Received 19.05.2025 Revised 21.08.2025 Accepted 23.09.2025

Vol. 21, No. 5
2025

Scientific Reports of the National University of Life and Environmental Sciences of Ukraine

Journal homepage: https://scireports.com.ua/en

UDC 636.592.09:591.3:616.3

Doi: 10.31548/dopovidi/5.2025.28

Morphological features of immune formations of the avian digestive tract

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Abstract. Immunocompetent structures of the digestive organs play an important role in protecting the body from bacterial and viral infections by providing an immune response. The aim of this study was to establish and summarise the morphological features of these structures in birds of different species, which would allow to determine their morphofunctional status, which is determined by the state of natural resistance and reactivity of the body, and to identify critical periods in the development of the immune system. To achieve this goal, a literature review of current research on the topography and microstructure of immune structures in the digestive organs of birds was conducted. It was established that the material basis of these structures is lymphoid tissue, the differentiation of which has regional characteristics, occurs in a specific sequence and proceeds in several stages. Its development depended on the age, species, sex, type of nutrition of birds and structural and adaptive features of the digestive organs. Immune formations were localised mainly in the mucous membrane of the digestive tract, and in birds of certain species also in the muscular and serous membranes. They consisted of T and B lymphocytes and their effector cells, which perform important cellular surveillance functions in protecting the body from foreign genetic information. It has been noted that they are in close contact with macrophages and function as a single lymphoid-macrophage system. The presented scientific research expands and supplements knowledge about the species, breed and morphological features of the structure of immune formations of the digestive tract of birds, which

Suggested Citation:
Mazur, N., & Dyshliuk, N. (2025). Morphological features of immune formations of the avian digestive tract. *Scientific Reports of the National University of Life and Environmental Sciences of Ukraine*, 21(5), 28-42. doi: 10.31548/dopovidi/5.2025.28.

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will allow specialists to objectively assess the effectiveness of methods of prevention and treatment of diseases in poultry farms

Keywords: immune formations; digestive system; lymphocytes; lymphoid tissue; lymphoid nodules

Introduction

The avian digestive tract is not only the primary organ for digestion and nutrient absorption but also a crucial link in ensuring the immune defence of the organism. Its wall contains numerous immune structures that form specialised structures of mucosa-associated lymphoid tissue (MALT), which are actively involved in protective reactions against pathogenic microorganisms that enter the body with food and water. Morphological study of these immune formations is important for understanding the mechanisms of immune response, assessing the resistance of birds, and developing effective veterinary and preventive measures in poultry farming.

Scientists B. Dukhnytskyi & V. Dukhnytskyi (2025) noted that poultry farming is a rapidly growing branch of animal husbandry that deals with the breeding, rearing, keeping and feeding of poultry for the purpose of obtaining eggs, meat and other products. However, one of the challenges is combating poultry diseases that negatively affect the immune system. The resistance of birds to disease is determined by the state of their immune system, which includes lymphoid organs, tissues and cellular elements capable of protecting the body from living organisms and substances that carry signs of foreign genetic information. According to S. Ceccopieri & J.P. Madej (2024), the immune system provides one of the most important adaptive functions of the body, aimed at controlling and maintaining its genetic integrity or homeostasis. The researchers also explained the significant development of immune structures in the digestive tract of birds by the absence of lymph nodes and the lymphoepithelial pharyngeal ring, as well as the prolonged retention of feed masses in certain sections of the digestive tract. Despite the scattered and uneven distribution of immunocompetent structures, the lymphoid-macrophage system responds to antigenic stimuli as a single entity, with a naturally enhanced response at the site of antigen entry.

M. Lu *et al*. (2023) found that the bulk of antigenic material (microorganisms and their waste products) enters the lumen of the digestive organs of birds with food and water. In response to their action, immune structures belonging to the peripheral (secondary) organs of the immune system develop in the wall of the digestive tract. Microscopically, they are represented by diffuse lymphocytic clusters without clear boundaries and lymphoid nodules without light and with light centres, in which the proliferation and differentiation of T and B lymphocytes, the main cells of immune processes, occurs. J. Mehrzad *et al*. (2024) found that proliferation is preceded by blast transformation of lymphocytes. As a result, T lymphocytes differentiate into several types: T killer cells (cytotoxic), which destroy foreign target cells and protect the body from neoplasms; T helper cells, which cooperate with B lymphocytes, without which their transformation into plasma cells is impossible; T suppressor cells, which block antibody formation; T memory cells, which store information about the antigen. Under the action of the antigen, B lymphocytes transform into plasma cells and memory B cells, and plasma cells produce immunoglobulins – components of antibodies that determine the development of humoral immunity. The researchers also noted that in addition to the four classic stages of lymphoid tissue formation characteristic of its morphological development, there is also a fifth stage, which reflects the involutive processes and reverse development of immune structures typical of the organs of the immune system.

J.-C. Weil *et al.* (2023) suggested that in adult birds, after the replacement of the lymphoid nodules of the cloacal sac with loose fibrous and fatty tissues, the function of B-lymphocyte formation is taken over by the peripheral organs of the immune system. G. Garagulya *et al.* (2022) emphasised that immune formations in the digestive organs are mainly associated with the mucous membrane, as it is constantly exposed to antigenic influences, although in some bird species they can also occur in the muscular and serous membranes. A significant part of the immune structures is macroscopically invisible, but in some areas of the inner lining, they are so developed that they form structures in the form of whitish thickenings (oesophageal and caecal tonsils, caecal diverticula, Peyer's patches, etc.). The functional basis of these formations is formed by lymphoid tissue – a collection of lymphocytes in the cells of the reticular tissue, which contains reticulocytes, ground substance and reticular fibres. N. Pendl & R.E. Schmidt (2024) identified four stages in the formation of lymphoid tissue. In the first stage, diffuse tissue is formed with the migration of lymphocytes from the hemocapillaries; in the second stage, cells are more densely arranged and pre-nodes are formed; in the third stage, primary nodes and their aggregates are formed, indicating readiness for the formation of immunocompetent cells; in the fourth stage, secondary lymphoid nodules with a light centre appear, which increase in size upon contact with antigens. This complex of morphological features indicates the functional maturity of immunocompetent structures. S. Zeinali *et al.* (2024) divided lymphoid nodules into two types: perivascular, which are located along the course of the haem- and lymph-microcirculatory channels and belong to the structures of the internal environment of the organism, and lymphoepithelial, which have a close connection with the surface epithelium of the mucous membranes of tubular organs.

The aim of the article was to study the immunocompetent structures of the mucous membranes of the oesophagus, stomach and intestines of various bird species to better understand the functions of their immune systems and improve approaches to prevention and vaccination. To achieve this goal, Ukrainian and foreign publications on the subject were analysed, and works with original research were selected that reveal the topography, macro- and microstructure of the immune formations of the digestive organs of birds. Particular attention was paid to works that used classical morphological methods (anatomical, histological, cytological, immunohistochemical, and statistical).

General characteristics of the digestive system of birds

The digestive system of birds is a long tube that begins at the beak and ends at the rectum with the cloaca (Fig. 1). It also includes digestive glands (liver and pancreas). The digestive tract consists of the oesophagus, stomach and intestines. In the lumen of the gastrointestinal tract, food lumps are broken down by the action of digestive juices, followed by the absorption of nutrients into the blood and lymph and the excretion of indigestible residues outside the body.

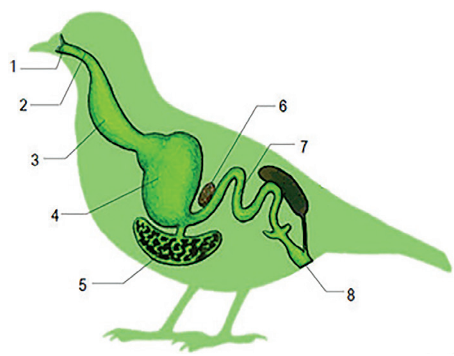

***Figure 1.** The digestive system of birds (diagram)*

Note: 1 – beak; 2 – oesophagus; 3 – crop; 4 – stomach; 5 – liver; 6 – pancreas; 7 – intestine; 8 – cloaca
Source: T.V. Kovtun (2023)

One of the initial digestive organs of birds, into which food enters and immune structures develop, as noted by A. Nahed *et al.* (2021) and

Z. Mosa & F. Al-Asadi (2022), is the oesophagus, which has the appearance of an elastic long tube (Fig. 2). It is capable of stretching in diameter, allowing large particles of food and insects to be swallowed. In granivorous birds, at the entrance to the thoracic-abdominal cavity, its wall expands and forms a protrusion – the crop, where food is stored and moistened. A.A. Alsanosy *et al.* (2021) showed in their studies that the crop also serves as a functional barrier to pathogens by lowering the pH through fermentation. S. Qinghui *et al.* (2020) noted that in most species of birds, the stomach is two-chambered and divided into glandular and muscular parts, which are connected by an intermediate zone (Fig. 2).

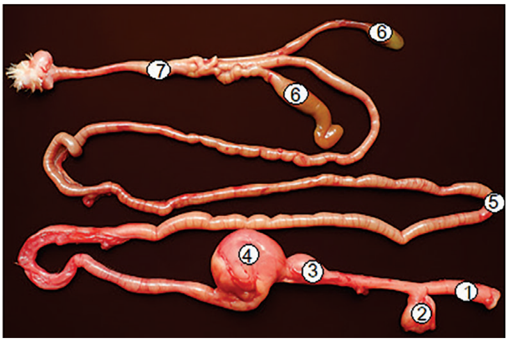

Figure 2. *Anatomical structure of the digestive tract of a domestic turkey (native preparation)*
Note: 1 – oesophagus; 2 – crop; 3 – glandular 4 – muscular parts of the stomach; 5 – small intestine; 6 – caeca; 7 – rectum with cloaca
Source: authors' own work

P.S. Selvan *et al.* (2008) reported the presence of a third pyloric part in wild birds, located at the border between the exit from the stomach and the entrance to the duodenum. It is represented by the pyloric sac, and in domestic birds this part is poorly developed. The glandular part of the stomach looks like a thick-walled tube with a well-defined mucous membrane with superficial and deep glands. The latter are grouped into lobules. In their work, Z. Umar *et al.* (2021), based on histological and histomorphometric analysis of ostriches (*Struthio camelus*) of different ages, showed age-related variability in the structure of the mucous membrane and glands of the stomach. The authors noted a gradual increase in the thickness of the mucosa, the depth of the crypts, and the density of the glands, indicating an increase in secretory activity with age. The data obtained complement the understanding of the functional specialisation of the glandular part of the stomach in birds and demonstrate the importance of the age aspect in assessing the morphology of the digestive tract. In granivorous, herbivorous, and omnivorous birds, they are multi-lobed with a complex branched duct system, while in carnivorous and insectivorous birds, they are single-lobed. In a comparative microscopic study, F. Taki-El-Deen (2017) examined the tongue, oesophagus, and stomach of two bird species, demonstrating significant differences in the structure of the mucous membrane and the organisation of the glands depending on the type of diet. It was shown that granivorous species are characterised by a more complex glandular apparatus, which corresponds to their need for prolonged mechanical and chemical processing of coarse feed. These data confirm the close relationship between the morphology of the digestive tract and the dietary specialisation of birds. The muscular part of the stomach has an elliptical shape with blind sacs located on opposite sides. It is where the mechanical processing of feed takes place, which is why its wall has a well-developed muscular coat. Simple tubular glands in the muscular part of the stomach produce a cuticle (keratin-like film) that covers the mucous membrane and prevents damage to its walls by solid particles. A study by W. Khamas *et al.* (2022), which evaluated the growth and development of digestive organs in two breeds of chickens with different growth rates, showed that significant dynamics in the development of the muscular stomach are observed already in the first four months of life. The authors found a direct relationship between the growth rate of the breed and the rate of formation of its morphological structures, in particular the muscular membrane and glands, which emphasises the role of genetic factors in the functional maturity of the digestive organs.

As noted by I.O. Kolomak (2023), the intestines of birds are divided into small and large sections of different lengths (Fig. 2). The small intestine, which is the longest, consists of the duodenum, jejunum and ileum. Their mucous membrane forms folds, villi and numerous crypts, which provide the main digestion and absorption of nutrients. The large intestine consists of two blind intestines and the rectum. They are mainly responsible for the formation and excretion of faeces. S. Zeinali *et al.* (2024) showed that the caeca varies in length depending on the bird species. It is short in blackbirds and long in chickens, turkeys, ducks and geese. The wall of the digestive tract of birds contains immune structures that have different locations and development of lymphoid tissue. Their topographical features and structural components are summarised in Table 1.

Table 1. *Sites of localisation and distribution of structural components of immune formations in the avian digestive tract*

Name of organ or part	Minor aggregations of lymphoid cells and solitary lymphoid nodules	Aggregations of lymphoid nodules (Peyer's patches)	Tonsils (islands or continuous layers of lymphoid tissue)
Oesophagus	+	-	-
Crop (Ingluvies)	+	-	-
Oesophagus-proventriculus junction	-	-	Oesophageal tonsil
Proventriculus (Glandular stomach)	+	-	-
Gizzard (Muscular stomach)	+	-	-
Gizzard-duodenum junction	-	-	Pyloric tonsil
Small intestine	-	+	-
Meckel's diverticulum	-	+	-
Caeca	-	+	Caecal tonsils/ diverticula
Rectum	+	-	-

Source: developed by the authors based on O.V. Byrka & M.M. Kushch (2010), L.P. Kharchenko & I.O. Lykova (2013), V.T. Khomich *et al*. (2020)

The highest concentration of lymphoid tissue is found in the tonsils, slightly less in Peyer's patches, and least in individual lymphoid nodules. The uneven development of this tissue and, accordingly, the immune formations in the avian digestive tract organs depends on the intensity of antigenic exposure, feed retention in certain areas, and the thickness of the epithelial covering of the mucous membrane. The morphofunctional features of the immune structures of individual organs of the digestive tract of birds are presented below.

Features of the topography and histostructure of immune formations of the oesophagus, crop and oesophageal tonsil

The microscopic structure of the oesophageal wall in birds of different trophic specialisations largely depends on how they obtain food. Its mucous membrane is lined with a multilayered squamous epithelium, which has varying degrees of keratinisation and contains glands whose size and shape depend on the feeding ecology. In particular, R. Sinha *et al.* (2023), studying the oesophagus of Japanese quails (*Coturnix japonica*), noted specific morphometric indicators of the mucosa and variations in the degree of epithelial keratinisation, indicating the adaptation of the organ to the peculiarities of food consumption. Similar conclusions were made by R.A. Al-Musawi & S.S. Ali Al-Khakani (2024), who, based on a comparative histochemical analysis of the oesophagus of a turtle dove and a buzzard, showed differences in the size and shape of the glands directly related to the type of diet and method of food procurement. R. Al-Musawi & S. Ali Al-Khakani (2024) found that in the grey turtle dove, they are absent in the cervical part of the organ. In many species of birds, diffusely scattered lymphoid cells and lymphoid nodules are located near the glands. The work of C. Casteleyn *et al*. (2010) provided a general overview of the localisation of lymphoid structures in chickens, emphasising the importance of the oesophagus as an area with a high concentration of GALT. N.J. Monisha *et al*. (2024a), analysing the histomorphometry of the digestive tract of broilers and roosters in Bangladesh, confirmed the presence of a significant number of immunocompetent cells in the oesophageal wall, which provides local immune protection. Research by M. Mahdy & E. Mohammed (2024) on domestic pigeons supplemented these data, demonstrating the diversity of the cellular composition of the mucosa depending on the age and functional activity of the organ.

Contact of the organism with the external environment and changes in the type of nutrition cause the development of subepithelial lymphoid barriers of the digestive tract in the first days of life after hatching, forming a local immune system. However, such a system is quite limited in the early stages of post-embryonic development and only intensifies with age. L. Horalsky & V. Gatskivsky (2009) found isolated lymphoid nodules with a diameter of 86 ± 9 μm to 172 ± 27 μm in the cervical part of the duck's oesophagus, while they were absent in the thoracic-abdominal part of the organ. Research by S. Kots (2009) shows that the mucous membrane of the oesophagus of birds of the heron family forms longitudinal wave-like folds with different configurations of bends and contains densely located oesophageal glands in the lamina propria of the mucous membrane. Lymphocytes in the middle and caudal sections of the grey heron's oesophagus are mainly located near the basement membrane of the secretory sections of the glands. The author suggests that these cells may migrate to the surface of the epithelial layer, where they work with gland secretions to protect the mucous membrane. Lymphocytes in the middle section of the oesophagus form clusters in the form of diffuse lymphoid tissue, and in the area of its transition to the stomach, there are 9 to 10 oval-shaped lymphoid nodules, which is probably associated with food retention during increased feeding.

Histological studies by H. Ali *et al*. (2023) showed that the shape of the folds of the mucous membrane of the oesophagus of pigeons differs in its individual parts and also depends on the age category of the birds. The cervical part of this organ in young pigeons had primary folds of the mucous membrane with a small number of secondary folds, while in adults, they were heavily folded and divided into primary, secondary and tertiary folds. Isolated clusters of diffuse lymphoid tissue were recorded in the plane of the folds. N. Hamoda & A. Farag (2018) also found lymphoid nodules in the oesophagus of pigeons, located in the lamina propria of the mucous membrane and the submucosal base. Some of them were also recorded in the muscular and serous membranes. According to the authors, the lymphoid tissue of the digestive tract can serve as an indicator for understanding the immune response after oral administration of vaccines.

The immune formations of the esophagus of waders are located in the lamina propria of the mucous membrane under the surface epithelium and near the glandular packets. They are mainly represented by a diffuse form and isolated lymphoid nodules (Kharchenko & Lykova, 2013). A similar location of immunocompetent structures was observed in the oesophagus of the African ostrich by O. Byrka (2017). M. Kovtun & L. Kharchenko (2005) identified diffuse lymphocytic aggregations and isolated lymphoid nodules in the oesophagus of sexually mature pheasants, quails, and rooks, whereas in chaffinches and bee-eaters only minor lymphocytic infiltration of the mucosa was observed. The immune formations showed a close morphofunctional association with the secretory portions of the glands, forming immunosecretory complexes. These complexes provided a protective barrier, enabling mucus on the epithelial surface to retain secretory immunoglobulins. In the region where the oesophagus transitions into the glandular part of the stomach in pheasants, quails, and rooks, well-developed clusters of lymphoid formations were observed. They were represented by lymphoid nodules, both without and with germinal centres, as well as diffuse lymphoid tissue. In the transitional zone of the bee-eater, only intensive diffuse infiltration of the mucosa was recorded, while in the chaffinch no lymphoid tissue was found. On this basis, the researchers suggested that in the bee-eater and the chaffinch, the oesophageal tonsil, as a distinct immune formation, is absent.

The lymphoid tissue of the esophageal tonsil of day-old quails is immature. Lymphoid nodules with pronounced centres of proliferation were recorded in it starting from 30 days of age. They are located in the mucous membrane singly and in the form of conglomerates (2-3 or more) (Kryvutenko, 1996). According to research by H. Sağsöz & N. Liman (2009), the oesophageal tonsil of quails begins to form on the 5th day after hatching. In day-old turkeys, the lymphoid tissue of the oesophageal tonsil is also undeveloped. Its development begins on the 30th day, and in 60-90-day-old birds, secondary lymphoid nodules appear, mainly in females, which is associated with their sexual maturation (Kryvutenko, 1984). According to research by L.O. Bugay (2008), in day-old muscovy ducks, the oesophageal tonsil was not macroscopically detectable, while in 5- and 10-day-old ducks, blurred spots were observed. Its most intensive growth occurred between 15 and 30 days and between 90 and 180 days. The oesophageal tonsil reached its maximum relative area in birds aged 30 days. In her studies, N. Petushinova (1985) noted that the lymphoid formations of the digestive organs of 49-day-old "Broiler-6" crossbred chickens are located in the caudal part of the oesophagus around individual terminal sections of the mucous glands in the form of more or less significant diffuse formations, and in the oesophageal tonsil there were up to 20 lymphoid nodules, which were limited by thin collagen fibres that were closely connected to the lamina propria of the mucous membrane. The same fibres penetrated into the thickness of the lymphoid nodules. According to research by N. Nagy *et al*. (2005), the oesophageal tonsil of 6-8-week-old chickens consisted of 6-8 separate units limited by a thin fibrous capsule. Each of them was located in the area of the bottom of the longitudinal folds and served as a "tonsil crypt". The surface epithelium of the tonsil location area was infiltrated with lymphoid, plasma, dendritic cells and macrophages.

According to morphological studies by N. Nagy *et al*. (2005), the oesophageal tonsil of chickens and ducks is divided into eight tonsillar units depending on the number of longitudinal folds, which lie in their own mucosal plate. Each tonsillar unit delimits a crypt lined with multilayered squamous epithelium infiltrated with lymphocytes. N. Arai (1987) noted in his studies that the oesophageal tonsil of chickens produces not only IgA, which is important for the protection of the mucous membrane, but also IgG for systemic immunity. In this respect, it is similar to the palatine tonsils of mammals. V. Indu & K. Lucy (2021) noted that the oesophageal tonsil of 12-week-old "White Leghorn" chickens contains large lymphoid nodules separated by internodular areas and bounded by a connective tissue capsule. G. Krok & N. Musyenko (1976) studied the development of lymphoid tissue in the area of the oesophageal tonsil of highly productive lines of chickens aged one, 10, 30, 60 and 90 days. It was shown that in this area of day-old birds, proliferation of reticular tissue was observed, and lymphoblasts and agranulocytes of varying degrees of maturity appeared. At 10 days of age, there was active proliferation of lymphoid elements located around the terminal sections of the glands. At 30 days of age, lymphoid tissue with diffuse clusters and lymphoid nodules with light centres was well developed and formed the oesophageal tonsil. In some areas, lymphoid elements reached the central lumens of the glands and migrated into their space. The oesophageal tonsil reached its maximum development in 60-day-old birds and contained numerous nodules with reactive centres.

The most complete macroscopic and microscopic study of the oesophageal tonsil in selected species of domestic and wild birds was conducted by V. Khomich *et al.* (2020). Macroscopically, this immune formation is evident in the chicken, quail, turkey, duck, goose, guinea fowl, common pheasant, hazel grouse, common peacock, Canada goose, magpie, hooded crow, and white stork as a thickened, whitish strip with a yellowish tint at the boundary between the oesophagus and the stomach. It is not visually noticeable in the willow ptarmigan, jay, common moorhen, Eurasian coot, and rock dove (feral pigeon). Depending on the development of the lymphoid tissue, the authors proposed dividing avian tonsils into diffuse and compact. In the former, the tissue occupied a significantly larger area than in the latter. Structural levels of lymphoid tissue organisation were found in the mucous membrane, with the diffuse form being widespread. The largest area of lymphoid tissue was observed in the domestic duck (68.64 ± 0.70%), and the smallest in the willow ptarmigan (2.31 ± 0.05%). Solitary lymphoid nodules and diffuse lymphoid tissue were also detected in the muscular and serous coats of the guinea fowl, goose, duck, Canada goose, common moorhen, and coot. Between the oesophageal tonsil and the glandular part of the stomach in the goose and Canada goose, there was an intermediate zone without oesophageal glands or lobules of deep glands, but with localised clusters of lymphoid cells in the mucous membrane. The researchers believe this transition zone is a species-specific feature of these birds. The composition of the lymphoid tissue in the chicken oesophageal tonsil included reticular cells, immunoblasts, lymphocytes, plasmocytes, monocytes, and macrophages. Among the lymphocytes, subpopulations were found that reacted to monoclonal antibodies with markers CD4+ (T-helper cells), CD8+ (T-cytotoxic/T-suppressor cells), and CD20+ (mature B-lymphocytes).

Features of the topography and histostructure of immune formations in the stomach and intestines

R. Matsumoto & Y. Hashimoto (2000) found clusters of lymphocytes located in three different areas of the lamina propria on the 20th day of incubation in the mucous membrane of the glandular part of the chicken stomach, namely under the surface epithelium, near the excretory ducts of the deep glands and in the wall of the glands themselves. In the third week after hatching, lymphoid nodules with a germinative centre were found in the deep glands. The latter was limited by densely located lymphocytes. The researchers noted that such nodules are formed as a result of the action of antigens present in the lumen of the stomach. N. Petushinova (1985) recorded lymphoid formations in the form of diffusely located cellular elements and lymphoid nodules (3-5 on the histological section) in "Broiler-6" crossbred chickens in the area of the transition of the muscular stomach to the duodenum. They were located among the crypts, under them and in the villi. They consisted of lymphocytes, macrophages and plasma cell precursors. According to N. Nagy & I. Olah (2007), the pyloric tonsil is a new peripheral organ of the immune system. According to their data, it forms a lymphoid ring in chickens.

According to morphological studies by S. Usenko (2023), immune formations in the glandular and muscular parts of the stomach of the waterfowl are represented by various forms of lymphoid tissue and occupy unequal areas. Such clusters are localised in the lamina propria of the mucous membrane and are formed by a diffuse form in the muscular part and all forms of lymphoid tissue in its glandular part. The lamina propria of the mucous membrane of the pigeon stomach contains diffuse lymphoid tissue, which is located mainly near and between the tubular glands. Similar accumulations of lymphoid tissue are found in the lamina propria and submucosal base at the border of the stomach and duodenum, forming pyloric tonsils, and lymphocytes from these accumulations penetrate the surface epithelium, forming lymphoepithelium. The latter covers the crypts between the villi. The wall of the glandular and muscular parts of the stomach of sandpipers is moderately infiltrated with lymphoid cells. Between the simple tubular glands of the lamina propria of the mucous membrane are unformed lymphoid nodules (Kharchenko & Lykova, 2013). In the grey crow, the mucous membrane of the glandular part of the stomach is infiltrated with lymphocytes and contains lymphoid aggregates located between the superficial tubular glands (Maksoud *et al.*, 2022). According to morphological studies by S. Kots (2009), in representatives of the heron family, the wall of the pyloric sac contains numerous immune formations that act as a protective "filter" when chyme moves from the stomach to the duodenum. They are located in the lamina propria of the mucous membrane, and isolated lymphoid nodules are also found in the circular layer of the muscular membrane.

After hatching, the intestines of chickens are sparsely populated with lymphocytes, so acquired immunity is practically undeveloped in the first days of life (Logvinova *et al.*, 2020). Protection during this critical period is the result of the activity of maternal antibodies or the innate immune system. IgA plays an important role in defence mechanisms, as it is associated with the mucous membrane and participates in the neutralisation of antigens in the intestine (Friedman *et al.*, 2003). The empty intestine of chickens contains immune structures represented by scattered Peyer's patches and Meckel's diverticulum. Peyer's patches form on the 5th day after hatching, and in birds 30 days old and older, there are 3 to 10 of them. Meckel's diverticulum forms in day-old chickens and contains lymphoid cells in its own mucosal membrane (Kalinovska, 2006). I. Kalinovska (2002) conducted a study of the blind intestines of 150-day-old Leghorn chickens. The author found that they contain cecal tonsils and Peyer's patches, which are macroscopically visible and located in the lamina propria of the mucous membrane, and Peyer's patches are also located in the submucosal base. The immune structures of the caeca are formed by connective tissue stroma, lymphoid tissue in the form of a diffuse form and lymphoid nodules, and a system of crypts. The latter are absent in some Peyer's patches. In the cecal tonsil, connective tissue stroma accounted for 12.38 ± 2.63%, lymphoid tissue for 71.01 ± 3.17%, and crypts for 16.60 ± 3.51% of their area.

O. Prokushenkova *et al.* (2012) noted that lymphoid structures in the duodenum of muscovy ducks appear 20-25 days after hatching in the form of diffuse lymphoid tissue, while secondary lymphoid nodules are found in sexually mature individuals aged 210-240 days. In the jejunum and ileum, the formation of such structures occurs in three periods: the development of diffuse lymphoid tissue (20-25 days), the formation of primary (25-60 days) and secondary lymphoid nodules (60-240 days). V. Logvinova & A. Oliyar (2021) identified four stages in the development of lymphoid structures in the wall of the small intestine of muscovy ducks. The first stage (5-25 days) is characterised by the development of diffuse lymphoid tissue. In the second stage (25-60 days), lymphoid nodules without centres and with light centres are formed. The third stage (60-240 days) is characterised by the formation of aggregated lymphoid nodules. At the fourth stage (90-240 days), the lymphoid nodules increase in size, as a result of which the lymphoid tissue occupies almost the entire area of its own mucosal membrane. Subsequently, groups of lymphoid nodules penetrate the muscular layer of this membrane and penetrate the muscular membrane of the small intestine, where they are separated by muscle layers. Lymphoid nodules in the muscular membrane of the intestine of muscovy ducks were also found by N. Dyshliuk *et al.* (2022).

T. Mazurkevych & V. Khomych (2019) conducted a study of the immune formations of the intestine of Blagovar cross broiler ducks from day-old to 420 days of age. It was found that they are represented by Peyer's patches, Meckel's diverticulum and cecal diverticula. One Peyer's patch was found in the duodenum and ileum, three in the jejunum of ducks from hatching to 240 days, two at 330 days, and one at 420 days. Each caeca contained 60 to 80 Peyer's patches arranged in a chain. Complete morphofunctional maturity of the cecal diverticula was observed on day 10, Peyer's patches of the duodenum, jejunum and cecum on day 15, and Peyer's patches of the ileum and Meckel's diverticulum on day 20. Lymphoid nodules were predominantly oval and elongated oval in shape. The linear indices of secondary lymphoid nodules were greater than those of primary nodules. Small and medium-sized lymphocytes, immunoblasts, proplasmacytes, plasmacytes, and macrophages predominated in the immune formations of the duck intestine. Ducks aged 180 days had stem cells (CD34+), which, according to the researchers, indicates the possible development of T and B lymphocytes in them, while in 30-, 150- and 180-day-old birds, T-helper lymphocytes (CD4+), T-cytotoxic/T-suppressors (CD8+), naive T-cells (CD44+), mature B-lymphocytes (CD20+), early B-lymphocytes (CD24+) and natural killer cells (CD56+).

Immune structures are located along the entire length of the intestine, localised in the lamina propria of the mucous membrane. The largest number of them is concentrated in the wall of the ileum. The epithelium of the intestinal villi of the small intestine contains a significant number of diffusely located lymphocytes. In the wall of the transitional zone of the small intestine to the rectum, there is Peyer's patch, which is represented by clusters of diffuse form and densely located lymphoid nodules. N. Hamoda & A. Farag (2018) found lymphocytic infiltration of the lamina propria and submucosal base of the mucous membrane and lymphoid nodules throughout the intestine of pigeons. The latter were located at the base of the short villi. Individual isolated lymphoid nodules were also found in the muscularis and subserosal layer. Lymphocytes infiltrated the simple cylindrical epithelium of the intestinal villi. The greatest infiltration and lymphoid nodules were observed in the ileum and caeca.

O.V. Byrka & M.M. Kushch (2010) noted that the Meckel's diverticulum of large grey geese is hook-shaped and located on the antimesenteric surface of the small intestine. Its own plate and submucosal base of the mucous membrane are infiltrated with lymphocytes, and lymphoid nodules are located at different depths. In some folds, small clusters of lymphoid cells form a pre-nodular form of lymphoid tissue. Secondary lymphoid nodules are also found in the muscularis and subserosal base of the serosa. According to research by N. Monisha *et al.* (2024b), there are more lymphoid nodules and a higher density of lymphocytes in the Meckel's diverticulum than in local chickens in Bangladesh. L.P. Kharchenko & I.O. Lykova (2013) reported that the mucous membrane of the Meckel's diverticulum of waders is densely infiltrated with elements of lymphoid tissue and contains large lymphoid nodules with pronounced light centres. Individual nodules are also located in the muscular and serous membranes. The lamina propria of the mucous membrane of the blind intestines of waders is moderately infiltrated with lymphocytes, and the mesentery also contains unformed lymphoid nodules. The latter are also located in the submucosal base of the rectum of waders.

Conclusions

The functions of the pperipheral organs of the avian immune system are aimed at creating biological protection for the body against antigenic influences. The absence of lymph nodes is compensated by well-developed immunocompetent structures associated with the mucous membrane of the digestive tract in the form of diffusely scattered lymphocytes and lymphoid nodules of varying degrees of maturity. The development of immune structures depends on the species, sex, age category, feeding and housing conditions, and feed specialisation of birds. They are mainly located in the lamina propria and submucosal base of the mucous membrane and appear as small clusters of lymphoid tissue and their aggregates. Immune formations lie under the epithelial layer, near the glands (oesophageal, gastric, Lieberkühn) and their excretory ducts.

Lymphoid cells from separate immunocompetent structures migrate into the surface and glandular epithelium and are found between epithelial cells and in the gland wall. In the areas of the digestive tract that are most exposed to antigenic influence, there are well-organised immunocompetent structures in the form of tonsils (oesophageal, caecal), Meckel's diverticulum, caecal diverticula and groups of lymphoid nodules (Peyer's patches). Establishing the characteristics of their functioning in birds is important for understanding the presence or absence of full-fledged specific immunity (cellular and humoral defence) at the local level in the digestive tract. The composition of immunocompetent structures indicates the diversity of cells (lymphocytes, plasma cells, macrophages, etc.) present in birds of all ages.

The physiological processes that occur in them emphasise the importance of such formations in the immune defence system. Knowledge of the structure of the immune formations in the avian digestive tract will help in developing more effective prevention and treatment of infectious diseases and local inflammatory processes of the mucous membranes. Based on the above, it becomes obvious that the study of the species and age morphology of these structures in birds is quite relevant and is not only of scientific interest but also has great practical significance. Promising areas for further research on this topic may include the analysis and generalisation of data on the morphological features of the immune structures of the digestive tract of other representatives of the animal world.

Acknowledgements

None.

Funding

None.

Conflict of Interest

None.

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Морфологічні особливості імунних утворень травного каналу птахів

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Анотація. Імунокомпетентні структури органів травлення відіграють важливу роль в захисті організму від бактеріальних та вірусних інфекцій надаючи імунну відповідь. Метою даної роботи було встановити і узагальнити морфологічні особливості цих структур у птахів різних видів, що дозволить з'ясувати їх морфофункціональний статус, який визначається станом природньої резистентності і реактивності організму та виявити критичні періоди в розвитку імунної системи. Для досягнення мети був проведений літературний аналіз сучасних досліджень з топографії та мікроструктури імунних утворень органів травлення птахів. Встановлено, що матеріальною основою цих структур є лімфоїдна тканина, диференціація якої має регіональні особливості, відбувається у певній послідовності і проходить у декілька етапів. Її розвиток залежить від віку, виду, статі, типу живлення птахів та структурно-адаптаційних особливостей органів травлення. Імунні утворення локалізовані переважно у слизовій оболонці травного каналу, а у птахів окремих видів ще й у м'язовій та серозній оболонках. До їх складу входять Т- і В-лімфоцити та їх ефекторні клітини, які виконують важливі функції клітинного надзору у захисті організму від чужерідної генетичної інформації. Зазначено, що вони мають тісний контакт з макрофагами і функціонують як єдина лімфоїдно-макрофагальна система. Представлені наукові дослідження розширюють і доповнюють знання щодо видових, породних і морфологічних особливостей будови імунних утворень травного каналу птахів, що дасть змогу спеціалістам обєктивно оцінити ефективність методів профілактики і лікування захворювань на птахівничих господарствах

Ключові слова: імунні утворення; апарат травлення; лімфоцити; лімфоїдна тканина; лімфоїдні вузлики