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The Comparative Anatomy of the Upper Digestive System in 26 Species of Zoophagous-Polyphagous Palearctic Birds

Anatomía Comparada del Sistema Digestivo Superior en 26 Especies de Aves Paleárticas Zoófagas-Polífagas

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SUMMARY: Birds are the most diversified organisms on Earth, with species covering various niches in each major biome, being essential to understand the modern ecosystem. This study concentrates on the diversification of the anatomical structure of the upper digestive tract for 26 species of zoophage-polyphagous birds and the anatomical differences in the digestive system to reveal aspects related to their evolution and diversification. The trophic spectrum of the selected birds includes several categories of food, or, as in the case of strictly carnivorous birds, to a single food category. After performing the dissections, the digestive tract was separated from the carcass and each digestive segment was measured and analysed. In this study, it was demonstrated that the birds' feeding behaviour influence the macroscopic particularities of the digestive system, more visible in the cranial portion (oropharyngeal cavity, esophagus, proventriculus and gizzard), with little descriptive information in the literature. The tongue is poorly developed and immobile in piscivorous birds, while the tongue of insectivorous birds is long and moves considerably away from the tip of the bill. The esophagus was stretchable and presents longitudinal folds on its entire surface in piscivorous species and not extensible in insectivorous birds.

KEY WORDS: Biodiversity; Crop; Esophagus: Proventriculus; Gizzard.

INTRODUCTION

The avian gastrointestinal tract is a continuous tube that opens at each end towards the outside world and is composed of a mouth, esophagus, crop, stomach (proventriculus, ventriculus or gizzard), small intestine, ceca, rectum, and cloaca (Klasing, 1999). Our study is focusing on the upper digestive system, to explore the anatomical differences of the beak, esophagus, proventriculus and the gizzard in some species of zoophagous-polyphagous birds, in order to highlight the differences that exist between species and to highlight some aspects of their evolution and diversity. Birds possess an incredible diversity within their genus that can reach impressive numbers of different species in a single genus (i.e. Accipiter) (Balkaya, 2016; Singh, 2018; Wu *et al*., 2021; Melo *et al*., 2022). Compared to mammals, birds do not have teeth or very strong jaw muscles and their digestive system is lighter compared with mammals. Instead, it presents a light beak (Erdogan & Iwasaki, 2014; Mahmoud *et al*., 2018). The anatomy and physiology of the digestive tract reflect in the bird the limitations of flight, the centre of gravity of the system being located within the coelom cavity to optimize manoeuvrability. In the course of evolution, the digestive system has undergone changes to facilitate flight: the teeth have disappeared, the digestive tract is shorter. Compared to mammals birds present heavier organs (liver, muscular stomach) gathered around the center of the weight (Denbow, 2000; Huang *et al*., 2022).

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MATERIALS AND METHOD

The biological material was represented by 63 cadaver specimens from 26 zoophage-polyphagous species. The birds we examined were donated by the Zoological Museum of the University Cultural Heritage of Babes-Bolyai University. The opening of the body was carried out in several stages. The protocol was made following the description in the veterinary necropsic diagnostic book (Catoi *et al*., 2014). The plucking of the corpses was carried out strictly in the area of the incisions. The cutaneous incision was carried out from the lateral commissure of the beak to the level of the cloacal orifice. On each side of the sternum, the initial abdominal incision is continued up to the level of the chondrocostal junctions. The abdominal wall is sectioned longitudinally up to the cloaca and is turned laterally. Before starting the dissections, we weighed each corpse individually and measured the length of the body from skull to the base of the body. The digestive system was examined only macroscopically, in situ, and separated from the carcass. The oropharyngeal cavity, esophagus, proventriculus, ventriculus (gizzard) was examined in order to point out the anatomical peculiarities. For our study, we selected carnivorous and omnivorous species, which we usually call zoophagous-polyphagous.

RESULTS

The shape and size of the beak are an example of the remarkable versatility of birds, suitable for the type of food or the manner of feeding. The beaks of the examined birds were of various sizes and shapes. Most of the birds were carnivorous species, but the long beak, as found in *Ciconia ciconia, Nycticorax nycticorax, Ardea alba, Ardea cinerea,* has the function of probing the water in search of prey. The short beak and curved at the tip, was found in Falconidae and Accipitridae and its function was to tear apart little pieces of prey. The birds of the Picidae family presented a long beak, suitable for the type of insectivorous diet.

The oral cavity (*Cavum oris*) was continuous rostro-aboral with the pharyngeal cavity resulting in a common oropharyngeal cavity in all individuals. A feature we observed in piscivorous bird species but not only, for example *Ciconia ciconia* (Fig. 1), *Nycticorax nycticorax, Phalacrocorax carbo, Ixobrychus minutus*, was the presence of oblique folds on the floor of the oropharyngeal cavity, indicating that this cavity may increase in volume. These folds also have delimited the cranial part of the esophagus. The roof of the oral cavity possesses a longitudinal cleft, the choanae, a direct communication between the oral and nasal cavities (Fig. 2). Compared to mammals, birds have no soft palate and pharyngeal isthmus, creating a common oropharyngeal or buccopharyngeal cavity. Caudal to the choana we found the infundibular fissure. The infundibular fissure or cleft represents the opening of the auditory tube in the oropharyngeal cavity .

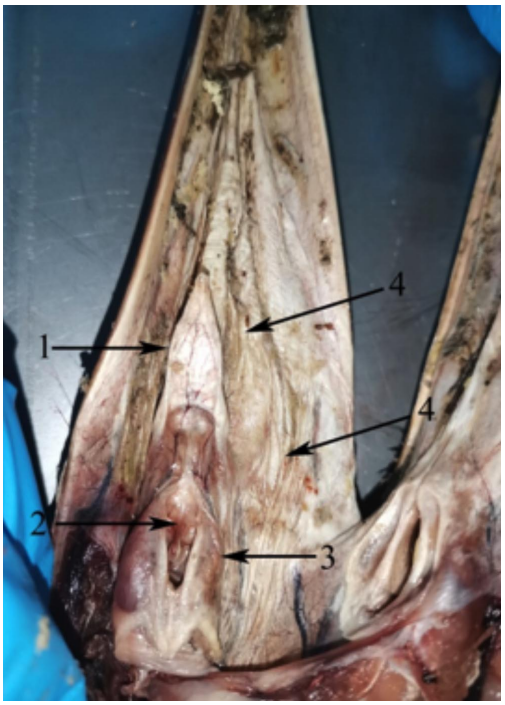

Fig. 1. Appearance of the lower jaw in *Ciconia ciconia*: the tongue with a spearhead appearance-1, the entrance of the trachea-2, continued with the laryngeal mound-3, the presence of longitudinal folds at the level in the lower jaw -4.

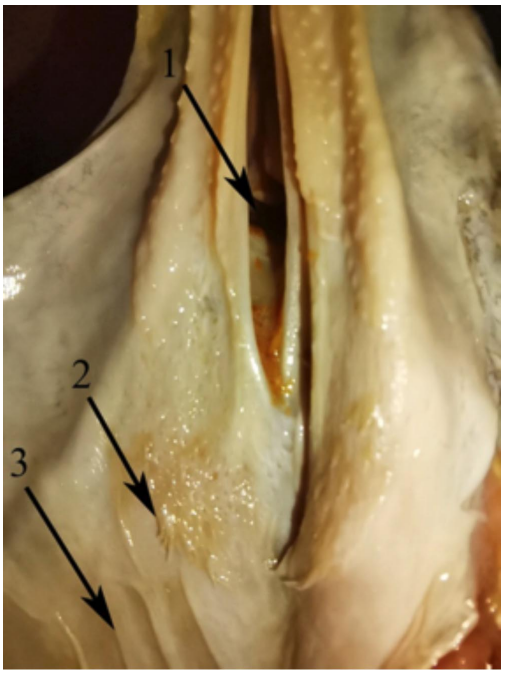

Fig. 2. Upper jaw *Gavia stellata:* choana-1; gland orifices-2; folded mucosa-3.

The morphological adaptations of the tongue (*Lingua*) varied depending on the

species. Some birds possess an immobile, short tongue, resembling an arrowhead, as seen in *Ciconia ciconia, Nycticorax nycticorax, Phalacrocorax carbo* while other species like *Ixobrychus minutus, Pandion haelietus, Ardea alba, Ardea cinerea* had a pointed and long tongue, reaching approximately the tip of the bill and showing little mobility. After the posterior part of the tongue, it is possible to identify the laryngeal mound, a reduced laryngeal structure, which has a narrow opening on the rostral surface, the entry into the larynx.

In raptors like *Falconidae, Accipitridae, Strigiformes*, we identified rigid, mostly conical and caudally directed papillae, distributed on both sides of choana and infundibular cleft, on the dorsal surface of the tongue and on the glottis. For the majority of studied raptors, we identified a row of conical papillae, with sharp pointed apices and with pointed ends facing toward the posterior part of the tongue, arranged in "V" shape. These conical papillae were absent in piscivorous pisces: *Ardea alba, Ardea cinerea, Ardea purpurea, Phalacrocorax carbo, Ciconia ciconia, Ixobrychus minutus, Podiceps grisegana*.

To be noticed is that the openings in the ducts of the salivary glands (*Glandulae salivariae*) were present in several species, mostly raptors (*Accipitridae, Falconidae, Strigiformes*), on the sides of the choana and the infundibular cleft, the ventral side of the lingual floor and at the terminal part of the tongue's body, on the lateral sides of the glottis (Figs. 2 and 3). Birds that live mostly on fish do not have these salivary openings.

A feature observed in piscivorous bird species but not only, for example *Ciconia ciconia, Nycticorax nycticorax, Phalacrocorax carbo, Ixobrychus minutus*, was the presence of oblique folds on the floor of the oropharyngeal cavity, indicating that this cavity is capable to increase in volume.

The esophagus is an organ with a tube-like appearance that extends along the neck from the oropharyngeal cavity to the proventriculus. It had the appearance of a thin-walled, easily extensible duct and presented a series of longitudinal folds, which help with distention. Compared with mammals, birds esophagus was divided into cervical and thoracic regions. In addition, it does not have an upper and lower sphincter than the esophageal level. For the majority of species investigated (*Pandion haliaetus, Dendrocopos major, Dendrocopos minor, Falco tinnunculus, Falco subbuteo, Falco vespertinus, Accipiter gentilis, Accipiter nisus*) the esophagus has a specific dilation the crop or ingluvius, prior to entering the thoracic cavity, an organ with variable shape depending on the species, formed by the enlargement of the esophagus (Fig. 4).

We observed that birds known to swallow the entire prey (*Nycticorax nycticorax, Phalacrocorax carbo, Ardea alba, Ardea cinerea, Ardea purpurea, Ciconia ciconia, Tyto alba, Buteo buteo, Buteo lagopus, Athene noctua*) have a slightly distended esophagus, and the longitudinal folds can also be found in the proventriculus

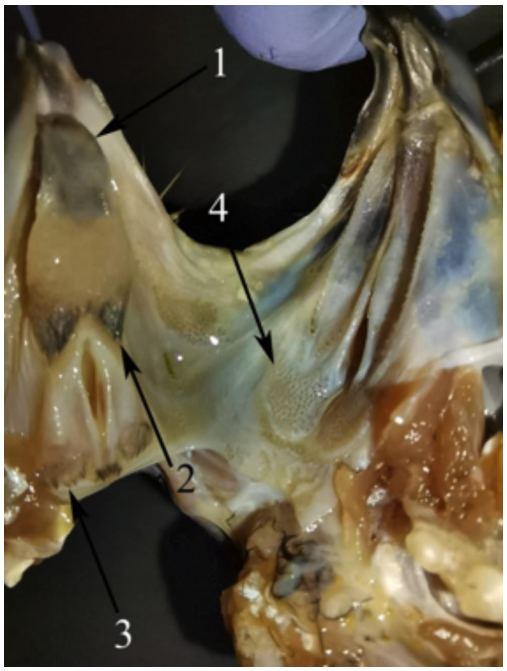

Fig. 3. Oropharyngeal cavity in *Falco tunniculus*: tongue-1, tongue aboral paillae-2, epiglotal papillae-3, glandular ducts-4.

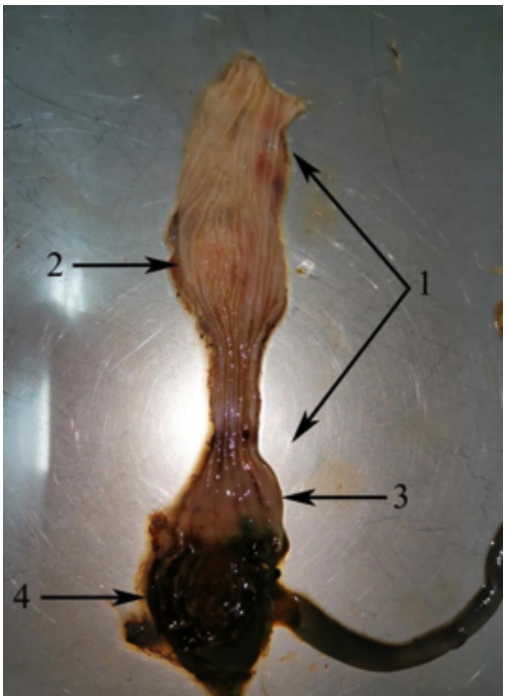

Fig. 4. Upper digestive tract *Accipiter nisus* esophagus-1, ingluvies-2, proventriculus-3, ventriculus-4.

(*Phalacrocorax carbo, Ardea alba, Ardea cinerea, Nycticorax nycticorax*). As well, the passage between the two compartments – the

esophagus and the proventriculus – is difficult to observe from the outside. Instead, on the inside of the proventriculus, about the transition between the two compartments, several orifices of the secretory glands may be seen on the surface of the mucosa, arranged between the longitudinal folds. In *Nycticorax nycticorax, Ixobrychus minutus*, longitudinal folds may also be seen on the surface of the glandular stomach, as a direct continuation of the longitudinal esophageal folds with an ill-defined passing between their mucosa. The middle zone, the isthmus, represents the transition from the glandular stomach to the muscular stomach. The proventriculus presented a visibly smaller size than the ventriculus with thinner walls and less rigid than of the gizzard. The topography of the crop depends strictly upon the species. For example in *Falco tunninculus, Falco subbuteo, Falco vespertinus, Accipiter gentilis* and *Accipiter nisus* the ingluvius is situated in the cranial part of the esophagus (Fig. 5), while in *Pandion haliaetus, Dendrocopos major, Dendrocopos minor* the crop in located the last portion of the esophagus.

The next organ, the stomach, is located on the left dorsal and ventral side of the thoracic abdominal cavity in most birds. In studied species of domestic birds the stomach has two compartments: the first segment is the proventriculus or the glandular stomach and the second is the gizzard or the muscular stomach, also known as ventriculus. Between these two segments, in all subjects we identified a supplementary segment called isthmus. The proventriculus or glandular stomach is located cranial to the muscular stomach, slightly orientated to the left, covered by the posthepatic septum and other abdominal organs. There was no distinct cardial orifice; on the internal side, at the transition from the esophagus to the proventriculus and at this level the esophageal folds dissapear. In *Nycticorax nycticorax, Ixobrychus minutus,* longitudinal folds are also present on the surface of the glandular stomach, as a direct continuation of the longitudinal esophageal folds. The middle zone, the isthmus, anatomically represents the transition from the glandular stomach (V*entriculus glandularis*) to the muscular stomach (*Ventriculus muscularis*). At this level the wall is thinner and less rigid than in gizzard.

The second segment, the gizzard, was identified ventrally on the left side of the coelomic cavity. The muscular stomach (*Ventriculus muscularis*) is positioned ventral to the glandular stomach, in contact with the sternum and the posterior portion of the lower thoracoabdominal muscles positioned on the middle left side of the coelomic cavity. In *Falco tunniculus* the glandular stomach was reduced in size, and the ventriculus resembled a pear like aspect (Fig. 6). In *Picus viridis*, between the glandular stomach and the gizzard we observed a gross strangulation (Fig. 7). *Ciconia ciconia* presents a poorly developed glandular stomach and at the surface of the mucosa we were able to observe many ducts of secretory glands. The koilin membrane, also called cuticula gastris, was identified on the surface of the muscular stomach in *Ciconia ciconia* (Fig. 8). The pyloric region was topographically different depending on the species, but for all the birds studied, it opens on the right side of the muscular stomach.

Fig. 5. Upper digestive in *Accipiter nisus*: ingluvies-1; esophagus-2; proventriculus-3, Ventriculus-4, duodenum-5.

Fig. 6. Upper digestive sytem in *Nycticorax nycticorax*: esophagus-1; 2. proventriculus-2; gizzard-3; pyloric orifice-4; duodenum-5.

DISCUSSION

Body length varies with the reference species, but because of the advanced state of carcass decomposition, measurements may differ from the values found in literature (Baltag *et al*., 2017).

As noted by van Wassenbergh & Baeckens (2019) and Lacasse (2015), there is a common understanding that the beak is specialized in feeding - a small, heavy beak can crush, a long beak has a probe-like function, the beak bent towards the tip tears the prey. Our results regarding the division of the beak are similar with the report of other authors (Denbow, 2000).

The anatomical features of the common oropharyngeal cavity, the communication between the nasal and oral cavity and the absence of the soft palate are similar with the results of other authors like Popovici *et al*. (2003) and Singh (2018). Caudal to the choanae, an infundibular fissure is present, located medially and represents the opening of the auditory tube (Denbow, 2000; Singh, 2018). The features observed by us regarding the oral cavity were also reported by Fidgett & Dierenfeld (2008). For the other listed species, these features were not found in the literature.

The abundance of secretory gland openings varies depending on the predominant diet of the species – piscivorous birds have few secretory gland openings (i.e. *Gavia arctica, Gavia stellata*), usually located near the beak, compared to birds which eat only mammals and birds (for example the family *Accipitridae, Falconidae, Strigidae*), respectively compared with birds that consume insects/seeds (*Picur viridis, Dendrocopos major* and *Dendrocopos minor*) (Denbow, 2000).

The tongue comes in different shapes and sizes. Variations in shape and size allow the tongue to manipulate, process and swallow prey (Abdel-Megeid *et al*., 2021). In general, the tongue of carnivorous birds is poorly mobile and presents cornified papillary formations at the base of the tongue, arranged in the shape of the letter V with an aboral opening (King & McLelland, 1979). Birds of the Picidae family are able to push their tongues out of their beaks for considerable distance to obtain insects and tree sap (King & McLelland, 1979). A particularity observed in piscivorous birds, the tongue cannot move and has the appearance of a spearhead of various sizes, as we have observed in *Nycticorax nycticorax, Phalacrocorax carbo, Ardea alba, Ardea cinerea, Ardea purpurea, Ciconia ciconia*.

The esophagus lies between the oropharyngeal cavity and the proventriculus. In all the studied species, this segment presents a series of longitudinal folds that help distension (Klasing, 1999).

The crop, a tubular organ formed by the enlargement of the esophagus, has been identified in several species studied, as

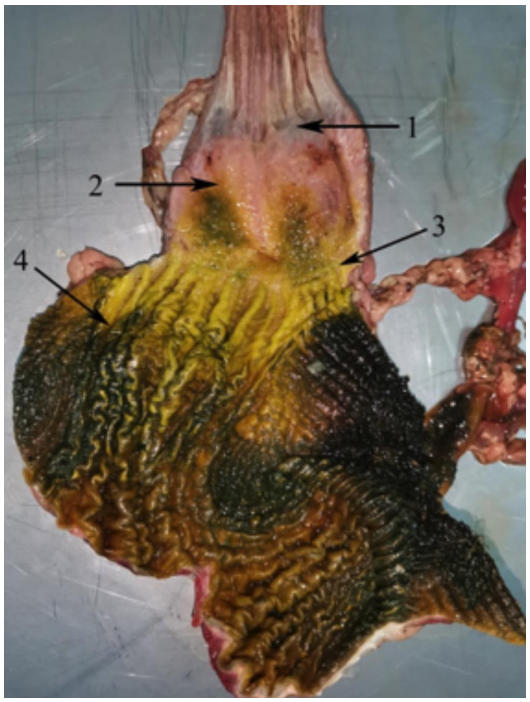

Fig. 7. Proventriculus and ventriculus in *Ciconia ciconia*: blurring of the oesophageal folds-1, glandular stomach-2, the isthmus-3 folded appearance of the cuticula gastris-4.

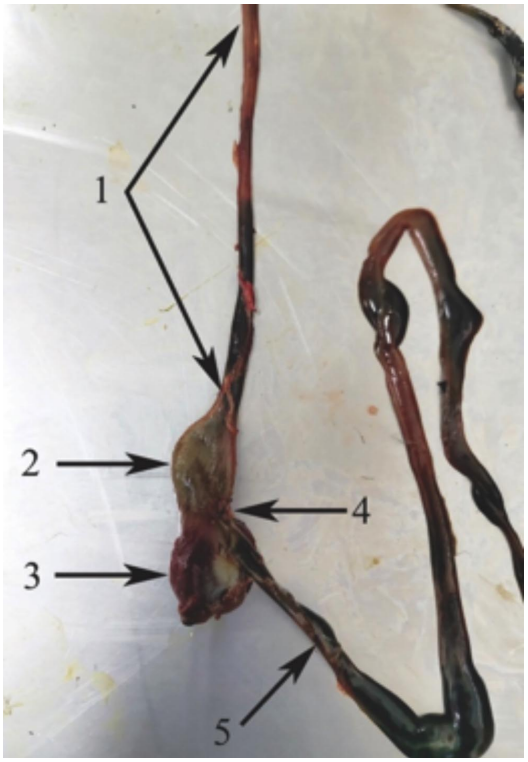

Fig. 8. Digestive tract upper portion in *Picus viridis*: esophagus-1; glandular stomach-2; muscular stomach-3; D-isthmus-4; duodenum-5.

observed in Falconidae and Picidae. The topography of ingluvies depends strictly upon the species: Falconiformes Piciformes order present the ingluvies located at the entrance to the thoracic cavity (Abumandour, 2013; Kieronczyk *et al*., 2016). In particular, the ingluvies observed in birds of the order Piciformes is not well defined; The lack of the crop was reported in penguins, owls and guls (Singh, 2018). Near the proventriculus, the esophagus increases in volume and then resumes its original shape before entering the proventriculus.

Birds have two compartments in their stomachs: the proventriculus and the ventriculus or gizzard. The proventriculus or glandular stomach is located cranial to the ventriculus or gizzard (Denbow, 2000). The proventriculus of the studied birds is small in size, positioned on the left ventral side of the thoraco-abdominal cavity. However, in dissections when the bird is open ventrally, a small part of the stomach can be identified because of the post-hepatic adipose septum (King & McLelland, 1979; Abumandour, 2013). The development degree of the proventriculus and ventriculus of raptors compared to other birds like granivorous or Psittaciformes is mentioned by Ford (2010) who highlighted it in the bald eagle. As we mentioned earlier, piscivorous birds have longitudinal folds, including at the proventricular level, with multiple openings of the secretory glands arranged between these folds.

The gizzard is placed on the left side of the midline and can be palpated as a firm, caudal positioned organ at the sternum. On an evolutionary scale, the stomachs of birds have adapted in accordance with their diet (McLelland, 1993; Mulè, 1991). McLelland (1979, 1990), claims that piscivorous and carnivorous birds show no obvious difference in the appearance of the two stomachs, easily distensible for swallowing whole prey. Birds that eat high-volume food compared to their size will have a large stomach (MacWhirter, 2009). The pyloric part is different, depending on the species, being situated either near the proventriculus-ventricle junction, or caudal to the ventricle, lateral to the esophagus-proventriculus-ventricle axis. In birds, as in mammals, the small intestine is subdivided into duodenum, jejunum and ileum. The intestinal length varies depending on the species, being shorter in the case of frugivores, carnivores and insectivores, and longer in the case of granivores, herbivores and piscivores (Mulè, 1991; McLelland, 1993; Klasing, 1999). Unfortunately, due to the advanced state of decomposition of the corpses, we were unable macroscopically to point out the separation of the actual segments (duodenum, jejunum and ileum).

CONCLUSIONS

As a result of the study, we can infer that the feeding habit of birds influences the macroscopic peculiarities of the digestive system, a noticeable aspect especially on the cranial segment of the digestive tract.

Based on analysis of trophic spectrum and anatomical characteristics, the main new observations are related to the tongue of piscivorous birds, which is poorly developed, with a spear-like appearance, located on the floor of the oropharyngeal cavity, immobile. Also in these birds we have identified folds with an oblique arrangement of the middle floor of the oropharyngeal cavity, an appearance which suggests this cavity is distensible.

The esophagus is adapted to the type of feeding, namely: birds which swallow whole prey have a distensible esophagus with longitudinal folds on its entire surface, including at the proventricular level. Insectivorous birds have longitudinal folds but do not have a similar distensible esophagus.

The stomach, underdeveloped in all the species studied and with the appearance of an elongated pear-like structure, was divided into two segments (the glandular stomach and the muscular stomach), separated by a small isthmus.

PREJA, A. I.; CIPOU, M. F.; MARTONOS, C. O.; STERMIN, A. N. & DAMIAN, A. Anatomía comparada del sistema digestivo superior en 26 especies de aves paleárticas zoófagas-polífagas. *Int. J. Morphol., 41(5)*:1336-1342, 2023.

RESUMEN: Las aves son los organismos más diversificados de la Tierra, con especies que cubren varios nichos en cada bioma principal, siendo esenciales para comprender el ecosistema moderno. Este estudio se concentra en la diversificación de la estructura anatómica del tracto digestivo superior para 26 especies de aves zoófago-polífagas y las diferencias anatómicas en el sistema digestivo para revelar aspectos relacionados con su evolución y diversificación. El espectro trófico de las aves seleccionadas incluye varias categorías de alimentos o, como en el caso de las aves estrictamente carnívoras, una sola categoría de alimentos. Después de realizar las disecciones, se separó el tracto digestivo de la canal y se midió y analizó cada segmento digestivo. En este estudio se demostró que el comportamiento alimentario de las aves influye en las particularidades macroscópicas del sistema digestivo, más visibles en la porción craneal (cavidad orofaríngea, esófago, proventrículo y molleja), con poca información descriptiva en la literatura. En las aves piscívoras, la lengua está poco desarrollada e inmóvil, mientras que la lengua de las aves insectívoras es larga y se aleja considerablemente de la punta

del pico. El esófago era estirable y presentaba pliegues longitudinales en toda su superficie en especies piscívoras y no extensible en aves insectívoras.

PALABRAS CLAVE: Biodiversidad; Cultivo; Esófago: Proventrículo; Molleja.

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