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Comparative histology and mucin histochemistry of the glandular stomach in the zebra finch (*Taeniopygia guttata*) and the desert finch (*Rhodospiza obsoleta*)

Reza Sayrafi*

Department of Veterinary Basic Sciences, Faculty of Veterinary Medicine, Amol University of Special Modern Technologies, Amol, Iran.

(*) Corresponding Author: reza.sayrafi@gmail.com

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Abstract

Finches are among the most commonly kept cage birds and are also used as laboratory models in certain areas of research. The zebra finch and the desert finch, while taxonomically grouped under the general designation of 'finches,' exhibit marked differences in their evolutionary lineages, ecological niches, and foraging habits. The present study aimed to characterize the histological and histochemical properties of the glandular stomach in these distinct species. Specimens from the proventriculus of five adult individuals per species were fixed in 10% buffered formalin. Tissues were processed for histological and histochemical analysis, utilizing Hematoxylin and Eosin (H&E), Masson's trichrome, Periodic Acid-Schiff (PAS), and Alcian blue (pH 2.5) staining. Histological analysis revealed a similar four-layered structure in the proventriculus of both species, comprising the mucosa, submucosa, muscularis, and serosa. The mucosa, characterized by numerous folds and a simple columnar epithelium, contained superficial simple tubular glands, with deeper tubuloalveolar glands situated beneath them, constituting a significant portion of the proventricular wall thickness. The submucosa was remarkably thin, followed by a muscularis layer composed of inner longitudinal, middle circular, and outer longitudinal strata, and an outer serosa. Histochemical findings indicated the presence of both neutral and acidic mucins in both species. In the zebra finch, neutral mucins were observed with greater intensity than acidic mucins. Furthermore, the zebra finch exhibited a stronger reaction to PAS staining compared to the desert finch.

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Introduction

In birds, the stomach plays a pivotal role in the gastrointestinal tract and consists of two anatomical parts. The first segment, the glandular stomach (proventriculus), is primarily responsible for chemical digestion through the secretion of gastric juices. The second segment, the muscular stomach (ventriculus or gizzard), functions as a muscular organ that mechanically grinds food particles and facilitates their thorough mixing with digestive secretions (Eurell and Frappier, 2006; Dyce *et al*., 2010).

The morphology and function of these stomach compartments vary widely among avian species, adapting to the nature and volume of their food intake. Consequently, the proventriculus is typically large and distended in carnivorous species, whereas it is notably smaller in granivorous birds (Khaleel *et al*., 2021).

In most avian species, the proventriculus is a tubular organ situated between the esophagus and the gizzard. As the glandular portion of the stomach, it serves as a temporary site for food storage and initiates digestion through the secretion of digestive juices before the ingesta passes into the gizzard. Histologically, the proventriculus contains superficial mucous glands and deep gastric glands, which secrete mucus, hydrochloric acid, and pepsinogen. These secretions facilitate the subsequent mechanical mixing of food within the gizzard. Pepsinogen is converted into pepsin, an enzyme that hydrolyzes peptide bonds in dietary proteins (Saran and Meshram, 2021).

Based on dietary habits, the avian stomach is categorized into three primary types. The first category comprises species consuming soft diets (e.g., owl and kestrel), the second includes those adapted to hard diets (e.g., sparrow and turkey), and the third encompasses birds with intermediate dietary regimes (e.g., goose, hoopoe, and darter) (Hassouna, 2001).

Interspecific differences in the histological and histochemical properties of the proventriculus are closely associated with diet. Given that dietary constituents significantly influence the structural and functional attributes of the digestive system, they consequently regulate digestive efficacy and the availability of essential nutrients (Jabbar and AlKhalissi, 2026).

Histological investigations of the avian proventriculus have demonstrated that this organ is composed of four principal layers: the mucosa, submucosa, muscularis, and serosa. In certain bird species, such as the chicken, the mucosal surface of the proventriculus is lined by simple columnar epithelium, which continues into the ducts of the submucosal glands. These glands are lined by epithelium ranging from simple cuboidal to short columnar in type. A single recognizable cell type has been described in this region and is thought to secrete both pepsinogen and hydrochloric acid. The lamina propria consists of typical loose connective tissue. The loose connective tissue of the submucosa is surrounded peripherally by the muscularis, which is composed entirely of smooth muscle. Externally, the proventriculus is enclosed by a serosal layer (Eurell and Frappier, 2006).

Despite sharing the common designation of finch, the zebra finch and the ground finch belong to distinct genera and species. Moreover, they differ in terms of habitat preference, feeding behavior, and dietary requirements. Anatomical and histological studies on certain digestive organs of the zebra finch have previously been reported. However, comparable information regarding the digestive organs of the desert finch remains unavailable. Accordingly, the current research was conducted to perform a comparative histological and histochemical evaluation of the proventriculus in these two finch species.

Materials and Methods

The present study was designed to comparatively evaluate the histological and histochemical characteristics of the proventriculus in zebra finches and desert finches. All animal procedures were performed in accordance with the guidelines of the Animal Ethics Committee of Amol University of Special Modern Technologies. Five adult birds of each species, representing both sexes, were used in the experiment. All birds were procured from pet stores and underwent health assessment prior to euthanasia. The animals were subsequently euthanized by an overdose of ketamine and xylazine for sample collection (Fig. 1).



Fig. 1. Anatomical appearance of the proventriculus of desert finch (a) and zebra finch (b): Red arrow: proventriculus.

Subsequently, the stomach of each bird was excised, and tissue specimens from the mid-region of the proventriculus were immediately placed in 10% buffered formalin. Following fixation, the tissues were dehydrated through ascending concentrations of alcohol, cleared in xylene, and embedded in paraffin. The paraffin blocks were sectioned using a rotary microtome (Diapath, Italy). The sections were then stained with hematoxylin and eosin (H&E) for general histological evaluation, Masson's trichrome for connective tissue identification, Periodic Acid-Schiff (PAS) for the detection of neutral mucins, and Alcian blue (pH 2.5) for acidic mucins (Suvarna and Layton, 2013).

Photomicrographs of the stained sections were obtained using a light microscope equipped with a digital camera (Olympus CX21 FS1; TrueChrome II).

Results

Histological and histochemical structure of the proventriculus in zebra finch

Histological examination of the proventriculus revealed four distinct layers: the mucosa, submucosa, muscularis, and serosa. The mucosal surface of the proventriculus exhibited finger-like folds of varying heights projecting into the lumen. These folds featured invaginations into the lamina propria, forming simple tubular glands (superficial glands) distributed along the surface epithelium. The mucosal surface was lined by simple columnar epithelium, characterized by relatively pale cytoplasm and basally located nuclei. Underlying this epithelium, the lamina propria consisted of loose connective tissue. An ultra-thin layer of smooth muscle, forming the muscularis mucosae, surrounded the deep proventricular glands. These large, deep-seated glands constituted the bulk of the proventricular wall thickness. The glands, arranged in oval or pyramidal lobules, possessed a tubuloalveolar structure. Most of these units were connected to secondary ducts, along which the primary secretory ducts were located. These primary secretory ducts opened into the lumen of the proventriculus. The alveolar units were composed of acidophilic cuboidal cells with central nuclei. In some areas, the cells displayed a serrated appearance due to their basal adjacency and apical separation. The cells in the secondary and primary ducts were columnar in shape, with the cells in the primary ducts being taller than those in the secondary ducts. The nuclei in these cells were often elongated and located at the base. The cytoplasm of the duct cells was foamy and slightly acidophilic.

The submucosa consisted of a thin to very thin layer of connective tissue, featuring large blood vessels in certain regions. The tunica muscularis was composed of an inner longitudinal layer, a middle circular layer, and an outer longitudinal layer of smooth muscle. The outer layer was very thin or discontinuous in some sections, and was occasionally not observed. The tunica serosa comprised a thin layer of loose connective tissue, containing large blood vessels, nerve fibers, and adipocytes.

Histochemical analysis using PAS staining revealed intense reactivity on the mucosal surface. The cells lining the superficial glands also exhibited a positive reaction. Furthermore, PAS reactivity was observed within the deep proventricular glands, particularly in the primary and secondary ducts.

Masson's trichrome staining revealed positive reactivity in the epithelial cells of the superficial glands, whereas a comparatively weaker reaction was observed in the primary and secondary ducts of the deep proventricular glands.

Alcian blue staining confirmed the presence of acidic mucins. Reactivity ranged from low to moderate in the mucosal surface epithelium and the primary and secondary ducts of the deep glands, while more intense staining was localized to the superficial gland cells and the deep glandular alveoli (Figs. 2-6).

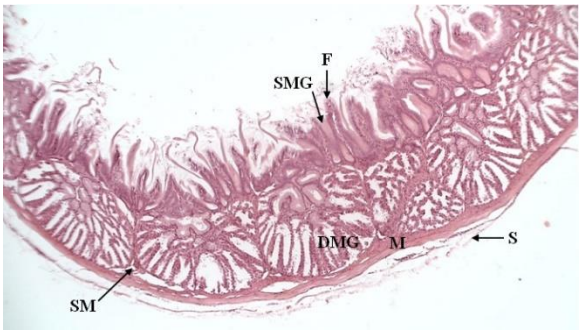


Fig. 2. Histological features of the proventriculus of zebra finch: F: fold, SMG: superficial mucosal gland, DMG: deep mucosal gland, SM: submucosa, M: muscular tunic, S: serosa (H&E; 100X).

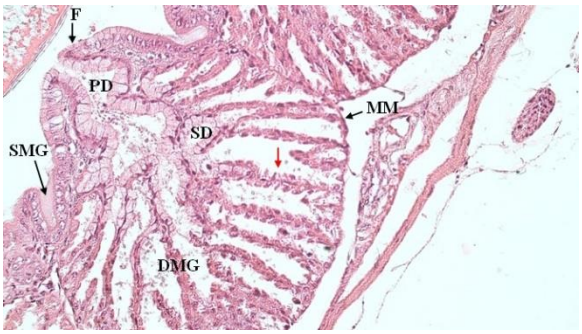


Fig. 3. Histological features of the proventriculus of zebra finch: F: fold, SMG: superficial mucosal gland, DMG: deep mucosal gland, PD: primary duct of the deep gland, SD: secondary duct of the deep gland, MM: mucous membrane, Red arrow: glandular cells were juxtaposed at their basal portions and showing a dentate appearance (H&E; 400X).

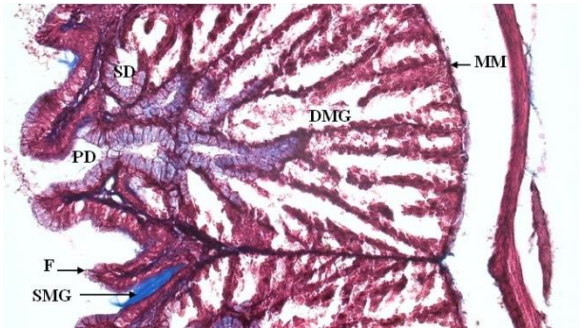


Fig. 4. Histochemical features of the proventriculus of zebra finch: F: fold, SMG: superficial mucosal gland, DMG: deep mucosal gland, PD: primary duct of the deep gland, SD: secondary duct of the deep gland, MM: mucous membrane (Masson's trichrome; 400X)

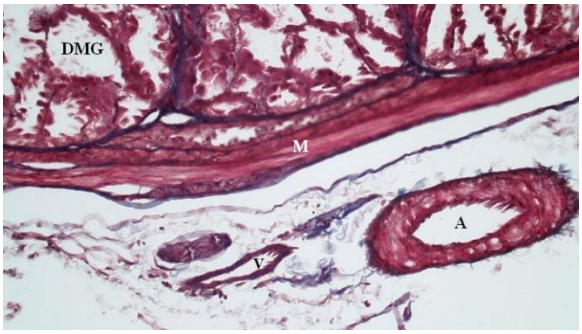


Fig. 5. Histochemical features of the proventriculus of zebra finch: DMG: deep mucosal gland, M: muscular tunic, A: artery, V: vein (Masson's trichrome; 400X).

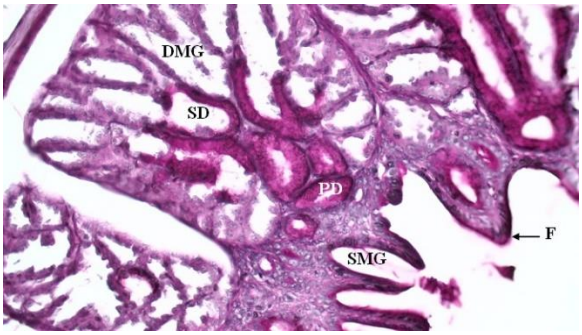


Fig. 6. Histochemical features of the proventriculus of zebra finch: F: fold, SMG: superficial mucosal gland, DMG: deep mucosal gland, PD: primary duct of the deep gland, SD: secondary duct of the deep gland (PAS; 400X).

Histological and histochemical structure of the proventriculus in desert finch

The proventricular wall comprised four distinct layers, ordered from the luminal to the serosal surface: tunica mucosa, tunica submucosa, tunica muscularis, and tunica serosa. The mucosal surface of the proventriculus was irregular, characterized by mucosal folds of varying heights and invaginations into the lamina propria. The epithelium was composed of simple columnar cells, featuring acidophilic cytoplasm and basally located nuclei. Within the lamina propria, which consisted of loose connective tissue, simple tubular glands (superficial glands) were distributed along the mucosal surface. The glandular cells exhibited a decrease in height from the superficial layer toward the base, transitioning from a columnar to a cuboidal morphology. The muscularis mucosae constituted an ultra-thin smooth muscle layer surrounding the deep proventriculus glands. The deep glands, organized

into oval lobules, constituted the majority of the proventricular wall thickness. These glands exhibited a tubulo-alveolar morphology and comprised both primary and secondary ductal systems. Primary secretory ducts originated within the secondary ducts, terminating at the lumen of the proventriculus. The epithelial lining of both primary and secondary ducts consisted of columnar cells. Notably, the cells within the primary ducts exhibited greater height compared to those in the secondary ducts. The cells featured predominantly elongated nuclei positioned at the cell base; additionally, the cytoplasm was characterized by a foamy and mildly acidophilic texture. In the alveolar regions of the deep glands, the cells exhibited a cuboidal morphology with centrally located nuclei and acidophilic cytoplasm. These cells displayed a serrated arrangement, characterized by closely apposed basal surfaces and distinct separation at the apical poles.

A thin layer of connective tissue constituted the submucosa, which contained various cross-sections of large blood vessels. The tunica muscularis comprised three distinct smooth muscle layers: an inner longitudinal, a middle circular, and an outer longitudinal layer. The outer layer was discernible only in certain sections and appeared markedly thin. Additionally, blood vessels and segments of the myenteric nerve network were observed interposed between the muscular layers. The serosa consisted of a thin layer of loose connective tissue that enveloped the proventriculus. Within the tunica serosa, large blood vessels, nerve fibers, and adipocytes were identifiable.

Histochemical analysis using PAS staining revealed positive reactivity on both the mucosal surface and the cells covering the superficial glands. Furthermore, the deep glands exhibited weak PAS reactivity, whereas the primary and secondary ducts demonstrated significantly greater staining intensity.

In the desert finch, Masson's trichrome staining exhibited positive reactivity in the superficial glands and the primary and secondary ducts of the deep proventricular glands, albeit with a lower intensity compared to the zebra finch.

Alcian blue staining, employed to detect acidic mucins, revealed positive reactivity within the mucosal surface epithelium, the superficial glands, and the primary and secondary ducts of the deep glands. Notably, this positivity was most intense within the cells of the deep glands compared to other regions (Figs. 7–11).

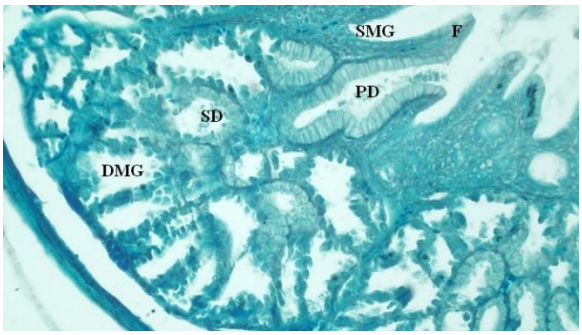


Fig. 7. Histochemical features of the proventriculus of zebra finch: F: fold, SMG: superficial mucosal gland, DMG: deep mucosal gland, PD: primary duct of the deep gland, SD: secondary duct of the deep gland (Alcian blue; 400X).

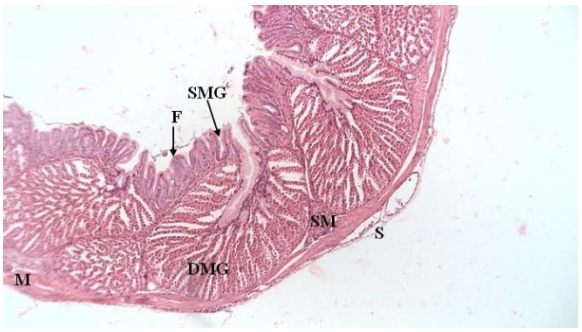


Fig. 8. Histological features of the proventriculus of desert finch: F: fold, SMG: superficial mucosal gland, DMG: deep mucosal gland, SM: submucosa, M: muscular tunic, S: serosa (H&E; 100X).

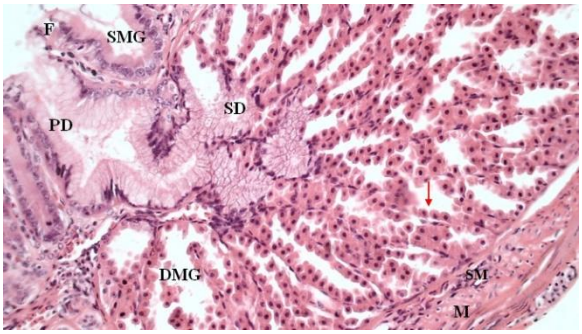


Fig. 9. Histological features of the proventriculus of desert finch: F: fold, SMG: superficial mucosal gland, DMG: deep mucosal gland, PD: primary duct of the deep gland, SD: secondary duct of the deep gland, SM: submucosa, M: muscular tunic (H&E; 400X).

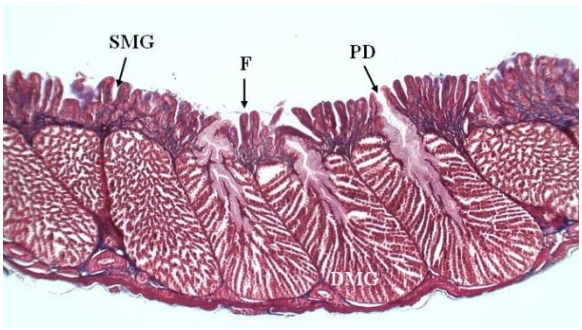


Fig. 10. Histochemical features of the proventriculus of desert finch: F: fold, SMG: superficial mucosal gland, DMG: deep mucosal gland, PD: primary duct of the deep gland (Masson's trichrome; 100X).

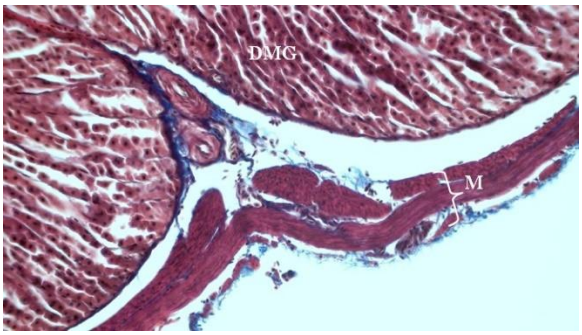


Fig. 11. Histochemical features of the proventriculus of desert finch: DMG: deep mucosal gland, M: muscular tunic (Masson's trichrome; 400X).

Discussion

Our findings demonstrated that the proventricular wall in both zebra and desert finches maintains a classical four-layered architecture. The observed proventricular structure aligns with typical avian morphological patterns. In contrast, the proventricular wall of the yellow-billed grosbeak exhibited a distinct three-layered structure, comprising the mucosa, muscularis, and serosa (Zhu *et al*., 2013). The proventricular mucosa in both species was lined by a simple columnar epithelium, a finding consistent with observations in various avian taxa (Ogunkoya and Cook, 2009; Kadhim *et al*., 2011; Hassan and Moussa, 2012, Al-Samawy *et al*., 2021; Abdel-Maksoud *et al*., 2022). This contrasts with the report by Rossi *et al*. (2005) regarding the partridge, which described a cuboidal epithelial morphology. The superficial glands in both species were of a simple tubular type, a characteristic also reported in the proventriculus of various passerines, such as Lichmera indistincta, Zosterops lateralis, Poephila guttata, and the cranial region of common starlings (Ogunkoya and Cook, 2009, Sayrafi and Aghagolzadeh, 2020). The deep proventricular glands of zebra and desert finches were tubuloalveolar, consistent with red jungle fowl (Kadhim *et al*., 2011). In contrast, the African pied crow and yellow-billed grosbeak feature compound tubular glands (Zhu *et al*., 2013; Udoumoh and Ikejiobi, 2017), whereas compound tubuloalveolar glands have been reported in three passerine species (Ogunkoya and Cook, 2009). The cells lining the tubuloalveolar glands of the proventriculus exhibited a dentate morphology, a feature previously reported in several avian species (Kadhim *et al*., 2011; Zhu *et al*., 2013, Sayrafi and Aghagolzadeh, 2020). The lobules of the deep proventricular glands were enveloped by muscular cells branching from the muscularis mucosa. In the studied species, the submucosal layer was thin to very thin in the zebra finch and thin in the desert finch. This histological finding aligns with observations in avian species lacking submucosal proventricular glands (Ogunkoya and Cook, 2009; Kadhim *et al*., 2011; Hassan and Moussa, 2012; Sayrafi and Aghagolzadeh, 2020). In contrast, a significantly thicker submucosa is characteristic of species possessing submucosal glands, such as the Iraqi falcon, hooded crow, and guinea fowl (Selvan *et al*., 2008; Hussein *et al*., 2020, Abdel-Maksoud *et al*., 2022).

Our findings suggest that the dominant structural component of the proventricular wall varies among avian species. In the common starling and three Australian passerine species, the deep proventricular glands constituted the widest dimension of the wall (Ogunkoya and Cook, 2009; Sayrafi and Aghagolzadeh, 2020). Conversely, in the Eurasian hobby and Iraqi falcon, the tunica muscularis emerged as the primary structural constituent (Abumandour, 2014; Hussein *et al*., 2020).

In both species, the tunica muscularis comprised three distinct layers: inner longitudinal, middle circular, and outer longitudinal. While the majority of avian studies report a two-layered muscularis (Rossi *et al*., 2005; Kadhim *et al*., 2011; Abumandour, 2014; Sayrafi and Aghagolzadeh, 2020; Abdel-Maksoud *et al*., 2022), our observations align with the findings of Banks (1992), who noted a tripartite muscularis (inner longitudinal, middle circular, and outer longitudinal) in fowl.

In both species, our description of the general structure of the tunica serosa aligns with that provided by most other authors (Ogunkoya and Cook, 2009; Kadhim *et al*., 2011; Hassan and Moussa, 2012; Deka, 2017). However, the tunica serosa in partridge consisted of connective tissue and a layer of cuboidal cells. Additionally, the presence of smooth muscle fibers was noted within the tunica serosa (Rossi *et al*., 2005).

PAS histochemical staining exhibited differential intensities between the two species; the zebra finch showed intense reactivity on the mucosal surface and within the deep proventricular glands, whereas the desert finch displayed significantly weaker PAS-positive reactions in both regions. The presence of PAS-positive mucin in the surface epithelium of both studied species corroborates previous findings in the common starling, guinea fowl, Iraqi falcon, and hooded crow (Selvan *et al*., 2008; Hussein *et al.,* 2020; Sayrafi and Aghagolzadeh, 2020; Abdel-Maksoud *et al*., 2022). Furthermore, the PAS-positive reaction observed in the superficial glands aligns with reports in the red jungle fowl, common starling, and guinea fowl (Selvan *et al*., 2008; Kadhim *et al*., 2011; Sayrafi and Aghagolzadeh, 2020). The PAS-positive reactivity observed in the ductular epithelium of the deep glands aligns with previous reports in the common starling and guinea fowl (Selvan *et al*., 2008; Sayrafi and Aghagolzadeh, 2020). This pattern, however, presents a nuanced contrast to the African pied crow, where the compound tubular glands reacted negatively to PAS, while the collecting ducts and the collecting tubules exhibited positive reactivity (Udoumoh and Ikejiobi, 2017). Such histochemical profiles underscore the functional importance of mucin secretion; specifically, the presence of mucin on the mucosal surface serves as a vital lubricant and forms a protective barrier against physical damage from luminal contents (Bansil and Turner, 2006; Udoumoh and Ikejiobi, 2017). Histological evidence indicated that an increased number of PAS-positive mucous cells within the epithelium reflects enhanced glycopolysaccharide synthesis and a greater protective capacity of the mucosal lining. A balanced diet supplies the essential nutrients required for proper epithelial differentiation and glycoprotein production, both of which are critical for maintaining mucosal barrier integrity and facilitating epithelial lubrication. Accordingly, the abundance of PAS-positive cells may be interpreted as a structural adaptation associated with strengthened mucosal integrity and elevated carbohydrate-rich secretory activity in the epithelium (Jabbar and AlKhalissi, 2026).

The mucosal gland epithelium exhibited positive Masson's trichrome staining in both species, although the reaction was more intense in the zebra finch. This pattern corroborates observations made in the red jungle fowl and common starling (Kadhim *et al*., 2011; Sayrafi and Aghagolzadeh, 2020).

Although the primary purpose of using Masson's trichrome staining in this study was to identify connective tissue, the presence of various dyes in this technique allows for the distinction between different tissue components (Humason, 1979).

Positive Alcian blue staining revealed a high concentration of acidic mucins in the glands. Notably, the reaction intensity exhibited a site-specific pattern, being most pronounced in the superficial and deep gland cells of the zebra finch, and the deep gland cells of the desert finch. This differential staining intensity suggests a functional heterogeneity in mucin secretion, potentially reflecting adaptive physiological responses to the specific environmental requirements or dietary habits of each species. Previous studies on sparrow hawks, crows, and starlings have reported that Alcian blue reactivity is largely confined to the tunica mucosa and superficial glands, with notably weak staining in the deep glands of starlings (Demirbag *et al*., 2015; Sayrafi and Aghagolzadeh, 2020). Similarly, in fowl, the glandular cells of the compound glands exhibit dual reactivity to both Alcian blue (pH 2.5) and PAS (Imai *et al*., 1991). In the present study, we observed a similarly broad distribution of neutral mucins, encompassing the superficial mucous cells, superficial glands, and deep glands of the proventriculus. This widespread presence aligns with the dual reactivity patterns observed in other avian species, suggesting a complex mucin profile in the proventriculus.

The composition of secretions varies depending on the function or requirements of the epithelial tissues in response to environmental factors. Generally, mucins are classified histochemically as either neutral or acidic. Both neutral and acidic mucins help protect the mucosal surface and create a durable mucosal

barrier in birds.

Diet composition, feeding habits, and the amount of food consumed are known to influence the histology of the digestive tract (Zaher *et al*., 2012; Abumandour, 2014). The avian gastrointestinal tract has evolved to take advantage of the physical and chemical characteristics of a wide variety of diet types. In other words, the differences in proventriculus structure may be related to diet. In birds that eat hard food, the proventriculus is relatively thin-walled and glandular while the gizzard is muscular and thick-walled. This gastric arrangement is typically found in granivorous, herbivores, insectivores, and omnivores (Gelis, 2005; Kadhim *et al.*, 2011; Abumandour, 2014). The numerous and extensive glands in the proventricular wall are due to the varied diet of these two species of finches.

In conclusion, while the overall proventricular histology of these two species aligns with established avian patterns, significant differences were observed. Specifically, the absence of submucosal glands, the mucosal location of proventricular glands, and the structural arrangement of the muscular layer distinguish these species from some other avian models. Histochemical analysis of mucins revealed interspecific variations. In the zebra finch, neutral mucins were more abundant than acidic mucins, and this species demonstrated a stronger PAS-positive reaction compared to the desert finch.

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Conflict of Interest

There are no conflicts to declare.

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