THE COMPARATIVE HISTOLOGY OF THE
ESOPHAGUS AND STOMACH OF
BIRDS OF DIFFERENT
FOOD HABITS

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ABSTRACT

A histological investigation was carried out on the esophagus and stomach of the following birds: kingfisher (Megaceryle alcyon saurina), California murre (Uria aalge californica), screech owl (Otus asio kennicotti), Peale's falcon (Falcoperegrinus pealei), and sparrow hawk (Falcospargerus spargerus). A number of stains were used to intensify the different structures present.

In the kingfisher, murre and owl the esophagus was a thin walled highly expansible tube of generally even calibre, whereas in the Peale's falcon the anterior part was dilated into a sac. The wall of the esophagus possessed the usual structure characteristic of this region of the digestive tube. Three types of glands have been distinguished in these birds. In the kingfisher and owl the simple oval glands were situated almost entirely within the epithelium. The glands and excretory duct were composed of similar cells with slight variations occurring in excretory duct lengths. In the California murre the glands were still simple but had sunken to the tunica propria with just the excretory ducts passing through the epithelium. The gland cells were narrower, and the duct cells resembled those observed in the owl and the kingfisher. These glands were all apocrine secretory. However, in the Peale's falcon and sparrow hawk secretion was holocrine. These glands were deeply embedded within the tunica propria and resembled the esophageal glands of the chicken. The excretory ducts were lined by squamous epithelial cells.

Although the birds examined possessed a variety of food habits: fish, mammals, birds and crustaceans; the food was essentially meat. However,
considerable variations in the structure of the esophagus were observed.

The proventriculus was comprised of: a mucosa, indented with minute gastric pits, a muscularis externa of three layers of smooth muscle, and a lamina adventitia that surrounded the entire tube. Within the mucosa the deep glands were situated. These were composed of large lobes, each enveloped in a dense capsule of connective tissue and internally consisted of simple tubules that radiated about a central excretory duct. The structure of the proventriculus was more or less uniform in the birds investigated, with only slight variations occurring in cellular arrangement and cellular size.

The gizzards in the birds examined were large spherical structures that filled a majority of the abdominal cavity. In the kingfisher, owl, Peale's falcon, and sparrow hawk, the gizzard was lined by a thin keratinoid lining that was secreted by the glands present in the gizzard mucosa. The muscularis externa was of approximately equal thickness throughout. In the murre, the keratinoid layer was five or six times as thick as in the above birds and the muscles showed a heavy development on the dorsal and ventral sides. This development took place toward a grinding mechanism that was necessary for processing the hard shelled crustaceans eaten by this bird.
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INTRODUCTION

Although active investigations of the alimentary tract in birds have been carried out for nearly two centuries our knowledge of this organ system still remains inadequate. The work of such men as Réaumur (1752) who concerned himself with the triturant action of the gizzard on introduced substances, Hunter (1786) who studied muscle movement and noises of stones in the gizzard, Cuvier (1805), Home (1814) and H. Milne Edwards (1857-1881) illustrates the early beginnings of inquiry into the mechanisms of the digestive tract. It was not until the work of Molin (1853) that the first methods of histological technique were introduced and investigations turned more to the finer structures of the organs. Among the earlier workers who engaged themselves in microanatomical investigations were Berlin (1852), Leydig (1857), Flower (1860), Bergmann (1862), Hasse (1865), Curschman (1866), Wiedersheim (1871), Garrod (1872) and Klein (1881). Even with their imperfect methods these men have made some advances to which only further knowledge can be added by continuous investigation and refinement in apparatus and technique.

It is the author's intention, in the study here presented, to add to accumulating knowledge concerning the alimentary tract of the birds.

For this investigation, two groups of birds have been chosen; one chiefly a piscivorous group and the other a carnivorous one. To represent the fish-eaters the western belted kingfisher (Megaceryle alcyon caurina Grinnell) and the California murre (Uria aalge california Bryant) were studied. The kingfisher is almost entirely a fish-eater while the California murre can exist equally well on fish or crustaceans.
(Taverner 1947). Of the carnivorous species chosen, the screech owl (*Otus asio kennicotti* Elliot) and the short-eared owl (*Asio flammeus flammeus* Pontoppidan) show preference for a diet consisting mainly of small mammals, while the Peale's falcon (*Falco peregrinus pealei* Ridgeway) and the black pigeon hawk (*Falco columbarius suckleyi* Ridgeway) are examples of the few birds that prefer birds as food. (Taverner 1947, May 1935, Darcus 1930). The sparrow hawk (*Falco sparverius sparverius* Ridgeway) although it belongs to the same genus as the Peale's falcon and pigeon hawk subsists contrary to the implications of its name, chiefly on insects and only occasionally captures a bird (Taverner 1947, May 1935).

In presenting this work, a comparative description will be given first of the anatomy and histology of the esophagus and stomach of each species followed by an attempt to correlate the histological structure of the tract with the food habits of that species.
The writer is indebted to Dr. W. A. Clemens and the members of the staff of the Department of Zoology, University of British Columbia for granting permission to carry out this investigation, especially to Professor G. J. Spencer for suggesting the problem and to Dr. I. McT. Cowan for the kindly interest that he has shown.

The author wishes to express her sincere appreciation for the helpful criticism and suggestions that Dr. J. A. C. Nicol has given in the preparation of this paper.

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HISTORICAL REVIEW

Several authors have described briefly the general anatomy of the esophagus and stomach of birds, but very few have touched upon the histology of these regions other than those of the domestic fowl.

Kingsley (1926) and Scheer (1948) in describing the anatomy, of the digestive tract of the bird spoke of the esophagus as an elongated tube with complex diverticulae. Kingsley (1926) stated that it was usual for the esophagus to be of uniform diameter but frequently in birds marked dilations were present. Wiedersheim and Parker (1907) expressed the opinion that modifications of the esophagus occurred as adaptations arising from food habits, the mode of life and the absence of teeth in birds. These workers found that in granivorous birds and in birds of prey either the whole gullet formed an expanded sac or a ventral outgrowth was present. This dilatation or outgrowth they referred to as the crop or ingluvies. Beddard (1898) stated that gallinaceous birds were provided with a crop while other birds possessed a slight, permanent or temporary dilatation that forshadowed the fully developed crop.

Of the literature pertaining to the histology of the avian esophagus and crop, the majority deals with the domestic fowl. Very little has been written about the histology of these structures in other birds.

Barthels (1895) described briefly the histology of the
of the esophagus of a number of birds, among which he mentioned *Uria lomvia* (a murre) and *Otus brachyotus* (the barn owl). Kaden (1932) on the other hand confined her work to a study of only the epithelium, glands and modes of secretion of these glands for a large group of birds.

For the murre (*Uria lomvia*) Barthels (1895) stated that the esophagus was thrown into about twelve folds which disappeared at the proventriculus. The epithelium was thick and consisted of small cells. The glands were small with long sharp necks extending through the epithelium. The muscle layer consisted of an external circular muscle layer as thick as the internal longitudinal muscle layer. Both of the above mentioned authors have worked on various species of the Family Strigidae (the owls). The esophageal wall of *Otus brachyotus* (the barn owl) was described by Barthels (1895) as highly folded and possessing a weakly developed mucosa. The epithelial cell was filled by a globular and slightly flattened nucleus. Kaden (1932) in discussing the epithelium of *Asio otus* stated that it consisted of flat cells with oval nuclei. The epithelium was thin and did not vary in thickness throughout the whole length of the esophagus. Barthels described the esophageal glands as oval structures lined with cuboidal epithelium and possessing short excretory ducts. Kaden stated that these glands were round or oval with their form and size remaining the same throughout the esophagus. The gland cell secretion was transparent and granular and stained with mucicarmine. The glands excreted directly into the lumen. Barthels (1895) stated that the lamina propria was made up of fibrous connective tissue with numerous round nuclei. Kaden (1932) said that it hardly existed. The muscularis externa was described by
Barthels (1895) as a faintly homogeneous layer consisting of an inner longitudinal and a very well developed outer circular muscle layer. Many blood vessels were present in the adventitia.

Kaden (1936) also described the structure of the epithelium and glands found in *Falco tinnunculus* (the tower falcon). The epithelium in this species was cornified and possessed a typical stratum lucidum in the region of the crop. The cells were large and very clear with round nuclei. The stratum lucidum disappeared gradually in the thoracic region but remained in the sinuses of the folds while the remaining epithelium showed strong continuous flattening. Complicated folded holocrine glands were present in this species. The folds were narrow and the cylindrical epithelium of the gland was so high that the lumen of the gland consisted only of thin branching tubes. The cells of the excretory ducts were flat squamous cells resembling the epithelial cells.

The stomach is divided internally into two regions. The anterior part Cazin (1886) Beddard (1898) Wiedersheim and Parker (1907) and Kingsley (1926) called the proventriculus because of its glandular development and the posterior, the muscular gizzard. Scheer (1948) on the other hand referred to the anterior section as the muscular gizzard and the posterior as the proventriculus. Cazin (1886) found in a number of birds of prey and in certain fish eaters that the proventriculus showed great development, its walls were extensible and its volume exceeded that of the gizzard. Often there was no division between the glandular portion and that of the gizzard. In the hawk the stomach consisted of a pocket which dilated at the inferior terminal portion into what Cazin called a "cul-de-sac". Beddard (1898) also found that the proventriculus was not always separated from the gizzard. In 1887
Cazin made a study of the histology of the stomach of some birds and for water birds and for birds of prey (sic) he described the proventriculus as a glandular area with each compound gland formed by an agglomeration of tubules in a blind sac of connective tissue. Each gland possessed two types of cells that never mixed within a single tube. The granular enzyme cells were always localized in the tubules at the periphery of the gland while the mucous cells existed in the central cavity and in the collecting canals that received the products of secretion of the enzymatic cells.

Bergmann (1862) distinguished between three types of proventricular glands. The first he described as those in which the gland tubes opened directly into a central cavity; the second in which the gland tubules entered a central cavity by way of secondary canals and a third, in which a number of little canals opened into the cavity of the stomach, one beside the other.

In 1888 Cazin described the mucosa of the proventriculus as consisting of fine outpushings, separated by deep ridges formed by the folding of the mucosa. Generally these folds were continuations of the esophageal furrows that passed to the gizzard.

Wiedersheim and Parker (1907) stated that the glandular stomach alone took part in dissolving the food and Scheer (1948) compared the proventriculus to the stomach of other vertebrates.

The second part of the stomach, the gizzard has attracted investigators for a long time. Indeed, as far back as 1752 observations have been carried out on the gizzard. All authors agreed that the gizzard had a mechanical function. Wiedersheim and Parker (1907) stated
that in correlation with this mechanical role a very peculiar and thick muscular wall provided with tendinous discs was developed. Kingsley (1926) said that the muscles of the gizzard wall were developed into two discs with tendinous centres. Cazin (1886b) did not observe tendinous areas in the gizzards of raptores and fish eaters. In these birds he found that the muscular wall was much reduced and had the same diameter throughout. Beddard (1898) also found that the gizzard was more muscular in grain than in flesh-and fish-eating birds. The degree of gizzard development according to Wiedersheim and Parker (1907) was in direct proportion to the consistency of the food. Gadow (1879) also indicated briefly the muscular grinding power of the gizzard in a number of birds. Grain eaters he found possessed the thickest keratinoid lining and strongest muscular wall while in the birds of prey modification was least marked.

The histology of the gizzard has been described by a few workers for several kinds of birds. Wiedersheim (1872) was the first observer who described the relation existing between the epithelium of the glands of the gizzard and the secretion contained in the interior of these glands. He showed that the parallel striations observed in cross sections of the mucosa were in direct relation with the "parietal" cells of the glandular tube. These striations represented little currents of secretions from the gland cells.

Cazin in 1887 described generally the mucosa of the gizzard of flesh eating birds as consisting of tubular glands. These glands secreted the cornified covering of the gizzard. The covering he found to be a thin soft membrane that could not be detached in the form of a
distinct sheet as the horny-lining of the gizzard of grain-eating birds.

Bauer (1901) confined his work chiefly to the duck where his aim was to establish more exactly the relation of secreted fibres that form the gizzard lining to the gland cells. In agreement with Hedinuis Bauer (1901) proposed that the various partially misleading terms like horny layer, cuticular layer and cuticula, used for the gizzard lining be surrendered in favour of a more precise expression and be referred to as a "keratinoid" layer.
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MATERIALS AND METHODS

For this work the following materials; two kingfishers, three California murres, three screech owls, a short-eared owl, three Feale's falcons, one sparrow hawk, and one black pigeon hawk were supplied by field workers from various parts of British Columbia.

In all but three instances, in which case two owls and one murre were obtained alive, material was supplied in the fixed condition. Immediately following death, the bird was dissected and the entire esophagus and stomach were removed and placed into the fixing solution. An attempt was made to begin fixation of the material before the heart ceased beating. Two incisions at the regions of the proventriculus and gizzard served to allow the fixative to enter the interior more rapidly. In this condition specimens remained until such time as they could conveniently be shipped.

Fixatives had to be picked that were easy to use, that acted rapidly, and in which materials could remain for extended periods of time without deleterious effects.

B.C. fixative and Bouins' fluid were chosen. The proportions of ingredients for B.C. fixative were first worked out by Dr. A.H. Hutchinson of the University of British Columbia. In the preparation of this fluid, he held in mind two things -

(1) To obtain a good general fixative and
(2) to develop a solution that could be used to greatest advantage in the field.
Thus he obtained a solution that fixed rapidly and one in which tissue could remain without destruction for periods of time up to three years or more. The proportions of materials for this fluid were as follows:

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<td>Methanol</td>
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<tr>
<td>Glacial acetic</td>
<td>250 cc</td>
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<tr>
<td>Formaldehyde</td>
<td>12 cc</td>
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<tr>
<td>Water</td>
<td>5 cc</td>
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This solution was primarily intended for plant histology, but with a slight modification of this formula, Professor G.J. Spencer was able to obtain a solution more suitable for animal cells. He modified the formula as follows:

<table>
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<th>Material</th>
<th>Volume</th>
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</thead>
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<tr>
<td>Methanol</td>
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</tr>
<tr>
<td>Glacial acetic</td>
<td>6 cc</td>
</tr>
<tr>
<td>Formaldehyde</td>
<td>12 cc</td>
</tr>
<tr>
<td>Water</td>
<td>100 cc</td>
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Although the above solution gave satisfactory results, Bouin's fluid gave a better over-all fixation.

Of the three living specimens obtained, the California murre and one owl were gassed and fixed in Bouin's fluid. The other owl was killed by asphyxiation. The foregut was removed and preserved in Helly's fluid, then post-chromed in a saturated solution of potassium dichromate at 37°C for 48 hours in an attempt to preserve the mitochondria.

For comparison small sections of tissues were removed from the fixative and treated for embedding. The material preserved in B.C. fixative was transferred for two or three days to dioxane, three changes; two changes of toluene, and one half to two hours each; and three
and three changes of tissue mat (55°C to 56°C) for one hour to one and one half hours depending on the size of the tissue.

Material fixed in Bouin's solution was washed first in 50 percent alcohol, then placed in 70 percent with added lithium carbonate until most of the picric acid was removed. From 70 percent alcohol it was transferred either into dioxane and the procedure followed as above; or it was dehydrated to 95 percent alcohol 2 changes; before clearing in toluene; or taken to absolute alcohol and cleared in cedar oil. If the sections were small enough, the cedar could be removed readily, thus yielding an easily cutting tissue. However, the majority of the sections used, difficulty was encountered with this method in removing the clearing agent during infiltration with wax. Final washing of the tissue in toluene prior to emersing in wax had little effect in removing the cedar oil from some sections unless the washing was greatly prolonged. For embedding two waxes were employed. Ordinary paraffin was used in the preliminary work; tissue mat (55°C to 56°C) was used for the majority of the preparations. Best results were obtained by dehydrating in dioxane, toluene and decreasing to a minimum the times of exposure of the tissues to heat.

The gizzards even with the above precautions could not be sectioned without further treatment. The keratinoid linings tended to crumble at the touch of the knife. Placing the gizzard blocks in a softening solution, consisting of aniline oil one part and glycerine nine parts, (Lendrum, 1944) prevented excessive crumbling and enabled the sections to be cut.
The material was sectioned from four to twelve microns. The slides were cleaned first with acid then with pure alcohol. The sections were flattened on a water bath, then affixed to a slide or warmed on a drop of water or 30 percent alcohol (Lillie 1948) directly on the slide on a metal sheet.

A selection of stains was made with the purpose in mind to intensify particular structures. Ehrlich's and Harris' haematoxylin and eosin were used as general stains. To stain mucin Mayer's mucicarmine (Bensley, 1938) was employed after haematoxylin. Methylene blue and eosin (Galigher 1934) were also tried for staining mucous. Some difficulty was experienced with this technique in determining a satisfactory schedule of staining times that would yield well differentiated results. Heidenhain's azan (Pantin 1946) and Mallory's triple stain (Pantin 1946) were also employed as general stains. Azan gave a most brilliant stain for connective tissue, reticulum, nerve ganglia and fibres, yet clear contrast between nuclei and cytoplasm in the smooth muscle could not be obtained. Mallory's triple gave excellent contrast but the method could not be relied upon since it created a different effect in each slide although it was surprisingly uniform in staining nerves. Mallory's phosphotungstic acid haemotoxylin (Bensley & Bensley 1938) produced fine differentiation and very clear contrast between cytoplasm and nuclei. This stain was capable of differentiating collagenic tissue, elastic fibres, fibroglia, myoglia, mitotic figures and bringing out with clearness cellular outlines. Several elastic tissue stains were used with good results. Van Gieson's stain showed white connective tissue and muscle well. It also stained nuclei and nuclear elements sharply.
The method used was as follows:

(a) Stain sections deeply with haematoxylin (one to two hours)
(b) Rinse in tap water.
(c) Stain in Van Gieson (ten cc of one percent aqueous solution of acid fuchsin to 100 cc of saturated aqueous solution of picric acid) one to three minutes and when pale wash briefly in water one-half second.
(d) Transfer to 95 percent alcohol followed by absolute alcohol.
(e) Clear in toluene and mount in balsam.

To bring out elastic tissue orcein (Bensley & Bensley 1938) and Verhoeff's (Galigher 1934) elastic tissue stains were tried. Orcein gave a very faint stain generally except where dense elastic tissue was present. Verhoeff's was not as delicate in staining dense elastic tissue but it brought out faint elastic fibres that were completely missed by orcein. As a counter stain Van Gieson was substituted for eosin in some cases.

For reticular fibres Foot's short method for silver impregnation of reticulum (Bensley & Bensley 1938) was employed with Mallory's triple and Van Gieson as counterstains.

Bodian's silver method for nerves (Bodian 1936) was excellent. Mallory's triple counterstain gave good contrast and seemed to intensify the nerve fibres and ganglia.

Altmann's mitochondrial stain (Bensley and Bensley 1938) was not successful.
OBERSERVATIONS

Esophagus -

Kingfisher (Megascroyle aloyon caurina)

The esophagus of the Kingfisher communicates anteriorly with the pharynx and passes posteriorly between the bronchi to join the pro-ventriculus. The tube lies dorsal to the trachea and is held loosely by connective tissue to the surrounding area (Plate I, fig. 1).

The esophageal wall is thrown into sixteen or eighteen longitudinal folds. At its base lateral folds are imposed upon the longitudinal ones, thus creating a zig-zagging appearance of the wall ridges. The esophagus is generally capable of great distension, but at this region its elasticity is further increased so that in addition a bulbous or crop-like dilation is also possible (Plate III, fig. 3b).

Primarily three coats constitute the structure of the wall, a mucosa consisting of a stratified epithelium and a lamina propria; a muscularis externa with an inner longitudinal and an outer circular layer; and finally a tunica adventitia. A muscularis mucosa is lacking and a submucosa could not be differentiated from the tunica propria (Plate IV, fig. 9).

The stratified epithelium is comparatively thick and extends eight or ten cell layers. In the germinative layer nearest the lamina propria the cells are polyhedral in shape with their large oval nuclei arranged perpendicular to the lumen. In these cells mitosis is
frequently observed. In the middle layer nuclei and cells become nearly spherical. The upper or surface layer shows the cells elongated and nuclei parallel to the lumen. At various points on the free surface the cells may be seen passing through the preliminary stages of degeneration. The nuclei become pyknotic, the cells show large vacuoles, die and eventually slough off. No cornification can be observed.

Within the epithelium and just extending to the lamina are the esophageal glands. These are simple oval shaped structures arranged side by side throughout the entire esophagus (Plate IV, fig. 10 d). There is no apparent difference between the basal gland cells and those lining the excretory duct (Plate V, fig. 11a,b). A similar effect is obtained for all the cells when stained with mucicarmine.

Schaffer (1924) made a detailed study of the morphological characteristics of digestive glands in mammals, and he developed a classification of the glands according to their structure. He distinguished between a homocrine gland, that is, one in which the secretory tubules are lined with cells of one type, and a heterocrine gland, one in which the secretory tubules are lined with cells of different types. He further divided the glands according to the number of layers present in the secretory epithelium as monoptychial, if the secretory epithelium is in one layer, and polyptychial if more than one layer is present.

On the basis of this classification the esophageal glands of the Kingfisher may be called homocrine monoptychial glands.

The gland cells are large cuboidal with spherical nuclei which at secretion become closely pressed to the distal wall, while the cytoplasm fills with granules (Plate V, fig. 11d). Upon secretion the
Apical parts break down and liberate the granules. Regeneration of the cells and granules begins once again.

Beneath the epithelium is a large lamina propria composed of dense collagen with many compressed fibroblasts (Plate VI, fig. 12 h). At its junction with the epithelium a reticular membrane or a group of reticular fibres surrounds the basal parts of the glands and passes across the peaks of the lamina papillae that extend between the glands. Under high power faint elastic fibres can be observed throughout the lamina. Small arteries, veins and nerve fibres (Plate VI, fig. 12 i) are scattered in the lamina propria.

The muscularis externa consists of two layer, an inner longitudinal, and an outer circular smooth muscle layer. In cross section the muscle cells appear to be of different shapes and sizes tightly packed within a bundle and enclosed in a connective tissue sheath (Plate VI, fig. 12 a). The nuclei are placed centrally, sometimes within a clear colorless vacuole (Plate VI, fig. 12 e). Usually one nucleolus and a peripheral chromatin net are visible. Each cell of a bundle is surrounded by reticulum and each bundle is enveloped in reticular fibres. The circular muscle consists of long spindle shaped cells lying parallel to one another. Their oval nuclei are placed in the widest part of the cell. Short reticular fibres can be seen more clearly in a longitudinal section of the muscle. The muscle bundles are held together by connective tissues interlaced with elastic fibres. Through this connective tissue layer and especially at the bases of the esophageal ridges are small blood vessels and nerves.

Enveloping the entire tube is the tunica adventitia which
consists of dense collagenous fibres and contains large blood vessels, and capillaries. Nerve fibres and autonomo ganglia supplying the esophageal wall are observed at intervals in the adventitia.

California murre (Uria aalge californica)

The esophagus of the California murre resembles generally that of the kingfisher (Plate III, fig. 4). The wall is thrown into longitudinal wavy folds that gradually smooth out at the junction of the esophagus with the proventriculus. The heavy folding provides for greater distension than was possible in the kingfisher. The usual three coats contribute to the structure of the wall; a mucosa, muscularis externa, and a tunica adventitia (Plate VII, fig. 14).

The epithelium in this bird is considerably thicker extending fifteen to sixteen cell layer, or more in places. The cells of the germinative layer are small and heavily staining with their nuclei filling most of the body. These nuclei lie close together in the germinatium but toward the free surface take on various shapes (Plate VIII, fig. 16 e). Cornification can not be observed anywhere. A slight flattening is present in some places, but it is more usual to see the cells at the surface swollen or enlarged (Plate VIII, fig. 16 e). Occasionally atrophication of the nuclei with subsequent sloughing off of the cells occurs.

The esophageal glands lie in the lamina propria with only their excretory ducts extending through the epithelium (Plate VIII, fig. 16 a,b). The cells lining the secretory tubule are tall, very narrow columnar cells.
with basal nuclei and granular cytoplasm (Plate VIII, fig. 16 d). The excretory duct cells are cuboidal almost round to oval in shape, and possess round nuclei (Plate VIII, fig 16 b). These cells resemble the gland cells of the kingfisher. The cytoplasm is lighter staining than that of the basal gland cells, and is less granular.

A dense collagen layer well supplied with blood vessels and lymphocytes, singly or in groups, constitutes the lamina propria which projects upwards into the epithelium by prominent papillae. The fibroblasts of the connective tissue are outstandingly abundant, and slightly compressed in shape. Many elastic fibres interlace with the collagenous fibres (Plate VIII, fig. 17 b).

No structure comparable to the musculaia mucosa could be observed, and the submucosa could only be differentiated arbitrarily.

The connective tissue of the lamina loosens at its junction with the muscularis externa, elastic fibres increase and blood vessels become more numerous. This layer extends to surround the muscle bundles of the externa. The muscularis externa consists of an inner longitudinal band, and an outer circular band of smooth muscle. The bundles are of varying sizes surrounded by collagenous and elastic fibres. The muscle cells are homogenous throughout the cytoplasm, with nuclei excentrically placed. There was no vacuolation present within the fibre, as in the kingfisher (Plate VI, fig. 12). The nuclei are thinner and more elongate, in fact, the muscle cells themselves are smaller (Plate VI, fig 13). Toward the junction of the esophagus with the proventriculus a third layer of muscle appears in the form of small longitudinal bundles dispersed in the tunica adventitia.
The tunica adventitia is a heavy layer of white connective tissue containing nerve fibres and ganglia of the autonomic nervous system that innervate the esophageal wall. Blood vessels of different sizes are also present in this layer. Surrounding the adventitia is a thin mesothelium.

Screech owl (*Otus asio kennechottii*)

Short-eared owl (*Asio flammeus flammeus*)

The esophagus of the screech owl lies to the right (Plate II, fig. 2) and is comparatively shorter than that of the other birds studied. None of the specimens examined showed any evidence of crop-like dilation (Plate III, fig. 5). Throughout its length the wall is faintly ridged, and thinner than in the kingfisher or murre (Plate IV, fig. 9; Plate VII, fig. 14; Plate IX, fig. 18).

As in the kingfisher and murre, the wall is composed of three coats (Plate IX, fig. 18).

A thin epithelium of about six or seven cell layers covers the ental surface of the esophagus. The germinativum layer is not very prominent. Cornification occurs slightly over the whole surface. In the short-eared owl the epithelium is about two times as thick as in the screech owl, and it does not show any cornification (Plate X, fig. 21 e).

The esophageal glands lie on a basement membrane (Plate XI, fig. 22 a) in the upper limit of the lamina and extend a little into the epithelium (Plate IX, fig. 19). They are in the screech owl (Plate X, fig. 20) simple oval shaped glands with very short excretory ducts, while in the short-eared owl, the ducts are considerably longer
The basal gland cells are tall, columnar and narrow, thickening slightly as they approach the excretory duct. These glands resemble those found in the kingfisher (Plate V, fig. 11; Plate X, fig. 20, 21) differing chiefly in the lengths of the excretory duct. In the screech owl the ducts are almost non existant, while in the short-eared owl they approach the size observed in the kingfisher. In the owls, are a little more alveolar in shape and do not extend as far into the lamina propria.

The lamina propria is formed of dense white connective tissue with a few compressed fibroblasts. Lymphocytes are rather scarce. Within the lamina, blood vessels pass to supply the wall.

A muscularis mucosa is missing, and the submucosa consists of merely a continuation of the lamina that joins the muscularis externa.

Two smooth muscle layers make up the muscularis externa; an inner longitudinal and an outer circular layer. The circular muscle is about two times as thick as the inner longitudinal muscle. These are held together by a loose connective tissue interspersed with elastic and reticular fibres. Surrounding the tract is a tunica adventitia, in which blood vessels and nerves are contained (Plate IX, fig. 18 d).

Peale's falcon (Falco perigrinus pealei)

Sparrow hawk (Falco sparverius sparverius)

Pigeon hawk (Falco columbarius suckleyi)

The esophageal tube of Peale's falcon (Plate III, fig. 6) shows a distinct enlargement at its anterior region a short distance behind the glottis. This enlargement or expansion is observed in all of
the specimens studied and may be referred to as the crop. At this point the ental surface of the wall is heavily and irregularly folded, but as the esophagus passes posteriorly the folds converge into longitudinal ones that remain as such for the rest of its length. The sparrow hawk, and the pigeon hawk (Plate III, fig. 7, 8) show essentially the same structure as the falcon. The usual three coats observed in the other birds make up the structure of the walls (Plate XII, fig. 23). A muscularis mucosa is once again entirely missing, and the submucosa can not be definitely placed.

The epithelium generally resembles skin and is thicker than any other so far seen, approaching up to twenty-five and thirty cell layers. A definite arrangement of transitional cell types is apparent (Plate XIII, fig. 26). The cells of the stratum Malpighii (Plate XIII, fig. 26 a) are densely arranged perpendicularly to the lumen. The cells of the middle layer become less compressed, their nuclei approach a spherical shape and appear to occupy a small part of the cell. In the surface layer the cells are highly flattened and the epithelium is very irregular. Cornification (Plate XII, fig. 23 a) is present along the whole inner surface of the esophageal wall. The epithelium is of about equal thickness in the falcon, sparrow hawk (Plate XVII, fig. 33) and pigeon hawk. It is irregular in the falcon and more heavily cornified than in the sparrow hawk. The pigeon hawk does not show extensive cornification either.

The lamina propria joins the epithelium by prominent and elongate papillae. These are regularly placed in the pigeon hawk. The lamina consists of a dense layer of collagenous fibres that extend from
the epithelium to the muscularis externa. Elastic tissue is most abundant nearest the epithelium. The fibres are so short and thin that it was very difficult to obtain a clear picture with Verhoeff's elastic stain. Either too much stain was removed from the fibres obtaining no result, or too much remained in the slide producing a black picture.

Embedded within the lamina are the glands of the esophagus. (Plate XII, fig. 24; Plate XIII, fig. 25). These are not simple glands as observed in the previous birds, but are large lobulated structures with the smallest in the pigeon hawk, and the largest appearing in the falcon. Surrounding the glands is a capsule of dense connective tissue. The gland cells are ridged with capillaries, and primary gland cells that extend into the ridges at regular intervals to give the gland its lobulated appearance (Plate XIV, fig. 27). The gland cells sit on a distinct basement membrane. They are tall columnar cells (Plate XIV, fig. 27 a) possessing faintly granular networks in their cytoplasm and small basal nuclei. The cells are of the holocrine secretory type, and after a meal are entirely absent from the wall (Plate XVI, fig. 32). From birds, shot at the time of feeding, various stages in secretion are observed. At the beginning of the secretory cycle, the apex of the gland cell breaks down, first, with a liberation of the cytoplasmic granules following (Plate XIV, fig. 28). As the cell becomes depleted of its cytoplasm (Plate XV, fig. 29) the nucleus and the remainder of the cell cytoplasm starts to move toward the lumen, leaving a few low cuboidal gland cells, blood cells, and lymphocytes at the basement membrane. As the nuclei move toward the excretory duct (Plate XVI, fig. 31) of the gland, they disintegrate and pass out with the cytoplasmic
secretion into the esophagus (Plate XV, fig. 30 c). The secretory duct is lined by squamous epithelium (Plate XV, fig. 30 b) and tends to close as does the space (Plate XVI, fig. 31 c) left after the gland completes secretion. An atrophied, almost indistinguishable gland lobule remains within the lamina together with a few blood vessels, and lymphocytes (Plate XVI, fig. 32 c,e). This condition may be observed in the esophagus of the bird shortly after the completion of a meal. Regeneration appears to take place from these indifferent or primary cells (Plate XVI, fig 32 d). A similar situation is present in the sparrow hawk (Plate XVII, fig. 34) and pigeon hawk. The submucosa or continuation of the lamina propria joins the muscularis externa which consists of two smooth muscle layers; an inner longitudinal one, and an outer circular one. The muscle layers are exceedingly thick in the sparrow hawk. A serosa of dense connective tissue surrounds the entire tube.
Proventriculus -

Kingfisher (Megaceryle alcyon caurina)

After its junction with the esophagus the proventriculus bends dorsally to enter the gizzard from the left side (Plate I, fig. 1). The longitudinal folds of the esophageal wall converge into 8 or 10 heavy rugae. The proventricular wall thickens from approximately 1.7 m.m. to 5.2 m.m. Tall columnar epithelium gradually supercedes the stratified squamous epithelium of the esophagus. A stroma of connective tissue, the lamina propria, supports the epithelium. Within the lamina propria a very diffuse muscularis mucosa may be detected at various points. The submucosa extends to surround the deep glands of the proventriculus and to join the muscularis externa. The muscularis externa is composed of an inner longitudinal, middle circular, and a third longitudinal smooth muscle layer. The entire tube is enclosed in a thin tunica adventitia (Plate XIX, fig. 36).

Macroscopic examination of the mucosa shows it to covered by a soft velvety lining that is pierced by minute pits. These pits form the gastric crypts or foveolae gastricae of the mucous membrane. The surface epithelium of the crypts consists of simple tall columnar cells possessing large spherical nuclei that fill the majority of the basal part of the cell. The cell is divided by a distinctly granular line into approximately two halves. The basal part possessing a spherical nucleus surrounded by a dense granulation and a bulbous apical part that is faintly granulated. The cells stained readily with carmine for mucus. These cells sit on a basement membrane that connects them
to the lamina propria.

The lamina propria consists of dense collagenous and reticular fibres and extends into the ridges between the gastric crypts containing in it many small capillaries that supply the epithelium.

Scattered diffusely throughout the lamina propria are smooth muscle bundles of varying sizes (Plate XXI, fig. 37c). These make up the muscularis mucosal layer of the proventricular wall.

The submucosa passes from the muscularis to surround the deep proventricular glands (Plate XX, fig. 37). The connective tissue of this layer becomes much denser and forms a capsule that encloses the glands. The fibroblasts are compressed and elongated. Macroscopically, the glands appear as simple lobes arranged side by side in the submucosa (Plate XXI, fig. 39). Upon microscopic observation each lobe is seen to be composed of many simple tubules that radiate from several excretory ducts (Plate XX, fig. 37). Surrounding each tubule is a continuation of the reticulum present in the outer capsule of the lobe. The excretory ducts are continuations of the gastric crypts into the deep glands. The cells lining the excretory ducts are simple columnar cells slightly smaller than the neck cells of the gastric mucosa, and do not yield a characteristic stain for mucus. They show an elongated nucleus placed almost centrally within the cell and a cytoplasm that gives a lighter non-granular stain than the neck cells of the crypt. The secretory lobules are composed of a single layer of cuboidal granular zymogenic cells (Plate XX, fig. 38c). The nuclei are spherical containing a very regular chromatin pattern. The position of the nucleus depends upon the activity state of the cell and may be central or basal.
The muscularis externa consists of three layers of smooth muscle, an inner longitudinal band, a larger circular band, and a third longitudinal layer of small bundles scattered in the dense connective tissue of the lamina adventitia.

California murre (Uria aalge california)

As the esophagus approaches the proventriculus, its longitudinal folds converge from twelve to seven folds or plicae. The plicae are deeper and more pronounced than those seen in the kingfisher. The esophageal wall increases gradually until a thickness of 5 mm. is reached at the middle of the proventriculus. Only about one half of this thickness contains proventricular glands. The stratified squamous epithelium is soon replaced by simple columnar epithelium (Plate XXIII, fig. 41d) that lines the gastric crypts in a single row. The crypts are denser than those in the kingfisher (Plate XXII, fig. 40a).

The tunica propria is much reduced between the gastric mucosa and the glands. The layer consists of dense collagenous and reticular fibres (Plate XXIV, fig. 43g). Present also within this layer are small blood vessels and nerves. A diffuse muscularis mucosa as observed in the kingfisher can be detected except that in this bird the muscle bundles continue in the connective tissue between the glands (Plate XXII, fig. 40c). The interlobular spaces are considerably increased and the proventricular glands are pushed nearer to the lumen of the proventriculus. The lamina propria in this case extends to surround the proventricular glands leaving the submucosa as a small region of loose connective tissue between the deep glands and the muscularis externa. Contained
in this layer are many small blood vessels and nerves regularly arranged in the gastric ridges between groups of glands present in each ridge (Plate XXIV, fig. 43e). The gland lobes are alveolar rather than tubular in shape and the central excretory cavity is much larger. The individual cells of the mucosal, secretory, and excretory regions do not show much variation from those of the kingfisher. The zymogenic cells of the murre (Plate XXIII, fig. 42b) are smaller than those found in the kingfisher and not as closely situated so that in a cross section of a tubule the distal parts of the cell are not in contact but produce a serrated appearance.

The muscularis externa consists of the three smooth muscle layers, an inner longitudinal, a middle circular, and a diffuse outer longitudinal one scattered in the tunica adventitia (Plate XXII, fig. 40f). A peritoneum covers the whole organ.

Screech owl (Otus asio kennicotti). Short-eared owl (Asio flammeus flammeus).

As the esophagus passes into the proventriculus, the wall of the tract thickens gradually from 0.7 mm. in the esophagus to 2.3 mm. at the middle of the proventriculus. The folds of the esophagus smooth out and no heavy folding of the proventricular wall can be observed. The lining is faintly wrinkled and pierced by small pits. As in the esophagus, three coats contribute to the structure of the wall; a mucosa, a muscularis externa, and a tunica adventitia. A muscularis mucosa is missing (Plate XXV, fig. 44).

A single layer of tall columnar epithelium lines the gastric pits of the mucosa. The epithelial cells are divided into a mucus
staining apical region and a paler basal part (Plate XXV, fig. 45a). The crypts are not regularly shaped as observed in the kingfisher and murre but are irregular (Plate XXV, fig. 45) and show some branching. In the short-eared owl the crypts are deeper and more regular in appearance, resembling somewhat the condition in the kingfisher. A tunica propria, heavily infiltrated with lymphocytes and consisting of dense white collagenous fibres forms a supporting tissue that extends from the epithelium to surround the deep proventricular glands. Immediately adjoining the glands the connective tissue becomes very dense in the form of a capsule around the lobe. The glands possess the same general structure; a single lobe composed of many tubules radiating about a branched excretory duct (Plate XXV, fig. 451). The zymogen gland cells are slightly larger than in the murre and produce a distinctly serrated appearance (Plate XXVI, fig. 46b). The excretory duct joins the gastric crypt (Plate XXV, fig. 45d) through which secretion takes place. A thin submucosa joins the lamina propria to the muscularis externa and extends for a short distance between the gland lobes. Within the submucosa and occurring at regular intervals between two adjacent lobes are a nerve, a vein, and an artery.

The submucosa joins the muscularis externa (Plate XXV, fig. 441) which consists of a large inner longitudinal layer, a larger circular middle layer and finally a few longitudinal bundles scattered throughout the serosa. Passing from the serosa through the muscularis to the glandular layer is an intricate nerve plexus, the myenteric plexus of the stomach. Ganglia (Plate XXVI, fig. 47c) are arranged at regular intervals in the tunica adventitia with fibres and nerve cells passing
through the muscularis to supply nervous innervation to the glands and the muscular wall.

A thin mesothelium surrounds the entire tube.

Peale's falcon (*Falco peregrinus pealii*)
Sparrow hawk (*Falco sparverius sparverius*)
Pigeon hawk (*Falco columbarius suckleyi*)

The folds of the esophagus converge to form four heavy plicae in the wall of the proventriculus. The surface mucosa possess a soft velvety appearance. The crypts in the mucosa are regular and placed one beside the other, thus reducing considerably the tunica propria (Plate XXVII, fig. 48a;b). This layer extends slightly between the gland lobes while the lobes are pushed close to the bases of the gastric crypts (Plate XXVIII, fig. 50). An identical situation can be observed in the sparrow hawk (Plate XXIX, fig. 51), while in the pigeon hawk the gastric crypts are considerably reduced and the tunica propria is increased. The tunica extends around the glands as a thin capsule of dense connective tissue. No muscularis mucosa is present. The glands are longer and narrower and they cover a greater area than in the other birds. In the falcon the wall is 6 mm. thick and it is almost entirely composed of glandular material. In the sparrow hawk the glands are smaller. The tunica propria is reduced and the muscle layer is a thin band surrounding the tube. From the gastric crypts one secretory duct extends into the centre of each tubular lobe of the deep proventricular glands (Plate XXVIII, fig. 50d,e). Around this duct the secretory tubules radiate. In the sparrow hawk the lobes are more
alveolar in shape (Plate XXX, fig. 52c). The cells of these tubules are closely arranged with all parts of one cell in contact with the adjoining cell reducing the lumen of the tubule (Plate XXVII, fig. 49b).

The tubules are not as dense in the sparrow hawk and the zymogen cells are smaller (Plate XXX, fig. 53a,b). The submucosa is a very small region joining the glands to the muscularis externa. The muscularis externa is reduced to thin bands of longitudinal and circular smooth muscle with additional longitudinal bundles scattered in the serosa. In the sparrow hawk the inner longitudinal muscle passes slightly between the gland lobes (Plate XXIX, fig. 51d) but in the pigeon hawk a large middle circular band of muscle is present and the inner longitudinal bundles do not enter between the lobes.

A tunica adventitia surrounds the tube.
Gizzard

Kingfisher (Megaceryle alcyon courina)

In the kingfisher the proventriculus enters the gizzard from the left dorsal side. The gizzard enlarges ventrally to fill the left and greater part of the right abdominal cavity. (Plate I, fig. 1)

Aside the entrance of the proventriculus’s and slightly to the right the duodenum leaves the gizzard. Externally a small swelling of the gizzard wall takes place and the intestine passes to fill the remaining part of the right cavity. Internally a sphincter consisting of five bulbous muscular projections covered by the keratinoid lining of the gizzard guards the exit of the duodenum. (Plate XXXI, fig. 5h)

From the liver, the falciform ligament continues along the ventral median and slightly left wall of the gizzard to join the mid ventral body wall and inner surface of the sternum, and divides the abdominal cavity into right and left regions. (Plate I, fig. lg). This continuation of the falciform ligament is often compared to the greater omentum of mammals, but is not homologous to that structure (Hyman 1947). "The ligament," Hyman (1947) P. 283) says, "is a mesentery peculiar to birds and arises as a secondary outgrowth from the serosa of the gizzard, to the ventral body wall and is probably due to the need for additional support for the heavy gizzard."

The wall of the gizzard thickens on the dorsal and ventral sides and becomes irregularly folded (Plate XXXII, fig. 58; Plate XXXIII fig. 59). The soft velvety lining of the proventriculus is soon replaced by the hard keratinoid lining of the gizzard. A single layer
of long simple tubular glands (Plate XXXIV, fig. 60 a) secretes the lining. The glands are present in the lamina propria and they connect with the pits of the gastric muscosa. Lining the crypts of the glands are low columnar or cuboidal cells (Plate XXXIV fig. 60 b), provided with basal nuclei and granular cytoplasm. From these cells the keratinoid secretion of the gizzard is poured into the lumen of the gland (Plate XXXIV, fig. 60 c). As the secretion reaches the surface it joins with that of the adjoining glands to form the hard continuous layer and presents striations representing the contributions of each glandular lumen. Within this layer some cellular debris can be observed.

The lamina propria (Plate XXXIV fig. 60 d) surrounds the glands of the gizzard and only extends far enough to connect with the band of smooth longitudinal and circular muscle, or muscularis mucosa (Plate XXXIV, fig. 60 e), or immediately below the glands. A submucosa of appreciable size joins the mucosa to the muscularis externa.

The muscularis externa is a thicker layer than that observed in the esophagus or proventriculus. A heavy inner smooth longitudinal layer that extends into the folds present in the gizzard composes a part of the muscularis externa. The circular muscle band is increased considerably and each bundle is surrounded by a connective tissue of collagen and elastic fibres. The entire gizzard wall is abundantly supplied with blood vessels. Present within the muscle bundle (Plate XXXV, fig. 61 a) close to the serosa, are large bundles of nerve fibres dispersed at intervals throughout the circumference of the gizzard.
Fat, blood vessels, and muscle bundles enclosing more nerve fibres compose the tunica adventitia. A mesothelium surrounds the tube.

**California murre - (Uria aalgae californica)**

The proventriculus enters the gizzard which continues for a short distance as a tube, before expanding into the bulbous structure of the gizzard. In this species muscular development (Plate XXXVI, fig. 62, 63) is quite marked with greatest increase in muscular thickness occurring on the dorsal and ventral sides. Between these two regions extends the narrow lumen of the gizzard. Beginning at the proventriculus and continuing around the cavity of the gizzard, the muscles become very thin on the lateral sides (Plate XXXVI, fig. 63). Beside the entrance of the proventriculus into the gizzard, the exit of the duodenum is situated. A sphincter (Plate XXXI fig. 55) consisting of a band of muscle surrounds the duodenal exit. At the right a slight bulging of the gizzard wall takes place. The keratinoid lining is thinner and greatly wrinkled. This may be the pyloric pocket that Cazin (1887) has described for some water birds.

A mucosa, muscularis externa and a serosa make up the structure of the wall (Plate XXXVII, fig. 64). A similar type of long simple tubular gland as observed in the kingfisher is present in this bifid. The glands possess essentially the same structure and appear to be of approximately the same size as those found in the kingfisher, but the keratinoid lining is about five or six times as thick (Plate XXXVII, fig. 64 a).
A simple cuboidal epithelium (Plate XXXVIII, fig. 65 b) covers the crypts of the gizzard glands. The cells possess large spherical nuclei and a granular cytoplasm. Surrounding the glands is a much reduced tunica propria which joins almost immediately a layer of smooth circular and longitudinal muscle bundles. Small blood vessels are present in the tunica at the bases of the glands. A complete layer of submucosa surrounding the tunica propria is not present. Instead, the tunica propria appears to intermingle with the muscle bundles, especially in the ridges that form the plicae of the gizzard. The fibroblasts of the tunica propria and submucosa are more abundant and not as compressed as those observed in the other part of this digestive tract. The muscularis externa is greatly increased in some places, particularly where folds (Plate XXXVII, fig. 64 d) of the gizzard wall are present. At these points the smooth muscle bundles extend into the ridges to the submucosa. The inner longitudinal muscle is of various thicknesses, while the outer circular layer is quite regular. Between the muscle bundles, blood vessels pass in the connective tissue surrounding these bundles. A serosa encloses the entire gizzard.

Screech Owl - (Otus asio kennicottii)

After its junction with the proventriculus (Plate II, fig. 2 i) the gizzard in the owl passes into the abdominal cavity and fills the left side almost completely. From the right anterior region the duodenum leaves to join the remainder of the intestine which fills the right side.
The thickness of the gizzard wall in this species varies to some extent. A thin layer of keratin lines the ental surface of the gizzard, the muscularis externa at some points is reduced (Plate XXXIX, fig. 66d) and a layer of fat envelops the exterior surface. The duodenal exit is slightly posterior to the entrance of the proventriculus. A sphincter (Plate XXXI, fig. 55) consisting of a mere puckering of that region guards the exit of the duodenum.

The wall is composed of essentially three coats, a mucosa, muscularis externa and a tunica adventitia (Plate XXXIX, fig. 66).

The proventricular glands end abruptly. The epithelium (Plate XL, Fig. 67a) continues for a short distance and gradually changes to the epithelium of the gizzard (Plate XLI, fig. 68a).

The simple tubular gizzard glands with slightly bulbous basal regions are arranged side by side in the lamina propria. These glands join to the pits in the mucosa and through this neck region they secrete into the lumen of the gizzard. The cells of the glandular crypts are the usual cuboidal or low columnar epithelium, with spherical nuclei, whereas the cells of the neck and apical regions of the mucosal folds are of the tall columnar type. The glandular cytoplasm is granulated. Also present within these cells are large colorless spheres, observed especially above and below the nucleus in the apical columnar cells, (Plate XLI, fig. 68f).

The tunica propria composed of dense collagenous tissue and abundantly supplied with fibroblasts, unites with the muscularis externa. A submucosa is absent.
The muscularis externa consists of an inner longitudinal smooth muscle layer and an outer circular muscle area which is greatly thickened at various points (Plate XXXIX, fig. 66 d). Nerve fibres occur frequently within the gizzard muscle and ganglia are present in the tunica adventitia. The tunica adventitia composed of collagenous fibres and far surrounds the entire tube.

Peale's falcon (Falco peregrinius pealei)
Sparrow Hawk (Falco sparverius sparvarius)
Pigeon Hawk (Falco columbarius suckleyi)

The gizzards of the Peale's falcon, sparrow hawk and pigeon hawk are more spherical in shape than those observed in the other birds. (Plate III figs. 6, 7, 8). The proventriculus enters the gizzard from the posterior side. Beside this entrance and to the left is the exit of the duodenum. In the Peale's falcon a sphincter (Plate XXXI, fig. 57), composed of two bulbous structures on one side and a fold of the wall on the other side, guards the opening to the duodenum. The muscular wall is reduced to a minimum, and the soft lining of the proventriculus is rapidly replaced by the keratinoid lining of the gizzard. Three coats contribute to the structure of the gizzard wall; a mucosa, muscularis externa and a tunica adventitia, (Plate XLII, fig. 69).

The proventricular glands are soon replaced by the simple tubular glands of the gizzard which join the surface gastric pits. The surface pits are covered by simple tall columnar cells, whose cytoplasm is distinctly divided into an apical pale, granular, cup-like
region, and a basal heavily granulated area, slightly above and below the nucleus, (Plate XLIII, fig. 70 c). Surrounding the glands is a loose collagenous and reticular area and enclosing small groups of glands is a dense band of connective tissue (Plate XLII, fig. 69 d) beneath which lies the submucosa. Essentially the same structure as in the falcon is observed in the sparrow hawk. The glands are grouped by a dense connective tissue band, but not in as pronounced a manner as in the peale's falcon, (Plate XLIV, fig. 71 d). In the pigeon hawk the connective tissue band is not observed. The glandular cells are low cuboidal cells lining the crypt of the gland in a single row (Plate XLV, fig. 72 b). The muscularis externa is greatly reduced in the falcon, whereas in the sparrow hawk and the pigeon hawk it is quite large. In the sparrow hawk it is composed mainly of a longitudinal band of muscle (Plate XLIV, fig. 71 e) and are thrown into heavy plicae. Penetrating the muscle are many blood vessels and nerves. The serosa is thick and contains large blood vessels and nerve fibres.
CONCLUSIONS AND SUMMARY

In the kingfisher, California murre, screech owl and the short-eared owl, the esophagus consists of a simple, thin-walled, greatly expandible tube of generally even calibre, while in the Peale's falcon an anterior enlargement that corresponds to or forshadow the fully developed crop of granivorous birds, is present. The wall possesses the usual structure characteristic of this region, a stratified squamous epithelium, a tunica propria and a muscularis externa composed of two layers of smooth muscle. The wall is generously supplied with glands and several gland types are present. In the kingfisher, screech owl and short-eared owl, oval glands composed of essentially the same type of cuboidal cells are situated in the epithelium with only a small portion of the basal part of the gland extending into the tunica propria. The excretory duct in the screech owl is short and nearly indistinguishable, while in the short-eared owl and kingfisher, the ducts are quite long. In the California murre the glands are still oval in shape, but have sunk below the epithelium into the connective tissue of the lamina propria with only the excretory ducts passing through the epithelium. The gland cells in this bird have become very narrow, tall columnar cells, thickening and shortening as they unite with the low cuboidal cells of the excretory duct. In the Peale's falcon, sparrow hawk and pigeon hawk, a different type of gland can be recognized. Large lobulated glands rather resembling the esophageal glands of the hen (Calhoun 1933) and composed of tall columnar mucous secreting cells like those found in the murre are observed. The excretory duct cells
are squamous cells of the epithelium. Schreiner (1900) found that if the number of glands in the esophagus increased too greatly, they tended to remove themselves from the surface area and sink to the underlying connective tissue. The cells of the excretory ducts would lose their secretory capacity. The glands in the Peale's falcon, sparrow hawk and pigeon hawk are holocrine secretory and sometimes are entirely absent from the esophageal wall. With mucicarmine, a characteristic colour for mucus is obtained for all of the esophageal gland cells, including the excretory duct cells of the kingfisher, owls and murre. According to Schaffer's (1924) classification, all of the glands are of the homocrine monoptychial type.

Essentially two methods of secretion, apocrine and holocrine for lubricating the food that passes through the esophagus, are distinguished. In apocrine secretion, present in the kingfisher, owls and murre, a continual secretion of mucus by the breakdown of the apical parts of the gland cells and in the holocrine type elimination of the entire gland content, including nuclei and cytoplasm, occurs. This holocrine secretion is characterized by the Peale's falcon, sparrow- and pigeon hawk. It would be difficult to state which of these two methods of secretion is more effective. In the apocrine type, secretion is always present while in the holocrine type, time is necessary for the regeneration of the gland.

When the food of these birds is considered, it will be noted that the diet of each bird is essentially flesh. The kingfisher feeds chiefly on fish, while the murre will eat crustaceans in addition.
(Taverner, 1947). The owls are generally predators on small mammals (Taverner, 1947) and the Peale's falcon and pigeon hawk eat birds (Taverner, 1947; May 1935). The sparrow hawk feeds almost entirely on insects (Taverner, 1947).

Although as stated above, the chief food of these birds is meat of one kind or another, considerable variation exists, especially in the structure of the esophagus. In the kingfisher, owls and murre, apocrine glands of similar cellular structure occur, yet the Peale's falcon and pigeon hawks, although they show a preference for birds, but will also eat small mammals, as do the owls, but have an entirely different glandular structure. Their glands are deeply sunk into the tunica propria and the excretory duct cells are transformed so that they resemble or are the cells of the epithelium. May, (1935), found that hawks were able to go a considerable length of time without eating and that many adult hawks did not capture food more than once in two or three days. The feeding habits thus may be a significant factor in the type of glandular cell present.

The stomach of the bird is divided into two regions, an anterior glandular proventriculus and a posterior muscular gizzard. The stomach shows less variation in structure than the esophagus.

The proventriculus is characterized by the presence of peculiar glands that are found generally in the stomachs of all birds. These are composed of masses of simple tubules placed adjacently to each other and radiating in all planes about a central excretory duct. The tubules are lined by a single layer of "zymogen" or digestive cells
that in the birds investigated are found to be all of the same type. Slight variations from species to species can be observed only in compactness, arrangement of tubules and in cell size.

The mucosa shows deep regular crypts and a reduced tunica propria in the kingfisher, murre, sparrow hawk and falcon, while in the owl the crypts are irregularly branched, and the tunica propria is of appreciable size. A muscularis mucosa is present in the kingfisher and murre, but is completely absent in the flesh-eating birds (the owl, falcon, pigeon hawk and sparrow hawk). Friedman (1939) states that in birds, both acid and pepsin are elaborated by one cell. The author also observed only one type of cell.

The gizzards generally possessed a keratinoid lining, a glandular layer that secretes the lining and a heavy smooth, muscular layer—that is more or less uniform in size in the kingfisher, screech owl, Peale's falcon and sparrow hawk. In the murre, modification of the gizzard takes place toward the development of a grinding structure whereby the muscles develop heavily on the dorsal and ventral sides and the central cavity becomes considerably reduced. The keratinoid lining is thicker than that of the other birds, reaching almost the thickness present in the grain-eaters.

It may be relevant to mention the experiment carried out by Broussay (1935) in which she changed the diet in a great horned owl from meat to vegetable and produced an alteration in the gizzard structure. This change was not distinguishable from the outside, from the rest of the stomach. The gizzard became partly separated by a constriction from the rest of the stomach. The mucosa showed newly developed rugae.
and longitudinal folds similar to those of a gizzard of a young grain-eating bird.

As far as the writer can determine no distinct relation can be drawn between the structure of the tract and the consistency of the food. Birds show considerable adaptability in their food habits.
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Fig. 1 Relation of the digestive tract of the kingfisher to the surrounding area.

a. Tongue
b. Hyoid apparatus
c. Esophagus
d. Trachea
e. Syrinx
f. Bronchus
g. Falciform ligament
h. Liver (cut)
i. Proventriculus
j. Gizzard
k. Duodenum
l. Ventral ligament
m. Rectum
PLATE II

Fig. 2 Relation of the digestive tract of the owl to the surrounding area.

a. Tongue  
b. Hyoid  
c. Esophagus  
d. Trachea  
e. Syrinx  
f. Bronchus  
g. Falciiform ligament  
h. Liver  
i. Proventriculus  
j. Gizzard  
k. Duodenum  
l. Ventral ligament  
m. Rectum
PLATE III

Diagrammatic representation of the relative shapes of the esophagus and stomach of:

Fig. 3 Kingfisher
   a. Esophagus  
   b. Crop evidence  
   c. Proventriculus  
   d. Gizzard  
   e. Duodenum

Fig. 4 California murre
Fig. 5 Screech owl
Fig. 6 Peale's falcon
Fig. 7 Sparrow hawk
Fig. 8 Pigeon hawk.
PLATE IV

Fig. 9 Kingfisher. Anterior esophagus. Mallory's triple 60X

a. Epithelium
b. Lamina propria
c. Muscularis externa
d. Tunica adventitia

Fig. 10 Kingfisher. Esophagus. Haematoxylin and carmine 140X

a. Epithelium
b. Lamina propria
c. Esophageal gland
d. Longitudinal layer of muscular externa
PLATE V.

Fig. 11 Kingfisher. Esophageal glands. Mallory's triple.
Oil immersion 1253X

a. Basal gland cell
b. Duct cell
c. Nucleus
d. Granular cytoplasm
e. Epithelium
f. Lamina propria
PLATE VI.

Fig. 12  Kingfisher. Longitudinal muscle. Short foot method for silver impregnation of reticulum with Van Gieson counterstain 630X

a. Longitudinal smooth muscle bundle enclosed in a connective tissue sheath.
b. Reticulum surrounding bundles of muscle
c. Circular muscle of muscularis externa
d. Short reticular fibres around each muscle cell
e. Nucleus
f. Clear area around nucleus
g. Lamina propria
h. Fibroblast
i. Blood vessel

Fig. 13  California murre. Longitudinal smooth muscle. Mallory's triple. 630X

a. Longitudinal smooth muscle
b. Nucleus
c. Loose connective tissue between the muscle bundles.
PLATE VII.

Fig. 14. California murre. Posterior esophagus. Mallory's triple. 60X

   a. Epithelium
   b. Lamina propria
   c. Muscularis externa
   d. Tunica adventitia

Fig. 15. California murre. Esophagus. Haematoxylin and carmine 140X

   a. Epithelium
   b. Lamina propria
   c. Esophageal gland
PIATE VIII.

Fig. 16  California murre. Esophageal glands. Mallory's triple 630X

a. Basal gland cell  
b. Duct cell  
c. Nucleus  
d. Granular cytoplasm  
e. Epithelium

Fig. 17. California murre. Lamina propria. Verhoeff's elastic tissue stain 140X

a. Lamina propria  
b. Elastic fibres  
c. Fibroblasts  
d. Lymphocytes  
e. Artery  
f. Vein
PLATE IX.

Fig. 18. Screech owl. Esophagus. Mallory's triple 60X

- a. Epithelium
- b. Lamina propria
- c. Muscularis externa
- d. Tunica adventitia

Fig. 19. Screech owl. Esophagus. Haematoxylin and Carmine 100X

- a. Epithelium
- b. Lamina propria
- c. Esophageal glands
PLATE X.

Fig. 20. Screech Owl. Esophageal gland. Mallory's triple 630X
a. Basal gland cells  
b. Excretory duct cells  
c. Epithelium  
d. Lamina propria

Fig. 21. Short-eared owl. Esophageal gland. Mallory's triple 630X
a. Basal gland cell  
b. Duct cell  
c. Nucleus  
d. Granular cytoplasm  
e. Epithelium  
f. Lamina propria
PLATE XI.

Fig. 22. Screech owl. Esophagus. Short foot method for silver impregnation of reticulum. 1hOX

a. Basement membrane
b. Reticulum surrounding the muscle fibres.
PLATE XII

Fig. 23. Peale's falcon. Anterior esophagus. Mallory's triple 60X

a. Epithelium
b. Lamina propria
c. Muscularis externa
d. Tunica adventitia

Fig. 24. Peale's falcon. Anterior esophagus. Van Gieson 60X

a. Epithelium
b. Lamina propria
c. Muscularis externa
d. Tunica adventitia
e. Esophageal gland
PLATE XIII

Fig. 25. Peale's falcon. Esophagus near the proventriculus. Haematoxylin and carmine 140X

a. Epithelium  
b. Lamina propria  
c. Esophageal gland

Fig. 26. Peale's falcon. Epithelium. Verhoeff's elastic tissue stain and eosin 630X

a. Stratum Malpighi  
b. Stratum corneum  
c. Lamina propria  
d. Fibroblasts  
e. Vein
PLATE XIV

Fig. 27. Peale's falcon. Gland before secretion. Verhoeff's elastic tissue stain and eosin 630X

a. Esophageal gland cell.
b. Primary gland cells
c. Connective tissue capsule
d. Capillary
e. Lamina propria
f. Fibroblast.

Fig. 28. Peale's falcon. Gland at beginning of secretion. Mallory's triple 630X

a. Esophageal gland cell
b. Nucleus
c. Beginning of the breakdown of the cytoplasm
d. Vein
e. Capillaries
f. Primary gland cell
PLATE XV.

Fig. 29. Peale's falcon. Esophageal gland nearing end of secretion. Haematoxylin and eosin 630X

a. Connective tissue capsule
b. Nuclei of gland cells
c. Broken down cytoplasm

Fig. 30. Peale's falcon. Esophageal gland secreting. Haematoxylin and eosin 630X

a. Glandular lumen lined with epithelium
b. Squamous epithelium
c. Glandular content being extruded
d. Lamina propria papillae
PLATE XVI

Fig. 31. Peale's falcon. Esophageal glands at various stages of secretion. Showing the excretory cavity through the epithelium. Haematoxylin and eosin 140X

- a. Esophageal gland
- b. Tunica propria
- c. Blood vessels
- d. Excretory duct cut at various levels
- e. Space remaining after secretion

Fig. 32. Peale's falcon. Esophagus after secretion. Verhoeff's elastic tissue stain 630X

- a. Epithelium
- b. Lamina propria
- c. Blood vessel
- d. Primary gland cells
- e. Lymphocytes
PLATE XVII

Fig. 33. Sparrowhawk. Esophagus. Mallory's triple 60X

a. Epithelium
b. Lamina propria
c. Esophageal gland
d. Muscularis externa with contraction bands showing in the circular layer.

Fig. 34. Sparrow hawk. Esophageal glands. Haematoxylin and carmine 60X

a. Esophageal gland
b. Epithelium
c. Lamina propria
d. Fibroblasts
PLATE XVIII

Fig. 35. Sparrow hawk. Gland during secretion. Mallory's triple 630X

A. Glandular epithelium.
B. Connective tissue capsule
Fig. 36. Kingfisher. Proventriculus. Short Foot method for silver impregnation of reticulum and Van Gieson 60X

a. Epithelium  
b. Lamina propria  
c. Muscularis mucosa  
d. Deep proventricular gland  
e. Submucosa  
f. Longitudinal smooth muscles  
g. Circular smooth muscle
PIATE XX

Fig. 37. Kingfisher proventriculus. Mallory's triple 140X

a. Foveolae gastricae
b. Lamina propria
c. Muscularis mucosa
d. Submucosa
e. Deep proventricular gland
f. Central collecting ducts
g. Capillary

Fig. 38. Kingfisher. Deep proventricular gland tubules. Mallory's triple. 630X

a. Cross section of tubule
b. Reticulum surrounding lobule and containing blood capillaries.
c. Zymogen cell
d. Nucleus (chromatin pattern very regular)
e. Interlobular connective tissue
f. Intralobular connective tissue
PLATE XXI

Fig. 39 Diagramatic three dimensional view of the proventricular wall.

a. Foveolar gastricae  
b. Plica  
c. Trough  
d. Excretory duct.  
e. Cross section of tubules  
f. Long section of tubules  
g. Lobular gland  
h. Intralobular tubule  
i. Interlobular connective tissue  
j. Intralobular connective tissue
PLATE XXII

Fig. lo. California murre. Proventriculus. Häagenshain’s-Azan 60X

a. Epithelium
b. Lamina propria
c. Muscularis mucosa
d. Deep proventricular gland
e. Submucosa
f. Muscularis externa
PLATE XXIII

Fig. 41. California murre. Proventricular excretory duct joining gastric crypt. Mallory's triple 120X
a. Gastric crypt
b. Excretory duct
c. Deep proventricular gland tubules
d. Columnar epithelium

Fig. 42. California murre. Proventricular gland tubules. Heidenhain's-azan 630X
a. Tubule (cross section)
b. Zymogen cell
c. Interlobular connective tissue
d. Intralobular connective tissue
Fig. 43. California murre. Proventriculus. Short Foot method for silver impregnation of reticulum. 60X

a. Gastric crypt
b. Lamina propria
c. Muscularis mucosa
d. Submucosa
e. Blood vessels and nerves in the base of the gastric ridges.
f. Muscularis externa
g. Central collecting cavity of deep gland showing basement membrane.
PLATE XXV

Fig. 44. Screech owl. Proventriculus. Mallory's triple 60X

a. Epithelium
b. Gastric crypt
c. Tunica propria
d. Deep proventricular gland
e. Muscularis externa

Fig. 45. Screech owl. Mucosa of proventriculus. Mallory's triple 140X

a. Epithelium
b. Gastric crypt
c. Tunica propria
d. Excretory duct.
e. Side branch of excretory duct.
PLATE XXVI

Fig. U6. Screech owl. Longitudinal and transverse section of the deep gland tubules. Heindenhain's-azan.

a. Interlobular connective tissue
b. Zymogen cell
c. Cross section of tubule
d. Longitudinal section of tubule

Fig. U7. Screech owl. Nerve ganglion. Bodian's silver stain.

a. Tunica adventitia
b. Circular layer of muscularis externa
c. Nerve ganglion of the myenteric plexus
PLATE XXVII

Fig. 48. Peale's falcon. Proventriculus. Mallory's triple 60X

a. Epithelium  
b. Tunica propria  
c. Gastric crypt

Fig. 49. Peale's falcon. Gland tubules cross section. Verhoeff's elastic tissue stain 630X

a. Zymogen cell  
b. Lumen  
c. Reticulum around tubule  
d. Blood cell
PLATE XXVIII

Fig. 50. Peale's falcon. Gastric mucosa. Mallory's triple 140X

a. Epithelium.
b. Tunica propria
c. Gland lobe
d. Excretory duct
e. Secretory tubules
PLATE XXIX

Fig. 51. Sparrow hawk. Proventriculus. Heidenhain's-azan 60X

a. Epithelium
b. Tunica propria
c. Deep proventricular gland
d. Muscularis externa
e. Tunica adventitia
PLATE XXX

Fig. 52. Sparrow Hawk. Proventriculus. Heindenhain's-azan 140X

a. Epithelium
b. Gastric crypt
c. Gland lobe
d. Excretory cavity

Fig. 53. Sparrow Hawk. Proventricular gland tubules. Heindenhain's-azan. 630X

a. Gland tubule
b. Zymogen cell
c. Intralobular connective tissue
PLATE XXXI  Drawings of the sphincters observed between the gizzard and the duodenum of the following birds: (Surface view, looking into the cavity of the duodenum.)

Fig. 54.  Kingfisher. Sphincter.  15X

a. Duodenal lumen
b. Five bulbous muscular projections from the duodenal lumen.

Fig. 55.  California murre. Sphincter 15X

a. Duodenal lumen
b. Muscle band surrounding the opening of the duodenum.

Fig. 56.  Screech Owl. Sphincter

a. Duodenal lumen. 15X
b. Muscle surrounding the opening.

Fig. 57.  Peale's falcon. Sphincter.

a. Duodenal lumen
b. Muscle surrounding the opening of the duodenum.
c. Bulbous projections from the duodenal cavity.
PLATE XXXII

Fig. 58. Kingfisher. Gizzard (thickest wall) Short Foot method for the silver impregnation of reticulum and Mallory's triple 60X

a. Keratinoid layer
b. Tubular gizzard gland
c. Muscularis mucosa
d. Submucosa
e. Muscularis externa
f. Blood vessel
PLATE XXXIII

Fig. 59. Kingfisher gizzard. (Thinnest wall) Mallory's triple 60X.

a. Keratinoid layer.
b. Tubular gizzard gland
c. Submucosa
d. Muscularis externa
e. Tunica adventitia
f. Artery
g. Vein.
PLATE XXXIV

Fig. 60. Kingfisher. Gizzard glands. Verhoeff's elastic tissue stain 630X

a. Gizzard gland
b. Cuboidal epithelium
c. Lumen of gland containing keratinoid secretion
d. Lamina propria
e. Muscularis mucosa
f. Blood vessel
Fig. 61  Kingfisher. Nerve fibre embedded in the smooth muscle of the gizzard. Mallory's triple 630X

a. Nerve fibre
b. Smooth muscle
c. Fat
PLATE XXXVI  Diagrammatic, longitudinal and transverse sections of the gizzard of the California murre, to show the gross arrangement of the muscle. (Dorsal side toward the top of the plate).

Fig. 62.  Longitudinal section of the gizzard

a.  Smooth muscle  
b.  Glandular layer  
c.  Keratin lining

Fig. 63  Transverse section of the gizzard.

a.  Smooth muscle  
b.  Glandular layer  
c.  Keratin lining.
PLATE XXXVII

Fig. 64. California murre. Gizzard. Haematoxylin and eosin 60X.

a. Keratinoid lining.
b. Glandular layer
c. Lamina propria
d. Muscularis externa
PLATE XXXVIII

Fig. 65. California murre. Gizzard glands. Haematoxylin and eosin. 630X.

A. Gizzard gland
b. Cuboidal epithelium
c. Lumen of gland containing keratinoid secretion
d. Lamina propria
e. Blood vessel
f. Muscularis externa
Fig. 66 Screech Owl. Gizzard. Haematoxylin and eosin 60X

a. Keratinoid layer
b. Glandular layer
c. Tunica propria
d. Muscularis externa
e. Tunica adventitia
PLATE XL

Fig. 67 Screech owl. Transitional area between proventriculus and gizzard. Haematoxylin and eosin 630X

a. Epithelium
b. Tunica propria
c. Fibroblasts
PLATE XL

FIG. 67

a
b
c
PLATE XLI

Fig. 68. Screech Owl. Gizzard glands. Haematoxylin and eosin 630X

a. Epithelium  
b. Keratinoid layer  
c. Capillary  
d. Neck of tubular gizzard gland  
e. Gizzard gland  
f. Colorless globules in the apical cells
PLATE XLII

Fig. 69. Peale's falcon gizzard. Haematoxylin and eosin 60X

a. Keratinoid layer.
b. Glandular layer
c. Tunica propria
d. Dense band of connective tissue enclosing groups of glands.
e. Submucosa
f. Muscularis externa
PLATE XLIII

Fig. 70. Peale's falcon gizzard glands. Haematoxylin and eosin 630X

a. Keratinoid lining.
b. Gizzard glands
c. Apical cells of the gizzard ridges
PLATE XLIV

Fig. 71 Sparrow Hawk. Gizzard. Mallory's Phosphotungstic Acid Haematoxylin 60X

a. Keratinoid layer
b. Glandular layer.
c. Tunica propria
d. Dense band of connective tissue
e. Muscularis externa
PLATE XLV

Fig. 72  Sparrow hawk gizzard glands. Mallory's phosphotungstic acid haematoxylin 630X

a. Keratinoid lining
b. Gizzard gland cell