbaum, 1792 (Santigosa et al. 2011).

The posterior intestine of the Altai Osman exhibited the lowest fold height and muscle thickness, yet the highest incidence of intraepithelial mononuclear leukocytes and goblet cells. Decreases in intestinal digestive function and increases in immune and osmoregulatory activity from the anterior to posterior compartment have been reported for many fish species (Okuthe and Bhomela, 2021; Alonso et al. 2013), including agastric fish (Ghosh et al. 2011; Domínguez-Castanedo et al. 2024). The supranuclear vacuoles found in the posterior epithelium are believed by several authors to be involved in the transport of macronutrients (peptides) and antigens (Peterson, 2015; Ikpegbu et al. 2014). The large number of goblet cells in the posterior compartment, compared to the anterior and middle compartments, is in turn associated with lubrication of the intestinal contents, which facilitates their evacuation (Cho et al. 2023). Therefore, there is a correlation between increased functional activity of the hindgut of fish and its morphological features. For agastric fish, such as Altai Osman, the hindgut has a much greater functional role in completing the digestion and absorption of nutrients.

Mononuclear leukocytes and eosinophil-like cells found throughout the Altai Osman digestive tract are part of intestinal-associated lymphoid tissue (GALT) (Rombout et al. 2011). Immunocompetent GALT cells play an important role in protecting the gut from foodborne pathogens, as well as maintaining a balance with the gut's own microbiome (Rombout et al. 2014). GALT immune cells are predominantly located in the lamina propria and submucosa. Their occurrence is usually maximal in the posterior intestine (Inami et al. 2009), which was confirmed for Altai Osman. Eosinophil-like cells have been found in many species of fish (Sukhee et al. 2024; Toledo-Cuevas et al. 2024) and are probably analogous to mast cells in mammals, being involved in the regulation of immunity and defense against parasites (Reite et al. 2005; Buddington et al. 1997). The development of GALT in the mid and posterior intestines of Altai Osman may suggest an immune response to diet components or parasitic infestations.

Conclusion

The Altai Osman digestive tract consists of four histologically distinguishable sections: the esophagus, anterior, middle, and posterior intestine, with the rectum morphologically indistinguishable from the posterior section. The esophagus is characterized by the presence of multilayered squamous epithelium, numerous goblet cells (approximately 15.6 cells/100 μm), and a thick layer of skeletal muscle tissue (263.1 μm in thickness). The foregut is the main site of digestion and nutrient absorption, as evidenced by the maximum mucosal fold height (811.6 μm), epithelium height (77.5 μm), and enterocyte nuclear area (27.4 μm^2). The posterior intestine shows the lowest fold height (278.2 μm) but the highest number of goblet cells (5.6 cells/100

µm) and intraepithelial lymphocytes (16.4 cells/100 µm), indicating its role in both nutrient absorption and immune defense. Gut-associated lymphoid tissue (GALT) elements, including intraepithelial leukocytes and eosinophil-like cells, were detected in all parts of the digestive tract. Their maximum occurrence was observed in the midgut and hindgut.

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