Microscopic Anatomy of the Digestive System of the Chicken

A study of the microscopic anatomy of the entire digestive tract of the chicken (*Gallus domesticus*) at different ages has never been undertaken. The author has never seen a related work illustrated with photomicrographs. These features added to the large compilation of literature included herein should make this a valuable source of reference to the anatomist.[1] It should be of added value to the English-speaking anatomist since previous to this time the more complete works were written in the German language.

This study was also considered with the idea that it would help solve a problem which has long confronted the pathologist. Since he is concerned with the effects of disease on organs, it is hoped that this paper will give him a standard for comparison.

REVIEW OF LITERATURE

Literature concerning the microscopic anatomy of the digestive tract of the bird is quite voluminous, but with few exceptions [Zietschmann (1911) and Bradley and Grahame (1951)] no author included the entire tract with all its appendages. In many cases the work covered chiefly gross anatomy with an occasional reference to the microscopic structure. Authors dealing with the gross anatomy alone included Huxley (1878), Wiedersheim (1907), Kingsley (1917), Johnston (1920), Kaupp (1921), Latimer and Osborn (1923), and Ellenberger and Baum (1943). Baum (1930) has made quite a complete study of the lymph system of the digestive tract of the chicken. Sturkie (1954) has in-

[1] The original was a thesis submitted to the Graduate Faculty of Iowa State College in July, 1931, in partial fulfillment of requirements for the degree Master of Science and was published in the Iowa State College Journal of Science 7:261–382, 1933.

cluded a limited amount of both gross and microscopic anatomy in his book on avian physiology. Strong (1939) published a bibliography of bird literature which includes all biological fields with a great many references to anatomy, histology, and embryology of the domestic fowl.

Mouth

Owen (1866), Wiedersheim and Parker (1897), Chauveau (1905), Zietschmann (1911), Kaupp (1918), Krause (1922), Schauder (1923), Grossman (1927), Boetticher (1928), and Bradley and Grahame (1951) spoke of the "horny" beak of the bird. Boetticher gave the time of beginning cornification as the sixteenth day of incubation. Krause gave a complete histological description of the beak. He divided it into four layers: bone, subcutis, cutis, and epidermis. Kingsbury *et al.* (1953) studied the histology of the beak of White Plymouth Rock embryos to follow the process of keratinization. According to Owen, "the beak consists of an upper mandible supported by the maxillary and premaxillary bones, and of a lower mandible formed by the lower jaw." Rosenstadt (1912), Schauder (1923), and Bütschli (1924) described the "Eizahn," a protuberance found on the upper beak of newly hatched chicks.

All recent authors are agreed that birds lack teeth. Blanchard (1860) described vestigial teeth in certain birds (parrots). Marsh (1881–82) stated that no true teeth had yet been found; and Ihde (1912), that further research along that line would be fruitless.

Owen (1866), Shufeldt (1890), and Marschall (1895) described the tongue muscles. Hollis (1901) gave particular attention to the skeleton of the tongue as associated with its function. Zietschmann (1911) described the relation of the shape of the tongue to the conformation of the mouth roof. Owen (1866), Wiedersheim and Parker (1897), and Ward and Gallagher (1926) spoke of it as a prehensile organ. Wiedersheim and Parker (1897), Schauder (1923), Bütschli (1924), Grossman (1927), and Otte (1928) described the tongue as pointed, especially horny at the apical end, and poor in muscle. Kaupp stated that the body of the tongue was made up of muscle and connective tissue. Schauder said the tongue corresponded to the form of the beak, while Marschall found that "the tongue of the chicken does not correspond to the form of the beak but has approximately the form of

a shoe sole and is soft." Kallius (1905) dealt with the embryology of the tongue of the sparrow.

It is the common belief that the sense of taste is not enjoyed by the chicken, but taste cells were found on the tongue and hard palate by Schauder (1923), in the beak and tongue by Krause (1922), and in the mucous membrane between the sides of the lower beak by Otte (1928). Botezat (1904 and 1906) found that chickens have a sense of taste resembling that of mammals. He found taste organs in the throat region. According to Bradley and Grahame (1951) taste buds are not present in the chicken. McLeod (1939) stated that the existence of taste buds had been both affirmed and denied but that such endings, if present, are probably concerned with touch rather than taste. Moore and Elliot (1944) found 27–59 taste buds on the tongue of the pigeon, 70.7 per cent of which were on the dorsal and lateral surfaces of the soft portion of the tongue caudad from the tongue fold.

According to Heidrich (1905), Kaupp (1918), Grossman (1927), Ward and Gallagher (1926), Otte (1928), and Bradley and Grahame (1951), the roof of the mouth is the hard palate. Marschall (1895), on the contrary, stated that all birds lack a palate; Heidrich, Ward and Gallagher, and McLeod (1939), that a soft palate was absent. Heidrich gave a detailed histological description of the different layers in the wall of the mouth. Chamberlain (1944) found the lateral walls of the mouth cavity are covered with keratinized epithelium similar to that of the beak.

Pharynx

All authors agreed that there was no exact line of demarcation between the mouth cavity and the pharynx. Killian (1888) stated that "birds have no naso-pharyngeal cavity." Grossman (1927) set aside the transverse row of papillae on the root of the tongue as a "convenient" mark for separating the two cavities while Heidrich (1905) designated a row of papillae in the palate for the same purpose. McLeod (1939) considered the mouth and pharynx as one continuous cavity, which he termed oropharynx. He stated that its posterior extent reaches the level of the third cervical vertebra. Foust (1952) chose the most posterior row of palatine papillae and the row at the base of the tongue as a dividing line between the mouth and pharynx. Heidrich (1905) and Zietschmann (1911) stated that the mouth-pharyngeal cavity is

covered by a "cutaneous mucous membrane." The latter added that a stratum corneum was found only on the roof of the mouth and on the caudal part of the dorsum of the tongue. Bradley and Grahame (1951) mentioned a stratified squamous epithelium lining the whole of the mouth and pharynx. Zietschmann did not find any muscularis mucosae in the mouth-pharyngeal cavity while Heidrich described it as beginning in the pharynx. Gadow (1891b) said that the pharynx was thin-walled; Heidrich, that it had no muscle, while Thomson (1923) designated the pharynx as a muscular region at the back of the mouth. Otte (1928) stated that instead of a soft palate a strong musculature was present. According to Schauder (1923), there were no voluntary muscles in the mouth except in the tongue.

Heidrich (1905) and Zietschmann (1911) described macroscopic papillae which have a matrix belonging to the tunica propria. Zietschmann stated that in the anterior part of the roof of the mouth there was little lymphoid tissue but that it increased posteriorly until the maximum was reached in the region of the opening of the Eustachian tubes. Killian (1888) has designated a certain area of adenoid tissue as "throat tonsil," especially in the region of the openings of the Eustachian tubes between the epithelium and the throat glands.

Salivary Glands

All authors who discussed the mouth parts at all mentioned salivary glands. Heidrich (1905), Zietschmann (1911), and Holting (1912) wrote the most complete works on the subject. The first two agreed, except on two points. Heidrich found basket cells while Holting did not, and Heidrich perceived some change in the gland according to the physiologic state while Holting failed to do so. Zietschmann differed from Heidrich on three points. Heidrich gave fifty as the number of openings of the lateral palatine glands and ten to fifteen openings for the anterior submaxillary gland, while Zietschmann gave "approximately one hundred" for the former and forty for the latter. Heidrich found muscle fibers in the gland capsule, and Zietschmann did not. Bradley and Grahame (1951), in their work, referred to Heidrich. Kovacs (1928) found the salivary glands to be uniformly constructed, in contrast to Heidrich, who described three different forms. Owen (1866), Marschall (1895), and Chauveau (1905) described them

as being little developed. McLeod (1939) found salivary gland tissue abundant in the chicken.

Other authors mentioned them briefly: Browne (1922), "true salivary glands are absent"; Thomson (1923) mentioned their role in lubrication; Schauder (1923) "numerous glands purely mucous"; and Grossman (1927) spoke of several glands being in the submucous tissue producing a mucous secretion which did not contain a digestive enzyme. Schauder gave the location of all the glands but did not include the histology of them. Halnan (1949) described the salivary glands as branched tubular glands. Kaupp (1918) gave the location of angular, sublingual, and palatine glands. Otte (1928) spoke of the first two and, in addition, the submaxillary and the spheno-pterygoideae salivary glands. Bütschli (1924) mentioned particularly diffuse glands of the tongue. Owen mentioned the following: "folliculi lingualis," "glandulae sublinguales," "glandulae submaxillares," "glandulae anguli oris," "folliculi preglottidei," 'folliculi post-nasales," and "amygdalae." Cholodkowsky (1892) described the glands of the lower mandible and the "glandula angularis oris." Wiedersheim and Parker (1897) compared the lingual and palatine glands of the bird to those of the reptiles. Chodnik (1948) studied the cytology of the salivary glands in relation to feeding. He found that the cells go through a physiological cycle coincident with the alternate accumulation and discharge of the mucous contents. Zietschmann described elastic fibers in the connective tissue propria in which the glands lie, as well as in the gland capsule itself. Leasure and Link (1940) made a study of the saliva of the hen.

Esophagus

In general, the esophagus has been described as a very elastic tube extending from the pharynx to the proventriculus and containing at its entrance into the thorax a dilatation called the *crop*. Kupfer (1908) used the term *pharynx* instead of *esophagus* to designate the part from the back of the mouth to the proventriculus. There are, however, two markedly contrasting views as to its structure. Barthels (1895), Heidrich (1905), Kaupp (1918), Browne (1922), Batt (1925), Kovacs (1928), Otte (1928), and Bradley and Grahame (1951) spoke of the outer layer of muscle as a longitudinal one, while Owen (1866), Gadow (1879), Cazin (1888b), Newton (1893–97), Marschall (1895), Zietschmann

(1911), and Otte (1928) mentioned an outer transverse or circular muscle layer. Heidrich observed that smooth muscle began quite a distance anterior to the esophagus.

Zietschmann (1911), Schauder (1923), and Kovacs (1928) found an esophageal tonsil near the lower extremity of the esophagus.

Another difference in opinion was manifested as to the number of layers in the wall. Kupfer (1908), Zietschmann (1911), and Otte (1928) said three; Marschall (1895), Batt (1925), and Grossman (1927), four; and Newton (1893–97), five.

The esophagus was described quite briefly by the following authors: Wiedersheim and Parker (1897), Browne (1922), Thomson (1923), Bütschli (1924), Ward and Gallagher (1926), and Grossman (1927). Schreiner (1900) and Schauder (1923) mentioned chiefly the longitudinal folds of the mucous membrane, smooth muscle, a longitudinally arranged elastic tissue sheath besides the muscularis mucosae, and the mucous glands. Of particular note in Barthels' (1895) work were "border cells," a detachment of the marginal edge of the mucosa.

Klein (1871) and Rubeli (1890) dealt with the structure, and Schumacher (1926) with the structure and development of the mucous glands. Batt (1925) stated that the mucous glands were most numerous in the upper esophagus. Michalka (1924) found pavement epithelium in the glands of the esophagus. Ivey and Edgar (1952) described the histogenesis of the esophagus and crop of the chicken.

Crop

It was agreed that the crop had the same general structure as the esophagus. Marschall (1895), Wiedersheim and Parker (1897), Chauveau (1905), Kaupp (1918), Browne (1922), Schauder (1923), Batt (1925), Ward and Gallagher (1926), and Otte (1928) merely stated that mucous glands were present. Barthels (1895) found no glands in the diverticulum of the crop. Schreiner (1900) found glands only on the "back side." According to Kupfer (1908) "the ventral surface of the crop and the side parts in the ventral surface are free from glands." Owen (1866) described "muciparous follicles" as being larger and more numerous than those of the esophagus. Gadow (1891b) found the crop to have a glandless lumen, and Kovacs (1928) found glands in the dorsal wall. Browne (1922) found them most

numerous near its openings. Schauder (1923) wrote that the middle part of the ventral crop wall had no glands. Klein (1871) and Bradley and Grahame (1951) found them absent in the crop. Zietschmann quoted Barthels, Gadow, and Schreiner on the matter of mucous glands and said in addition that the crop lacked lymphoid tissue. Mayberry (1935) followed the gross development of the crop of the chick embryo from the seventh to twenty-first day.

Proventriculus

Bischoff's (1838) work brings forcibly to one's mind the advancement made in histology in the last century. A quotation from his work follows: "The mucous membrane of the proventriculus which is present here and which is separated from the little sacs is in the form of small pyramidal pouches or villi in which I could not observe any epithelium but only a granular structure. . . . If one sections it with a fine pair of scissors and flattens it out. . . ."

In general the proventriculus was described as having a mucous membrane lined with simple columnar epithelium and containing in the tunica propria superficial tubular glands, a muscularis mucosae next, and between it and the lamina muscularis were the deep propria glands [Zietschmann (1911), Bradley and Grahame (1951)]. In contrast to this, Batt (1925) described the deep propria glands as being between the muscularis mucosae and the epithelium. There were differences of opinion as to the structure of the glands. Browne (1922), Batt (1925), Grossman (1927), Otte (1928), and Bradley and Grahame (1951) described the deeper glands as tubular. According to Cazin (1887b and 1888a), the glands were "by no means tubular." Cazin (1887c) mentioned them as "culs-de-sac." Kovacs (1928) stated that the deep glands were sac-formed. Schreiner (1900) and Zietschmann (1911) found them to be multilobar. Recent papers on the proventriculus have all included a description of the macroscopic papillae containing a cavity into which the deep glands empty [McLeod (1939), Ellenberger and Baum (1943), Chamberlain (1944), Elias (1945), and Sisson and Grossman (1953)]. Wilczewski (1870) stated that the glands increased in size near the esophagus and decreased near the gizzard, while Marschall (1895) found the glands to decrease at both extremities. According to Gadow (1891b), glands were located in approximately

fifty scattered rows. Newton (1893–97), Wiedersheim and Parker (1897), and Ward and Gallagher (1926) mentioned particularly the large amounts of glandular tissue in the proventriculus. Dawson and Moyer (1948) described elongated threadlike argentophile cells scattered over the surface of the lobules or arranged radially between the tubules of the chicken proventriculus. Chodnik (1947) described the deep glands as tubular and found the superficial columnar epithelium similar to the intestinal epithelium. He found some transitional neck cells between the two.

Kovacs (1928) stated that "the glands may be likened to fundus glands"; Browne (1922), that the proventriculus was "analagous to true stomach in mammals"; Bütschli (1924) compared the proventriculus to the cardiac portion of the mammalian stomach; Batt (1925) stated that there were no acid or peptic cells in the proventriculus but that they resembled the parietal cells of mammals; and Kaupp (1918) found them similar to the fundic glands of the horse.

The same differences of opinion as to the muscle layers existed here as in the case of the esophagus. Cazin (1888b) admitted that a longitudinal layer might be seen on the outside of the external circular layer. He also found the muscularis mucosae to contain both a longitudinal and transverse layer. Zietschmann (1911) made this statement, "Of twenty-six investigated kinds of birds, only one, *Iotames calidris,* lacked the longitudinal layer." In Oppel's (1895) work on the muscular layers of the proventriculus he described an outer longitudinal layer (often rudimentary) and an inner circular layer comprising the lamina muscularis and an inner longitudinal layer and the muscle around the glands as making up the muscularis mucosae. Zietschmann stated that the outer longitudinal layer ended at the beginning of the gizzard.

Zietschmann (1911) described a lymphocytic infiltration of the propria which included many eosinophils. Hässe (1866) found only a trace of elastic elements visible. Laroche (1926–27) quoted Cazin. Swenander (1902) studied *Gallus domesticus* in comparison with other birds. Owen (1866), Chauveau (1905), and Schauder (1923) gave slight consideration to this organ. Schreiner's (1900) work included quite a detailed cytological study of the epithelium. At the point of the folds, prismatic cells had a height of thirty microns. The basal part of the cell was small, granular, and contained an oval nucleus. Other vacuolated cells which took a deeper stain were described. He also found the

cells to diminish in height as the fold widened. Hibbard (1942) studied the Golgi apparatus in both proventriculus and gizzard of chicken embryos and growing chicks.

According to some authors there is a so-called "intermediary piece" between the proventriculus and the gizzard. Batt (1925) said it was analogous to the mammalian pylorus. Hässe (1866), Cazin (1886b), Zietschmann (1908), Schauder (1923), and Kovacs (1928) stated that it was characterized by the lack of the deep propria glands of the proventriculus. Cazin (1886a) described the tubular glands as longer than the surface glands of the proventriculus. Cazin (1888b) stated that the exudate was more complex. Schauder and Zietschmann agreed that it lacked the hornified layers of the gizzard, while Kovacs characterized it by its keratinized layer. Marschall (1895) found a sphincter of circular muscle fibers separating the proventriculus and gizzard, while Bradley and Grahame (1951) designated the constriction only as a demarcation. Bütschli (1924) stated that a "clear intermediary piece is seldom inserted between the two sections."

Ventriculus

Most authors agreed on the general structure of the gizzard: its peculiar musculature, a thin submucosa, and the mucous membrane with its glandular layer and its keratinized secretion forming an inner layer. Owen (1866), Gadow (1891b), Newton (1893–97), Wiedersheim and Parker (1897), Cornelius (1924), Grossman (1927), Otte (1928), and Bradley and Grahame (1951) described the internal layer as hard, thick, yellowish, horny, and keratinized. Zietschmann (1911) said it was falsely called a horny layer and Hedenius (1892) described it as a keratinoid layer medial between keratin and albumin. Cazin (1887a) stated that it was not analagous to tegumentary coverings.

According to Bütschli (1924), this layer was strata-like and contained cast-off cells, and Hässe (1866) mentioned parallel lines in it. Cazin (1886b) described a "secretion in the form of colonnades between which the secretion from the superficial epithelium is poured."

Browne (1922) spoke of a "horny epithelium" and stated that there were no true glands present. Otte (1928) said that the true mucous membrane lay under the inner membrane and that the glands therein resemble the stomach glands of mammals. Schauder (1923) and Kovacs (1928) compared them to pyloric glands of

mammalian stomachs. Hässe (1866), Cazin (1886b), and Bütschli (1924) described the glands as tubular; Cazin (1886a), as long cylindrical culs-de-sac. Hässe (1866), Zietschmann (1911), Cornelius (1924), and Kovacs (1928) mentioned the cluster arrangement of the glands.

Cazin (1888b) stated that the cells were arranged obliquely to the axis of the tube. Pilliet (1886) stated that the gland cells were not cylindrical and Zietschmann (1911) that they were cubical to flat. Wiedersheim (1872) described secretion cells which appeared on the edge of the glands in profile. He also included a microscopic study of the secretion cone and secretion hook, the two latter being in contact with the cell itself. Zietschmann stated that the glands were shorter where the mucosa was thinner. He also found elastic tissue to be confined to an area beneath the gland region. Cazin (1885), in writing of the development of the cornified layer, stated that on the sixteenth day of incubation the glands approached the adult form. Dawson and Moyer (1948) found a few oval or triangular argentophile cells in association with the epithelium of the gland tubules. Kaupp (1917) stated that walls of gizzards of granivorous birds were very thick, while Magnan (1911a) contended that the muscle masses were reduced to a minimum. Batt (1925) mentioned a thin outer longitudinal muscle layer. Sisson and Grossman (1953) described three muscle layers — inner oblique, middle circular, and outer longitudinal.

Both Garrod (1872), who wrote a paper on the mechanism of the gizzard, and Ashcraft (1930), in writing of the activities of the alimentary canal of the fowl, stated that in hunger the proventriculus and gizzard were vigorously and continually contracting, but they did not discuss the minute structure of the gizzard. Bauer's (1901) work on the histology of the gizzard was chiefly done on the duck. Cazin (1887b) dealt with the embryonal development.

Marschall (1895) and Kaupp (1918) designated a valve and Otte (1928) a fold in the mucous membrane as separating the gizzard from the duodenum.

Marschall (1895) also stated that the wall of the gizzard became thinner as it approached the duodenum. According to Bradley and Grahame (1951), the keel of the gizzard contains striated muscle. They described coarse transverse striations varying from 25μ to 90μ apart. According to their reports, nuclei crossed by the striations were distorted. According to Zietschmann (1911), the

border zone was rich in lymphocytes. Oppel (1896–1914) stated that this transitional zone corresponded to the pyloric region of mammals. Zietschmann called it the pyloric gland zone of the gizzard.

According to Oppel (1896–1914), one cannot speak of a pyloric sphincter between the ventriculus and the duodenum. He also stated that the circular muscle of the intestine could be considered as a continuation of the diminished muscles of the ventriculus. Zietschmann (1911) stated that the surface of the gland layer in this intermediary portion became uneven and the glands were farther apart and took on an aspect of villi. Oppel described the glands in this areas as club-shaped and curved at their lower end – not a beginning of Lieberkühn's glands. Kovacs (1928) described an alteration of the glands and the presence of lymphoid infiltration possessing follicular character.

Small Intestine

Zietschmann (1911), Batt (1925), and Clara (1926a) agreed in general on the structure of the small intestine (duodenum included): the mucous membrane was lined with simple columnar epithelium interspersed with goblet cells; the villi were tongue-shaped, longer and more numerous in the duodenum; a submucosa in which the blood vascular system was contained; and two layers of muscle – an inside muscularis mucosae, the middle circular and outer longitudinal layers of the lamina muscularis. Cloetta (1893) stated that there was no submucosa and that the blood and lymph vessels were in the tunica propria.

Two bile ducts and three pancreatic ducts opening into the duodenum were described for the chicken by all authors with the exceptions of Batt (1925), who described one bile duct and two pancreatic ducts, and Chamberlain (1944) and Sisson and Grossman (1953), who indicated that there might sometimes be only two pancreatic ducts. According to Gadow (1879), the entrance of the ducts into the intestine was marked by a small warty projection which contained a valve.

Newton (1893–97) described a villus as a structure containing a prolongation from the submucosa, a lacteal, arteries and veins, and smooth muscles. Bujard's (1906) work indicated a change in the villi according to age. Clara (1927b) found the villi to present a picture of geometric regularity upon cross section.

Cloetta (1893) described the epithelial cells of the glands as

being smaller than the epithelial cells of the villi. He also found goblet cells nearer the tip of the villus as the age of the birds increased. Chodnik (1947) found the goblet cells of the domestic fowl to differ from those of mammals in that they always presented the form of a neatly shaped goblet. He followed the cycle of the Golgi apparatus and mitochondria in relation to secretory activities. Ackert *et al.* (1939) found that the numbers of goblet cells in a unit area (122μ × 10μ) along the side of the villi of the duodenum varied from 2.9 in a 2-day-old chick to 9.0 in a 320-day-old bird. Birds of 71 and 124 days had 9.3 and 10.7 goblet cells per unit area, respectively. Zietschmann (1911) found that the epithelial cells contained a cuticular border. Moog (1950) observed that the striated cuticular border of the duodenum of chicks up to 2 days old exhibited large quantities of alkaline phosphomonoesterase indicating a powerful phosphatase-synthesizing mechanism present at hatching. Bradley and Grahame (1951), Greschik (1922), and Clara (1926b and 1927a) agreed that there were cells of Paneth, while Cloetta doubted their presence. All authors with the exception of Kaupp were agreed that Brunner's glands were lacking. Kaupp (1918) made the following statement: "Openings of simple intestinal tubular glands, the duodenal glands, or the glands formerly known as Brunner's glands, are located between the villi."

Otte (1928) described Peyer's patches in the bird intestine, and Retterer and Lelièvre (1910a) found areas having the appearance of Peyer's patches.

Zietschmann (1911) found that elastic fibers were not demonstrable in the gland layer and were comparatively few in other layers. Batt (1925) described a layer of white fibrous tissue between the outer longitudinal and the inner circular muscle. According to Batt there were valvulae conniventes present; also lymph nodules were fewer in the remainder of the small intestine than in the duodenum.

Browne (1922) made the statement that the intestine was uniform in caliber throughout, while Cloetta (1893) and Otte (1928) found the duodenum to have a wider lumen.

Gadow (1891b), Newton (1893–97), and Thomson (1923) mentioned the ileo-cecal valve, and Zietschmann (1911), an iliac sphincter. Marschall (1895), Wiedersheim and Parker (1897), Ward and Gallagher (1926), and Grossman (1927) described the small intestine briefly.

Large Intestine

The term *large intestine* was seldom used. Some used the term *colon,* while others used the term *rectum* to include the portion from the caeca the cloaca. Still others used the terms combined —*colon and rectum.* McLeod (1939) suggested the term *colorectum.* In this paper *rectum* will be used to refer to this portion.

Caeca

Zietschmann (1911) and Looper and Looper (1929) made the most complete studies of the caeca. The general structure corresponded to the small intestine. According to Eberth, as reported by Oppel (1897), Zietschmann (1911), and Kaupp (1918), there was an elevation in the caeca about two to four millimeters from their origin. Muthmann (1913) found so-called "caecal tonsils." Looper and Looper found that lymph nodules first appeared at about fourteen days in the tunica propria two millimeters from the origin of the caeca, and in the tunica propria and submucosa of the blind ends. Prior to this age, the lymphoid tissue was scarce and diffuse. Berry (1900) found lymphoid tissue diffused throughout the mucosa. Looper and Looper (1929) and Bradley and Grahame (1951) described many lymphoid nodules in the caeca. Batt (1925) stated that there were "few small lymphatic nodes" and Zietschmann (1911) that follicles seldom appear.

Looper and Looper (1929) found the muscularis mucosae to be absent in many places, while Batt (1925) stated that it was well developed.

Looper and Looper found many eosinophils throughout the wall, and Muthmann (1913) stated that cells with large granules were present in large quantities. Bittner (1924) and Otte (1928) divided the caeca into three parts: a neck with many villi, a middle portion with few villi, and the vesicular blind end which was thin walled and free from villi. Zietschmann (1911) and Browne (1922) stated that the villi were short or absent in the dilated portion. According to Batt (1925), the mucous membrane was thrown into folds which gave the appearance of villi.

Oppel (1895) referred to Eberth as finding ciliated epithelium in the folds and extending into the glands. Maumus (1902) attempted to verify this but failed. He concluded they were probably artifacts.

Zietschmann (1911) found goblet cells to be lacking in spaces where lymphoid tissue was numerous.

Other important facts brought out by Looper and Looper (1929) were: the submucosa was occupied by or obliterated by lymph nodules where the lymphoid tissue was present in the tunica propria; circular layers of muscle were displaced by lymphoid tissue in the blind end; reticular connective tissue fibers extended into the circular muscle layers and encircled the fibers; most important of all, the mucosa of the distal two-thirds underwent a degenerative change as fowls became older. The regression involved the atrophy of the epithelium and glands accompanied by the appearance of lymphoid tissue. This had, in turn, been replaced by sclerotic fibrous tissue in the blind ends of the caeca in a 3-year-old specimen.

Marschall (1895), Wiedersheim and Parker (1897), Schauder (1923), Ward and Gallagher (1926), Grossman (1927), and Otte (1928) gave slight consideration to the caeca. Maumus and Launoy (1901), Röseler (1929), and Mangold (1931) dealt primarily with the physiology of these organs.

Rectum

Regarding the structure of the rectum, little has been said beyond the fact that it was very similar to the small intestine. Owen (1866) stated that the villi of the rectum were coarser, shorter, and less numerous than those of the small intestine. Greschik (1912), on the contrary, found them to continue the same height to the anus. Zietschmann (1911) in describing the "cloacal end of the rectum" agreed with Owen (1866) and added that the villi "afterwards take on the greatest length of anywhere in the intestine." Marschall (1895) and Grossman (1927) described numerous villi with glands emptying between them. Greschik mentioned simple tubular glands, and Zietschmann stated that the glands were longer than in the rest of the intestine. Zietschmann (1911), Greschik (1912), and Clara (1926a) found lymphoid tissue in the rectum. According to Greschik, the submucosa was weakly developed and in many cases not apparent.

Cloaca

Bütschli (1924) found a sphincter marking the limitation of the rectum. Owen (1866) and Otte (1928) made the statement that the rectum terminated in a valvular circular orifice. Kaupp (1917) agreed with them by saying that there was a strong oblique fold of the mucous membrane where the large intestine emptied

into the cloaca. According to Retterer (1885) and Jolly (1915), there was no demarcation between the two.

Gadow (1891a), Schauder (1923), Thomson (1923), Bütschli (1924), Ward and Gallagher (1926), and Bradley and Grahame (1951) described three compartments in the cloaca. The most anterior was named *coprodaeum,* the middle one *urodaeum,* and the posterior one *proctodaeum.* Retterer (1885) spoke of a "rectal vestibule" in describing the anterior compartment. Owen (1866) stated that the rectum terminated in a rudimentary urinary bladder. McLeod (1939) did not favor the use of the terms *coprodaeum, urodaeum,* and *proctodaeum* because he felt such divisions did not coincide with the facts. He preferred to describe the cloaca as a tubular cavity incompletely divided into an anterior functional and a posterior non-functional part by a circular fold of mucous membrane. Bennett (1944) studied 181 White Leghorn chickens and found three compartments: the coprodaeum, which was the largest; the urodaeum, the smallest; and the proctodaeum. He found definite folds separating the urodaeum from the other two compartments. Foust (1952) also described three compartments in the cloaca as did Chamberlain (1944) and Sisson and Grossman (1953).

According to Gadow (1891a), the coprodaeum had the same mucous membrane as the rectum, and Zietschmann (1911) described a one-layered epithelium extending as far as the anal opening. Bradley and Grahame (1951) found Paneth cells to the end of the proctodaeum.

Anus

Retterer (1885) described a sphincter of smooth muscle outside of which was a voluntary transverse cloacal muscle. Marschall (1895) described the anal opening as an oblique slit, while Gadow (1891a) stated that it was a round opening.

Liver

Few writers have given much attention to the microscopic anatomy of the bird liver. Krause (1922) studied the liver of the pigeon as representative of the livers of birds and found it to be very similar to the mammalian liver. He found indications of changes in the cells according to the secretory condition. Batt (1926) also noted the similarity to the mammalian liver. Zietschmann (1911) stated that the liver of the bird had a smaller lobule

design than the mammal. According to him central veins were lacking. Batt stated central veins and a portal system were present.

Chodnik (1948) stated that the liver of the domestic fowl is much simpler than that of mammals and has no true lobular structure. He also found prominent morphological changes in both Golgi material and mitochondria to be connected with cellular activity and secretory phenomena. Elias and Bengelsdorf (1952) have presented some new ideas on the structure of the liver. They believe that the vertebrate liver is a "solid mass of hepatic cells, perforated by more or less cylindrical lacunae which contain the sinusoids." The hepatic plates or lamina are walls separating these sinusoids. In chickens they found all hepatic plates to be two cells in thickness. They described the chicken liver as "sacculosinusoidal." These same authors also found the nuclei of the liver cells of germ-free chickens from the Lobund Laboratory at Notre Dame University to be the most extremely basally or parietally located of any vertebrate specimen examined. Bradley and Grahame (1951) found the chicken liver to be simpler than mammalian liver and more like reptile liver. According to their work the liver cords form columns arranged in a tubular manner about a bile capillary.

Zietschmann (1911) found elastic fibers only in the vessel walls. Batt (1926) described a scant reticulum in the liver of the bird. Shore and Jones (1889) described the liver parenchyma as dense with obscure cell outlines. In young chickens the cell structure was clearly tubular with five rows of cells to the tubules. Shore and Jones further indicated that there was no distinction between interlobular and intralobular vessels. Shore (1890–91) found the liver cells of baby chicks to be excavated by spaces for oil droplets. He suggested a relationship between the color of the liver and the yolk. Doyle and Mathews (1928) stated that the color of the liver changed from the yellow of the baby chick liver to the red or maroon of the adult liver by the time a chick was a week to ten days old. Dalton (1933) studied the mitochondria and Golgi network in the hepatic cell of the chick.

Gall Bladder

The wall of the gall bladder, as described by Zietschmann (1911), consisted of an adventitia with many blood vessels and some lymph follicles, an outer longitudinal and inner circular

muscular layer, and a mucous membrane with many folds. The propria was filled with lymph cells. According to him, "the surface epithelium resembles that of the liver," and the surface was pouched and contained short crypts. Otte (1928) found many tubulose glands in the tunica propria. Bradley and Grahame (1951) described only a thin longitudinal muscle layer in the gall bladder.

The structure of the ducts was similar to that of the gall bladder. The ducts contained, according to Zietschmann (1911), a one layered cylindrical epithelium, while goblet cells and special glands were lacking.

Pancreas

Zietschmann (1911) found the pancreas to differ little from that of the mammal. Pugnat (1897) described three lobes, each possessing a distinct excretory duct. Clara (1924) described, in addition to the two lobes in the loop of the duodenum, a splenic lobe. He did not find a separate excretory duct for it. Clara found this splenic segment to be of a lobular structure, while the other two were not. According to Pugnat, the pancreas was a ramifying and reticular tubulo-acinar gland. Krause (1922) described more islets of Langerhans in the dorsal lobe than in the ventral, while Clara (1924) and Nagelschmidt (1939) found more in the splenic lobe of the pancreas. According to Zietschmann, the islets of Langerhans showed nothing special in the bird, while Clara described a "pseudo-islet" similar in structure, but different in staining affinity. According to Batt (1926), they were smaller than the islets of the mammalian pancreas but similar in structure. Böhm (1904) did not find a pronounced accumulation of Langerhans cells. He did not find the islets to be set off from the surrounding pancreas, while Batt described a delicate fibrous capsule surrounding them. Lucas (1947) observed that the islets were small in both relative amounts and size in embryos and young chicks. As chicks grew older he found a rapid increase both in size of islets and in amount of islet tissue. He reported the islets to vary in size from one with a few cells up to one 363μ by 458μ. Lucas also observed a lumen as large as 23μ in diameter in one islet. Other islets presented only a slitlike lumen. Clara (1924) had previously found a lumen in the islets of birds. Lucas also found intranuclear inclusions in the islands of the White Leghorn chicken. They first appeared in birds of 30 days and were present in 75 per cent

of those between the ages of 31 to 40 days. By the time the birds had reached 101 days or more, 99.4 per cent of them exhibited inclusion bodies. He found no relation to sex, lymphomatosis, or other possible causes.

Oakberg (1949) made a study of the ratio of pancreas weight to body weight and determined the number of islets in different areas in various aged White Leghorn chickens. He confirmed the observations of Nagelschmidt (1939) and Miller (1942) that there were two types of islets in birds, one "dark" composed of alpha and delta cells, the other "clear" made up of beta and delta cells. Miller made his observations on the pigeon pancreas. Oakberg (1949) found from 150 alpha islets at one day to 2,000 at 100 days and 3,500 beta islets at one day to 40,000 at 300 days regardless of sex. More alpha islets were present in the proximal portion of the body of the pancreas. Beta islets were distributed throughout. Alpha islets were larger in males. In the splenic lobe both types of islets were larger than in the body of the pancreas. Clausen (1953) in studying the phylogeny of the islet of Langerhans found two types of islets in birds, clear islands of the regular type and dark islands which are specialized organs similar to "Gangorgane," a secondary island found in some lower forms. Chodnik (1947 and 1948) made a study of the relation of zymogen granules, Golgi material, and mitochondria to the physiological activity of the pancreas cells. Zietschmann (1911), Krause (1922), and Bradley and Grahame (1951) found few centro-acinar cells, while Pugnat (1897) stated that there were no centro-acinar cells. According to Pugnat, the pancreatic cell was small. Batt found basket cells forming a reticulum about the acinar cells. Zietschmann described scant elastic tissue between the gland tubes.

Zietschmann (1911) stated that the pancreatic ducts were similar in structure to the bile ducts. Batt (1926) mentioned a simple columnar epithelium lining the main duct and involuntary muscle fibers in its walls.

Bursa Cloacae

The bursa cloacae (bursa of Fabricius) has given rise to much speculation in regard to its function. According to Retterer and Lelièvre (1913b), it had previously been given the names: egg reservoir, third caecum, anal gland, anal pouch, urinary vessel, bladder, genital apparatus, seminal vesicle, prostate, Cowper's

gland, and one author even described it as a pouch characteristic of the female which received the sperm of the male. Microscopically this organ has in general been described as having a serosa, a muscular tunic of smooth fibers, and a mucous membrane of longitudinal folds made up of a mass of lymphoid and epithelial tissue. Retterer (1885) described a thick serosa; Osawa (1911), a thin serosa; and Jolly (1915) stated that the capsule was made up of a thin connective tissue layer and a thin smooth muscle layer. Gadow (1891a) also mentioned the smooth muscle. Retterer (1885) found the exterior muscle layer longitudinal and the internal transverse, while Osawa found the opposite arrangement. Retterer (1885) stated that there might be as many as 40 to 50 follicles in a single fold. Jolly (1915) stated that there were 12 to 14 folds in the chicken.

There were two opposing views on the structure of the follicle: one that there was a connective tissue network and blood vessels in the medullary portion [Stieda (1880), Retterer (1885), and Osawa (1911)]; the other that connective tissue and blood vessels did not penetrate the medullary part [Wenckebach (1889 and 1896) and Schumacher (1903)]. Retterer and Lelièvre (1910a) described an abundance of elastic fibers in the "interfollicular walls."

There were some differences of opinion regarding the epithelium. Jolly (1915) mentioned only cylindrical epithelium; Schumacher stated that the epithelium varied from cuboidal and tall columnar to pseudostratified columnar; according to Osawa (1911) the epithelium was stratified with the surface layer cylindrical. Wenckebach (1889) did not find any goblet cells. Gadow (1891a) found few goblet cells in the epithelium of the bursa cloacae.

Forbes (1877) could not find a valve or flap over the opening to the bursa cloaca. Retterer (1885) stated that the posterior face of the uroanal fold overhung the opening into the bursa in the murre (*Uria aalge*).

Retterer (1893), Jolly (1910, 1911a, and 1913a), and Retterer and Lelièvre (1913a) concerned themselves chiefly with the development of the bursa cloacae. Retterer and Lelièvre (1910b and 1913b) stated that the medullary portion was of epithelial origin. According to Retterer (1885), its size at its maximum development was probably 2.5 cm. in length, 2 cm. in width, and 1.5 cm. in thickness. Jolly (1913b) stated that the beginning of

involution coincided exactly with the appearance of sexual maturity, while Riddle (1928) found involution usually complete coincident with sexual maturity. According to Kaupp (1918), Schauder (1923), Otte (1928), and Bradley and Grahame (1951), its maximum growth was reached between four and five months. Bittner (1924) compared the bursa cloacae to an acorn at five months and a hemp seed or a pea at one year. Others such as Gadow (1891a), Marschall (1895), Wiedersheim and Parker (1897), Thomson (1923), and Ward and Gallagher (1926) discussed its retrogression briefly. Jolly (1911c and 1915) wrote more in detail on the subject. On the matter of its physiological function, Boyden (1922) referred to Jolly (1911b), who ascribed to it a hematopoietic function. Jolly (1911b) and Jolly and Levin (1911) found that fasting had a rapidly degenerative effect on the bursa cloacae.

Diverticulum

The remnant of the yolk stalk was described as an appendage to the small intestine. Owen (1866), Retterer and Lelièvre (1910c), and Otte (1928) observed this diverticulum in many birds. Zietschmann (1911) stated that in all birds, except the goose, it disappeared completely after birth. Muthmann (1913) found it to remain during the entire life of the bird. Latimer (1924) and Bradley and Grahame (1951) found it to be constantly present in the chicken. Maumus (1902) stated that the cells lining the so-called third caecum were a continuation of the intestinal canal. Much lymphoid tissue was present. As age increased macrophages became numerous, the villi diminished, and the longitudinal muscle fibers near the blind end seemed to disappear little by little. Maumus made the statement that the disappearance of the muscle varied with the activity of the macrophages. Generally it began to disappear about the third month and had completely disappeared in the greater part of Gallinacea two months later.

The disappearance of the yolk sac itself was considered by Schilling and Bleecker (1928) to be almost complete by the fourteenth day. Schauder (1923) stated that it underwent involution at the sixteenth day in the chick. Latimer (1924) found the yolk sac, with one exception, up to and including the thirty-eighth day, and thereafter frequenly up to the two hundred thirty-seventh day.