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THE PLASTICITY AND MORPHOFUNCTIONAL ORGANIZATION OF THE DIGESTIVE SYSTEM OF WADERS (CHARADRII) AS MIGRANTS

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The Plasticity and Morphofunctional Organization of the Digestive System of Waders (Charadrii) as Migrants. Kovtun, M. F., Lykova, I. O., Kharchenko, L. P. — The results of the macro-micromorphological structure of the digestive system of the waders and comparative analysis with the migrants of the Aves are presented. It was revealed that the digestive system of waders at the anatomical level has a universal structure typical for representatives of class Aves. As a result of histological studies of the structure of the digestive tract, it was found that the feature of the wall of the waders small intestine is the dense location of the crypt in its own plate of the mucous membrane throughout its length. High proliferative capacity of cambial crypt cells and their multilayered location provide high secretory and regenerative activity of enterocytes, which helps to restore the mucous membrane and intensify the digestive processes, especially during the active feeding of the waders at the migration stopover points. At this time, the length and mass of the intestine, the mass of the stomach and the liver increase, what is considered as a reaction to a large number of feeds in the intensive feeding of birds and indicates the plasticity of their digestive system. It is shown that the change in the morphometric parameters of the waders digestive system organs depending on the migration situation is an integral part of the adaptive mechanism of the migratory birds, which provides the basic need of the organism — fat accumulation. The content of general liver lipids, abdominal fat and thoracic muscles in 6 species of tundra warblers with varying degrees of fat accumulation at the migration stopover points in the Azov-Black Sea region was studied.
Key words: waders Charadrii, short- and long-distance migrants, digestive system, plasticity.

Introduction

Migration of birds, as a bilological phenomenon, evoked interest not only zoologists-ornithologists, but also practically all the representatives of all the fields of biology as well as astrophysics, zoogeography cybernetics. Nevertheless many aspects of the phenomenon till the present time are explained at the level of hypotheses: historical background, evolutionary consequence, geographic attachment, mechanisms of orientation, energic provision.

The highest interest at this aspect is represented by long-term migrants, performing transatlantic flights, and whilst doing this, experiencing a number of negative factors. Performing migrations, the birds annually connect ecosystems of different geographic zones into a certain chain, which makes them important, and, possibly, unique component of biosphere (Alerstam, 2008). The object of this study was waders of Charadrii suborder, whose representatives are short- and long-distance migrants. Therewith, waders belong to one of the most studied taxonomic groups, and are ecological indicators of wetlands state. A number of authors consider waders as model species for studying the migration process.

Different issues of waders biology were illustrated in quite a large amount of papers. Various aspects of the ecology and behavior of birds at nesting sites, migration routes, migration stops, trophic specialization were covered. The results were partially summarized by Dutch ornithologists (Kam et al., 2004).

Waders are demanding to habitats, and especially — to places of migration stopover points. It is necessary to replenish energy reserves not only for flight to nesting sites, but also for successful breeding for tundra species of waders at *migration stopover points* (Yohannes et al., 2010; Hobson, 2010). Therefore the most important characteristic and the requirement to migratory stopover sites is the trophic base (Maillet, Weber, 2009; Chernichko, Kirikova, 1999).

The digestive system of waders and, in particular, the adaptive mechanisms of the organs of this system in connection with distant transatlantic flights have been investigated by small number of authors (Stein et al., 2005; McWilliams, Karasov, 2001, 2005; Piersma, Gill, 1998). In particular, the work of Thomas Pirsma on the example of *Limosa lapponica* (Linnaus, 1758) showed that distant migrants decrease the mass and size of the digestive system before the onset of migration, since during the flight their functions are minimized. After the end of the flight, the sizes of the organs and their functions are restored (Piersma, Gill, 1998). Similar data are provided by A. Dekinga at the example of *Calidris canutus* (Linnaus, 1758). Dependence of the size of the digestive system on the composition and consistency of feeds on wintering and nesting sites in the tundra zone was also studied (Dekinga et al., 2001). The example of *Limosa lapponica* also showed that, at the beginning of the migration stopover point, the organs of the digestive system (stomach, intestines, liver) increase, and at the end of it, partial atrophy is observed with a parallel increase in pectoral muscles and fat deposits (Landys-Ciannelli et al., 2003). Some researchers note the seasonal variability of enzyme activity (Stein et al., 2005). It is also shown that migratory species of birds are characterized by the ability to switch to mono feed and expand the range of feeds (Maillet, Weber, 2009; Chernichko, 2010, Khomenko, 2003), including atypical forage objects (Schmaltz et al., 2018). At the anatomical level, the digestive system of waders was investigated; studies at the histological level are not known to us.

Summarizing these materials, it can be stated that successful migrations of birds are facilitated by two groups of factors: ethological, including orientation mechanisms; trophic, providing energy for flight and reproduction. It is easy to see that these factors work in parallel and contribute to the plasticity of the digestive system of migrants.

The main tasks of the study was to investigate the morphofunctional organization of the digestive system of waders to reveal the factors that ensure its plasticity, and on this basis to discuss the features of their structure that allow waders to migrate long-distances.

Material and methods

The material (table 1) was collected during expeditions with ornithologists from the Azov-Black Sea ornithological station to the wetlands of the Zaporizhia and Kherson Regions. Other species of birds were collected in the territory of the Kharkiv Region. To obtain a comparative material, representatives of Passeriformes, Gruiformes, Anseriformes, Apodiformes orders were investigated.

All manipulations with the studied birds were carried out according to the provisions of the "European Convention for the Protection of Vertebrates, which are used for experiments and other scientific purposes" (Strasbourg, 1986), "General ethical principles of animal experiments" (Kyiv, 2001).

Investigation of the anatomical structure of the digestive system of birds was carried out on a fresh material, or fixed one by 5–6 % aqueous solution of neutral formalin.

Morphological studies involved the definition of morphometric indices of the body of birds (Busse, 2000) and organs of the digestive system (Davletova et al., 1986). The degree of fat content of birds was determined according to the method of T. I. Blumental and V. R. Dolnik (Blumental, Dolnik, 1962). Investigation of macrorelief of the internal surface of the digestive tract was carried out on fixed samples using a stereoscopic microscope MBS-10. Images were taken by a digital camera Samsung. Biometric processing of the obtained material was carried out according to generally accepted methods. Histological studies were carried out in accordance with generally accepted methods. The morphometry of the digestive tract walls was carried out using an ocular micrometer AM-9-2. Material for illustrations was taken by a digital camera DCM300 (USB2.0) under trinocular microscope XSP-139TPJNOES (Japan). The obtained data were processed statistically with usage of Students t-criterion.

Table 1. List of investigated species of birds Charadriiformes

Species	Status of stay in the studied region*	Number of individuals	Research methods				
			macro-morphometric	macroscopic	histological	micro-morphometric	biochemical
Family Charadriidae Genus *Pluvialis* Brisson, 1760 *Pluvialis squatarola* (Linnaeus, 1758)	M	2	–	+	+	+	–
Genus *Charadrius* Linnaeus, 1758 *Charadrius hiaticula* Linnaeus, 1758	M	2	+	+	+	+	–
Family Recurvirostridae Genus *Recurvirostra* Linnaeus, 1758 *Recurvirostra avosetta* Linnaeus, 1758	N	2	–	+	+	+	–
Genus *Himantopus* Brisson, 1760 *Himantopus himantopus* (Linnaeus, 1758)	N	2	+	+	–	–	–
Family Scolopacidae Genus *Tringa* Linnaeus, 1758 *Tringa ochropus* Linnaeus, 1758	M	3	+	+	+	+	–
Tringa glareola Linnaeus, 1758	M	6	+	+	+	+	+
Tringa nebularia (Gunnerus, 1767)	M	3	+	+	+	+	–
Tringa erythropus (Pallas, 1764)	M	2	+	+	+	+	–
Tringa stagnatilis (Bechstein, 1803)	M	2	+	+	–	–	–
Tringa totanus (Linnaeus, 1758)	N	2	+	+	–	–	–
Genus *Actitis* Illiger, 1811 *Actitis hypoleucos* (Linnaeus, 1758)	M	2	+	+	–	–	–
Genus *Philomachus* Anonymous [= Merrem], 1804 *Philomachus pugnax* (Linnaeus, 1758)	M	25	+	+	+	+	+
Genus *Calidris* Anonymous [= Merrem], 1804 *Calidris minuta* (Leisler, 1812)	M	6	+	+	+	+	+
Calidris temminckii (Leisler, 1812)	M	2	+	+	–	–	–
Calidris ferruginea (Pontoppidan, 1763)	M	18	+	+	+	+	+
Calidris alpina (Linnaeus, 1758)	M	20	+	+	+	+	+
Genus *Limicola* Koch, 1816 *Limicola falcinellus* (Pontoppidan, 1763)	M	3	+	+	–	–	–
Genus *Gallinago* Brisson, 1760 *Gallinago gallinago* (Linnaeus, 1758)	M	3	+	+	+	+	–

* N — nesting; M — migratory.

Results

The digestive system of the representatives of the bird class at the anatomical level has a universal structure. The differences, if they are, relate mainly to the morphometric parameters and are mainly due to food objects. Migrant birds do not have significant anatomical rearrangements of the digestive system organs. Adaptive changes, presumably, occurred at the histological and biochemical levels.

Macro- and microscopic structure of waders digestive system organs. Esophagus

The length of the esophagus of waders, as in other birds, depends on the length of the neck. The relative length of the neck to the total length of the digestive tract gives an idea of the length of the neck (as a whole). In the investigated species of waders this indix is in the range of 10–15 %. Beyond this framework, it is only *H. himantopus* — 18.11 % and *Ph. pugnax* — 17.10 %. Goiter in the investigated species of waders is absent. *Ph. pugnax* has esophageal expansion. This is not a feature of waders, since the absence of goiter is also observed in other migratory birds. The dependence of certain morphological characteristics of the esophagus on the size of feed objects and their consistency is known. Because of this, the diameter of the empty esophagus of waders varies from 0.8 mm to 2.1 mm; the thickness of esophagus walls varies from 0.8 mm to 1.6 mm. The relief of the mucosa of the esophagus of waders is corrugated; inter-species variability of the mucosal relief is noted in terms of size, shape and structure of the folds. But this is not specific for waders, since it also occurs in other groups of birds. The presence of unbranched folds of the mucous can be considered, to some extent, a feature of macrorelief of the esophagus mucous membrane of waders. But there is no explanation for this from the functional side. The own plate of the mucous membrane of the esophagus is represented by loose connective and reticular tissues, where a large number of esophagal glands that secrete mucus are located. (fig. 1). The muscular membrane of the esophagus of waders is of two-layers, in migrants from the order Passeriformes it is three-layered. The vessels of the microcirculatory bed in the mucosa of the esophagus form two well-developed networks — the superficial and deep. The latter is located on the border of the submucous base of the mucosa and muscle membranes. We believe that such an organization of the microcirculatory bed provides a rapid regeneration of the epithelium.

Stomach

Wader stomach is two-sectional as in majority of birds and migrants, i. e. the stomach has glandular and muscular sections. In waders, the relative mass of the stomach is obviously greater than that of representatives of other groups of birds, including some migrants. Its weight in the investigated species of waders is on the average 3.3–4.4 % of body weight, the glandular stomach is 0.1–0.5 %. In birds of migrants from the group Passerine mass of the stomach is not more than 3 % of the body weight. Two types of relief of the mu-

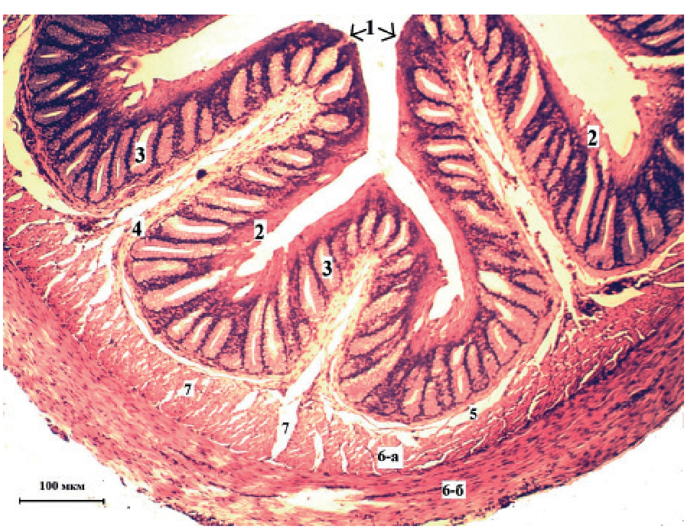

Fig. 1. The esophagus wall *Tringa ochropus*, cross cut, caudal section. Histopreparation (hematoxylin and eosin, x100). 1 — folds; 2 — epithelial layer; 3 — esophageal glands; 4 — muscle plate; 5 — submucosal basis; 6 — muscle (a — inner longitudinal layer; b — outer circle layer); 7 — layers of connective tissue.

cous membrane of the glandular stomach of waders are distinguished: 1) with concentrically arranged plates around the apertures of the excretory ducts of the glands (*R. avosetta, G. gallinago, T. nebularia, T. erythropus, T.ocropus, T. glareola, T. tetanus, H. himantopus);* 2) with a smooth surface of the mucosa around the excretory ducts of the glands (*C. minuta,C. temminckii, C. ferruginea, C. alpina, L. falcinellus*).

The thickness of the wall of the muscular stomach of waders varies and amounts to 4.5 mm to 15 mm. In the representatives of passerines, the thickness of the wall of the muscular stomach is much smaller. Waders, like other birds, have on the opposite sides of the muscular stomach so-called blind bags. Their function is the accumulation and mixing of food. The inner surface of the wall of the muscular stomach of waders is lined with a thick cuticle (the thickness of the layer is 0.2–0.3 mm), which is due to fodder specialization, i. e. the composition of waders feed includes crustaceans, insects, mollusks, grain cereals (fig. 2). In the cavity of the muscular stomach of waders we identified gastrolits (small pebbles, sand). The mucous membrane of the muscular stomach of waders, like other birds, is lined with single-layer prismatic glandular epithelium, which forms simple unbranched tubular glands. In migrant birds that feed on insects with a stinging apparatus, a peculiar demarcation zone has been identified which is formed by the connective tissue of a special plate of the mucous membrane that separates the two glandular genera — superficial and deep. A comparative analysis of the stomach structure of waders with migratory birds of the orders Passeriformes and Apodiformes and with birds of other orders of the Aves did not reveal features typical for waders, as migrant birds.

Intestine

It is known that the intestines of birds are relatively short, slightly differentiated into divisions. On the border between the thin and large intestines are paired blind intestines. The large intestine is represented by only one short intestine. The mucous membrane of the intestine forms a large number of different in shape and size villi, which facilitates rapid absorption of nutrients. The structure of the intestine of the investigated wader species fully corresponds to the general scheme of the macro- and microscopic structure of the intestine of representatives of the *Aves* class. Let us focus on some features that characterize the anatomical and histological organization of the intestines of waders as migrants.

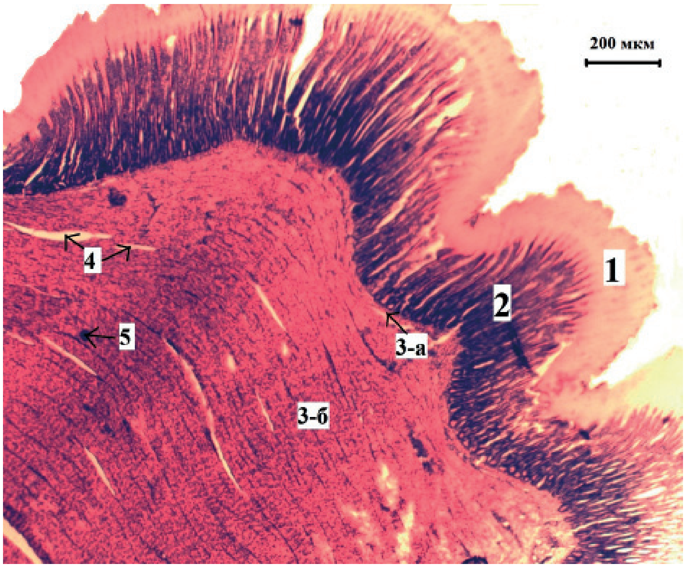

Fig. 2. The wall of the muscular stomach *Tringa nebularia* cross cut. Histopreparation (hematoxylin and eosin, x40). 1 — cuticle, 2 — tubular glands; 3 — muscle (a — inner longitudinal layer; b — outer thick circle layer); 4 — layers of connective tissue; 5 — blood vessels,

The investigated species of waders had the intestine, the length of which was 2.2–4.8 as long as the length of their torso. At the same time, the duodenum was 11.97–24.15 %, the jejunum and iliac guts 69.5–72.3 %, the cecum — 11.2–19.24 %, the rectum — 2.8–9.3 % of the total length of the intestine. Almost the same indicators, or very close to them, were inherent in birds migrants from other orders. It is established that in all the migrant birds we studied, the intestinal loops are located compactly near the center of mass of the body, which apparently improves their aerodynamics. The investigated species of waders are characterized mainly by the lamellar type of the relief of the mucous membrane of the small intestine with a complex zigzag-like labyrinth system. In this case, the lamellar relief varies in shape and dimensions of the plates and the density of their arrangement (fig. 3). Analysis of the architectonics of the mucosal relief allows us to state that the processes of digestion and absorption of nutrients are carried out along the entire length of the small intestine, and the zigzag-like arrangement of the plates of the mucous membrane facilitates the retention of digestive enzymes and the prolongation of their action (Lykova, Kharchenko, 2016).

Histological examination of the wall of the small intestine of waders showed that the plates of the mucous membrane are covered with a single-layer prismatic epithelium. In the epithelial layer there is a large number of goblet cells, the number of which increases in the caudal direction. On its own plate, the mucosa of the small intestine in most of the investigated waders, several layers of crypts are observed (fig. 4); in birds-migrant order Passerine crypts are located one layer along the entire intestine.

In the waders studied, a significant number of mitosis figures in cambial cells were found in the crypt epithelium. Obviously, the high mitotic index of cambial cells on the bottom of intestinal crypts indicates a high rate of proliferation of enterocytes which ensures a constant renewal of the epithelium of intestinal plates. A rapid process of regeneration of the intestinal epithelium is provided by multi-layered placement of crypts, which contributes to the intensive digestion process during migratory stops. In all investigated species of waders, we detected Meckel's diverticulum located on the antimisenteral surface of the caecum loop. In migratory birds of the Passerine order this organ is absent, but it is present in other orders of birds. According to the results of histological studies, it was revealed that all the walls of the Meckel diverticulum wall are infiltrated by lymphoid structures, which makes it possible to consider the wader Meckel diverticulum as the peripheral organ of the immune system (Kharchenko, Lykova, 2013).

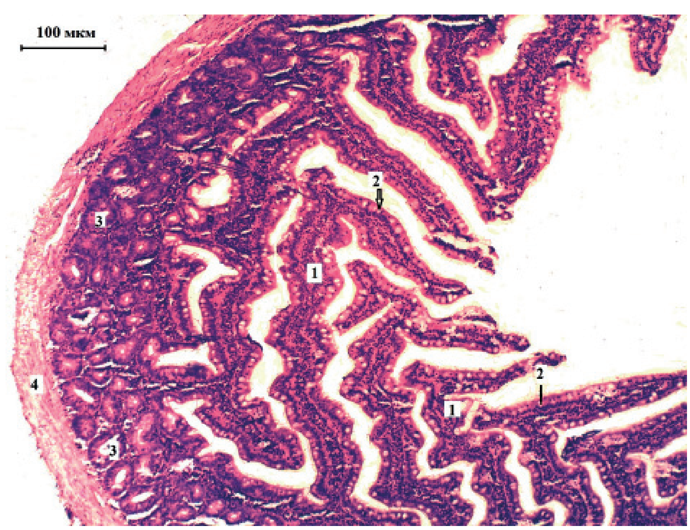

Fig. 3. The wall of the jejunum *Calidris ferruginea*, cross cut, cranial section. Histopreparation (hematoxylin and eosin, x100). 1 — plates of the mucous, located zigzag; 2 — goblet cells; 3 — intestinal crypt; 4 — muscle.

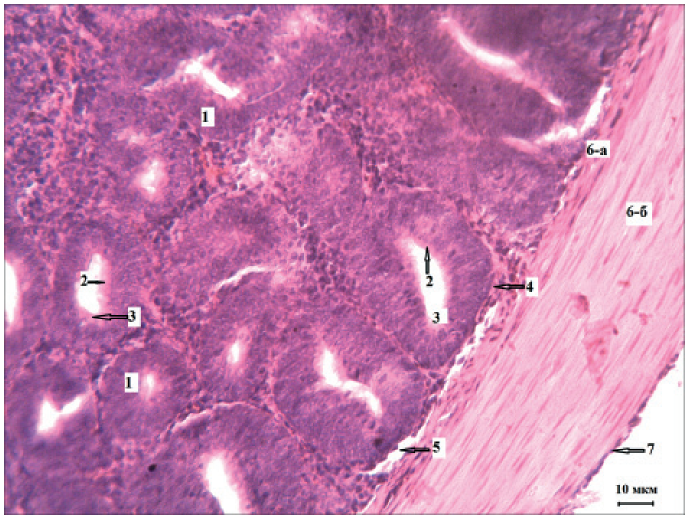

Fig. 4. Crypt in the wall of the duodenum *Tringa nebularia*, cross cut. Histopreparation (hematoxylin and eosin, ×250). 1 — crypt; 2 — corpuscle enterocytes; 3 — alveolar extension of the bottom part of the crypt; 4 — separate muscle cell myocytes; 5 — submucosal basis; 6 — muscle (a — inner longitudinal layer; b — outer circle layer); 7 — gray serum.

The rectum represents the large intestine of waders; on the border between the small intestine and the rectum are located paired blind guts. The length of the blind colon in various species of waders is quite variable: in most species, it lies within the boundaries of 11.2–18.2 % of the total length of the intestine, but in representatives of the *Tringa* genus, it is 0.7–4.6 %. It is known that the structure and function of the blind intestines of birds depends on trophic specialization: in herbivorous birds, symbiotic digestion takes place, that is, with the participation of microbial flora; in insectivores they are filled with lymphoid tissue. In waders the blind intestine, as evidenced by our histological studies, is a lymphoid-epithelial organ (fig. 5). The composition of the superficial epithelium of the blind intestines revealed many special enterocytes, which indicates their osmoregulatory function (Kharchenko, Lykova, 2013). However, this is not a specific feature of waders.

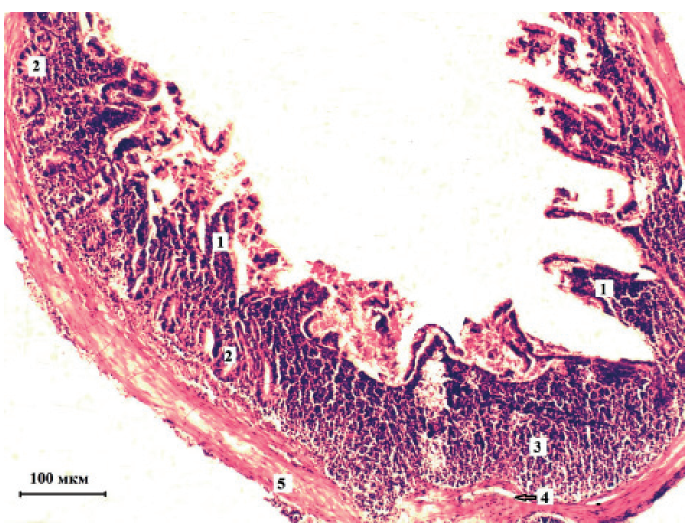

Fig. 5. The wall of the cecum *Philomachus pugnax*, the area of the body, cross cut. Histopreparation (hematoxylin and eosin, x100). 1 — mucosal plates; 2 — crypt; 3 — lymphoid tissue; 4 — submucosal basis; 5 — muscle.

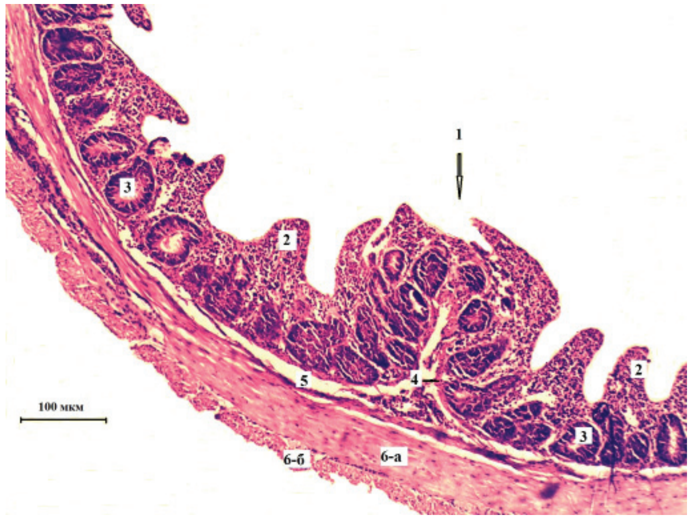

Fig. 6. The wall of the rectum *Tringa glareola*, cross cut, cranial section. Histopreparation (hematoxylin and eosin, ×100). 1 — fold of the wall; 2 — mucosal plates; 3 — crypt; 4 — muscle plate; 5 — submucosal basis; 6 — muscle (a — inner circle layer; 6 — outer longitudinal layer).

The mucosa of the rectum of waders, like other parts of the intestine, is lined with a single-layered glandular epithelium; in which goblet cells predominate that actively produce mucus (fig. 6).

Digestive glands of waders on the anatomical and histological structure are not much different from those of other birds. Their liver consists of two parts; the right side is larger than the left one. The weight of the liver of the investigated species of waders was 2.77–5.27 % of the total body weight of birds. The pancreas is located in the loop of the duodenum, its mass is 0.35–0.73 % of the total body weight of the birds.

Discussion

Summarizing the above, with respect to the anatomical and histological organization of the digestive system of waders as migratory birds, it can be asserted that it fully corresponds to the general scheme of the morphofunctional organization of the digestive system of representatives of the Aves class. Obviously, migration, as a biological phenomenon, did not lead to significant rearrangements in the digestive system.

Amongst investigated birds, there were some, which nestle on the research territory *(R. avosetta, H. himantopus, T. totanus)* while other species continue to migrate and the explored area served as a migration stop for them. Analysis of the results of an anatomical and histological study indicates that the range of migratory flights does not affect the anatomical structure of the digestive system of waders. However, as in the works of other authors, we have shown that certain factors (foraging stereotype, food objects, and trophic specialization) significantly affect the individual characteristics of the digestive system of birds, in particular, morphometric indices. For example, we have revealed that the intestine is 10–20 % shorter in birds that take food in flight (*Apus apus, Riparia riparia, Merops apiaster*) in comparison to birds of the same size and body weight, but with a different stereotype of foraging behavior. Even among the birds of the first group there is a variability of the relative length of the intestine: it is greater in *M. apiaster*, and the smallest in *A. apus*. Obviously, this difference can be associated with a different degree of attacking method of obtaining feed in flight. The noted well-developed blind colon in waders cannot be considered as a feature that is characteristic of migrants:

firstly, not in all migrants they are equally well developed; secondly, in *Asio otus* (not a migrant) they have large relative sizes. According to the literature, and of our own data, the plate type of the mucosal surface relief of the waders intestine is not unique, it also occurs in other migratory and sedentary birds. The marked seasonal variability of the morphological and morphometric indices of individual organ structures, in our opinion, indicates the plasticity of the digestive system of waders, as distant migrants. It is the plasticity of the digestive system, along with the ethological factors, that provide waders with a variety of food.

Plasticity of waders digestive system organs

Plasticity implies the ability of the organs of the digestive system to change certain quantitative parameters when changing diet, food objects and trophic base of migration stopover points. The study was conducted on representatives of three species of tundra waders (*C. alpina, C. ferruginea, Ph. pugnax*) during their stay and feeding at the migration stopover grounds in the Azov-Black Sea region. We studied the body mass index, morphometric parameters of the digestive system, and analyzed their dynamics in the process of fat accumulation, during the migration stopping. For the study, three individuals of males and females of each species with the same body and wing length were selected.

The results revealed that at the end of the migration stopping the mass of waders increases by 27.6–77.7 %. Moreover, in males of all types — by 55.9–75.7 % and in females *C. ferruginea* — only by 22.3 %, which is probably due to the fact that females fly to the migration stopover points a little later (Chernichko, 2010). This assumption is supported by the fact that an increase in body weight in males and females *Ph. pugnax*, which arrive at this stopover point at the same time, practically does not differ — 33.1 % and 36.4 %, respectively. It was found that the increase in body weight is mainly due to the intensive fat accumulation of the subcutaneous and abdominal fat, to a lesser extent — the accumulation of lipids in the muscles, and due to the increase in the weight of the organs of the digestive system. Thus, the increase of stomach mass is due to the thickening of the muscular stomach walls; intestine mass grows as a result of the enlargement of linear parameters and wall thickness; the mass of digestive glands increases due to the fat accumulation (Lykova, 2014).

It was revealed that at the end of the migratory stopping in all investigated species of waders, the absolute intestinal mass increased from 0.27 to 1.07 %, which was 8–45 % of the intestinal mass at the beginning of the stopping. During migration stopping, the length of the intestine increases by 5.8–12.3 % in all wader species studied ($p < 0.01$). The increase in the length of the intestine is mainly due to the hollow club intestine. The above results on waders are similar to the data on migratory species of Passeriformes (Mc Williams, Karasov, 2001, 2005).

Architectonics of the relief of the duodenal mucosa during the migration stopping does not change. In the hollow club intestine, all investigated species of waders have a tendency to increase the height and density of the mucous plates, which obviously enhances the absorbtion surface.

The weight of the liver during migration stops in investigated waders increases by 25–64 %, the total mass of the pancreas increases by 12–35 %. It is known that changes in the diet of birds during migration lead to a change in the activity of digestive enzymes (Mitchell et al., 2000).

The increase in the morphometric parameters of the digestive system organs at migratory staging sites provides a rapid update of their functions after long flights, starvation and promotes the intensity of digestion, renewal and accumulation of energy reserves for the continuation of migrations to nesting sites.

Thus, the ability of the organs of the digestive system to change their morphometric parameters (decrease-increase) depending on the migratory situation can be qualified as an integral part of the adaptive mechanism of migratory birds, in which, obviously, microscopic, biochemical and ethological factors prevail, providing the main necessity of organism — fat accumulation.

Fat accumulation in waders bodies during the migration stop at Azov-Black sea region

The above-mentioned increase in wader body weight during migratory stops by more than 80 % is due to the accumulation of fat, only a small part — due to an increase in the morphometric parameters. It is known that for birds during long flights the main source of energy is fat reserves. The energy of flight of migratory birds is sufficiently studied (Dolnik, 2009; Gavrilov, 2012.), and the energy properties of fats are described in detail in biochemical literature (Leninger, 1985).

It is known that the optimal form of energy storage in an animal organism is triacylglycerols, which are synthesized in the cytoplasm of hepatocytes and adipocytes from glucose, keto acids, amino acids and accumulate in adipose tissue of different organs. When oxidized to CO_2 and H_2O, they release the greatest amount of energy in comparison with carbohydrates and proteins. The physicochemical properties of triacylglycerols are determined by the fatty acids that are included in their composition (Leninger, 1985). The main energy material for all tissues and organs, except the brain are saturated fatty acids. Unsaturated fatty acids (monoenovye and polyene), except for energy, perform a number of other functions in the body. Most unsaturated fatty acids are not synthesized in animals, including waders, but come from feed. This, according to the data of some authors, determines the choice of migrating birds to the trophic bases at migration stopover sites (Weber, 2009).

We conducted a study of the content of polyunsaturated fatty acids in the total liver lipids, abdominal fat and pectoral muscles of 6 species of tundra waders with different degrees of fat accumulation at migration stops in the Azov-Black Sea region.

According to the obtained data the mass of the body of the investigated wader species increased by 30.8–70.7 % during the migratory stay, which indicates an intensive accumulation of fat. According to other authors, the body weight of waders can be increased up to 80 % during the migration stopping (Atkinson et al., 2007; Khomenko, 2003).

The content of total lipids in the liver of the investigated waders was 1.96–2.44 % at the beginning of the migration stop, then at the end it increased to 4.3–8.7 %, increasing by 1.5–4.5 times. The content of total lipids in the abdominal fat tissue of the investigated waders was 29.2–40.5 % at the beginning of the migration stopping, then at the end it increased to 61.2–78.2 %, increasing 1.6–2.4 times. The content of total lipids in the pectoral muscles of the investigated waders was 2.5–3.2 % at the beginning of the migration stop, then at the end it increased to 8.3–10.1 %, increasing 2.7–3.95 times.

Conclusions

The features of anatomical and histological organization of the digestive system of waders testify to the adaptive lability of a number of their morphometric and structural features. However, such lability is characteristic of other representatives of the class, including sedentary bird species, and therefore cannot be considered as a direct consequence of adaptation to migration. Nevertheless, lability is an integral part of adaptations to migrations. Therefore, adaptation to migration is a multifactorial complex mechanism that includes not only macro and micromorphological features of the digestive system, but also general organizational factors: ethological, biochemical, and physiological. It seems that fat accumulation plays a central role in this process and some properties of essential fatty acids supplied with food cause mechanisms of adaptation of the bird's organism to long-term migrations. More specifically, the topic of fat accumulation in waders and sources of essential fatty acids during migratory stops, we consider in the following paper, connected to these questions.

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