THE HISTOLOGY OF THE DIGESTIVE TRACT OF THE CHIMAEROID FISH, *HYDROLAGUS COLLIEI* (LAY AND BENNETT)

by

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INTRODUCTION

Taxonomy and distribution of chimaeroids

Taxonomically the chimaeroid fishes are included in the Chordate class Chondrichthyes which is divided into the two subclasses, Elasmobranchii and Holocephali. The subclass Elasmobranchii includes the order Selachii, the sharks, and the order Batoidea, the rays. The subclass Holocephali has only one living order, Chimaerae, which includes five genera and twenty-nine species given by Bigelow and Schroeder (7, p.314-458) as follows:

Subclass Holocephali and order Chimaerae

Bathyalopex	abbreviatus (Gill), 1883.
	plumbeus (Gill), 1877.
Callorynchus	callorynchus Starks, 1906.
	capensis Dumeril
	elephantinus Gray, 1854.
	milii Bory de St. Vincent, 1823.
Chimaera	cubana Howell-Rivero, 1936.
	deani Smith and Radcliffe, 1912.
	jordani Tanaka, 1905.
	monstrosa Linnaeus, 1758.
	owstoni Tanaka, 1905.
	phantasma Jordan and Snyder, 1900.
	pseudomonstrosa Fang and Wang, 1932.
Harriotta	curtiss-jamesi Townsend and Nichols, 1925.
	raleighana Goode and Bean, 1895.
Hydrolagus	affinis (Brito Capello), 1867.
	africanus (Gilchrist), 1922.
	alberti Bigelow and Schroeder
	barbouri (Garman), 1908.
	colliei (Lay and Bennet), 1839.
	eidolon Jordan and Hubbs, 1925.

lemures Whitley, 1939.
media Garman, 1911.
mirabilis (Collott), 1904.
mitsukurii Dean, 1904.
novae-zealandiae (Fowler), 1911.
ogilbyi (Waite), 1898.
purpurescens Gilbert, 1905.
waitei Fowler, 1908.

Chimaeroids are widely distributed, with the species of *Callorhynchus*, however, limited to the southern seas and those of *Chimaera* largely to the northern. *Hydrolagus colliei* occurs only off the Pacific coast of North America from California northward.

Chimaeroids range from surface water, (*H. colliei*) to depths as great as 1,300 fathoms (*H. affinis*), the latter being the most abyssal of the Chondrichthyes (16, p.11-21).

The size range of adult chimaeroids is from 60 cm. (*H. mitsukurii*) to 175 cm. (*H. purpurescens*). *H. colliei* is about 70 cm. long in the adult, the female being slightly larger than the male (16, p.6-13).

The chimaeroids are reported to have a mixed diet, ranging from seaweeds to other fishes, including also worms, echinoderms, molluscs, and crustaceans (23).

Spawning takes place at all seasons of the year. After internal fertilization, the eggs are layed singly in capsules and the developing young remain in the egg case for nine months to one year. It is thought that the egg cases become attached to rocks or heavy sea-weed by means of their filamentous ends. The only reasonably complete account of chimaeroid life history is that of C. monstrosa written by Legendre (23;16, p.11-21).

Literature on the histology of chimaeroid fishes

Only fragmentary knowledge exists on the histology of the subclass Holocephali. The first contribution to the microscopic anatomy of a chimaeroid fish was provided by Leydig in 1851; however, micrological techniques had not advanced far enough at that time to allow a detailed study (24). The digitiform rectal gland of C. monstrosa was described by Mazza and Perugia (25). Oppel discussed some generalized features of the histology of the intestine, mouth, pancreas, and liver of chimaeroids in his treatise on comparative histology (30, vol.2, p.8-402). Neuville described the morphology of the valvular intestine of C. monstrosa in detail in 1901 (28).

In 1906 Dean published his monograph, "Chimaeroid Fishes and their Development". This work deals primarily with the embryology of chimaeroids but also includes sections of taxonomy, life history, distribution, fossil chimaeroids and an extensive bibliography (16).

The morphology of the urogenital organs of C. monstrosa was described by Burlend (10). The lateral line system was studied by Ruud (34). Morgera studied the testes and Leydig's canal in C. monstrosa (27). Craigie studied the blood vessels of the brain of H. colliei (13). The oral epithelium of C. monstrosa was described by Studnicka (36). The histology of the spleen of C. monstrosa was described by Scattizzi (35), and the gills were described by Citterio (12). Bargmann in a review of the kidneys of fish, discussed the kidney of C. monstrosa (6).

Histological features of chimaeroids were reviewed by Jacobshagen (20, vol.3, p.563-724).

Prasad described and compared the nidamental glands of H. colliei, Raja rhina and Platyrhinoides triseriatus (32). The venom apparatus of H. colliei was described by Halstead and Bunker (18).

After a thorough search of the literature, I failed to find any detailed description of the histology of the central nervous system, integument, eye, olfactory organ, heart, digestive tract, digestive glands, thymus, thyroid, pituitary, interrenal and chromaphil tissues. The digestive tract was selected for the present study because, once described, it could serve as a reference point in the investigation of the digestive glands and other studies planned for the future. The digestive tract was of particular interest because of the relatively large amount of work done on the digestive tract of other fishes and the possibility of a comparative approach in the analysis of the data.

MATERIALS AND METHODS

Twelve *Hydrolagus colliei*, five males and seven females, were captured alive in the West Sound of Orcas Island of the San Juan Archipelago by means of an otter trawl. The specimens were kept in live boxes under the dock of the Friday Harbor Laboratory of the University of Washington for about twelve hours without feeding and were then killed for dissection by injecting 10 ml. of 10% formalin directly into the brain.

The body cavity was exposed by a ventral median incision extending lengthwise from the mouth to an area immediately to the right of the anus. The heart, dorsal aorta, and dorsal and ventral gastric arteries were then injected with fixative. The entire digestive tract was carefully removed and cut into pieces which were placed into fixative. The time from injection of formalin into the brain until immersion of the tissue into fixative never exceeded five minutes.

Zenker-acetic and Bouin fixatives were used, with six hours as fixation time for Zenker-acetic tissues and twenty-four hours for Bouin tissues. Both fixatives gave good results.

Paraffin embedded sections were stained by four different methods: Harris' hematoxylin-eosin for general observations, Mallory's triple stain for collagenous fibers, Foot's method for reticular connective tissue and the MacCallum-Verhoff stain for elastic fibers.

OBSERVATIONS

Gross anatomical features

The digestive tract can be divided into five regions anatomically: the buccal cavity, pharynx, esophagus, valvular intestine, and large intestine.

The entrance to the buccal cavity is ventral and is partly covered with folds of skin which form flaps over the dental plates. The maxillary dental plates are formed by seven thick ridges joined one to another by thin, almost transparent, portions. The two solid and lateral mandibular plates meet anteriorly at the median line. The free edges of these plates are nearly vertical for about 3 mm., their buried portions extend about 14 mm. more horizontally into the buccal wall. At the level where the dental plates become buried, their internal surface is covered by a thin white buccal mucosa with low evenly distributed papillae being replaced by pronounced longitudinal folds about 10 mm. behind the mucosal margin. The folds at first give off diagonally disposed branches, but more posteriorly are mainly longitudinal.

The buccal cavity is flattened dorsoventrally and is the widest area of the digestive tract. Average measurements taken on five adult specimens were:

greatest width, 22 mm.; length from anterior margin to end of papillae, 13 mm.; length from start of folds to first gill opening, 14 mm.

The pharynx (level of first gill opening to last gill opening) is flattened dorsoventrally but less wide than the buccal cavity. There are four internal branchial openings in each ventrolateral wall. The lining of the pharynx, like that of the buccal cavity, is light bluish in color in freshly dissected specimens, with low folds branching and anastomosing in an irregular fashion. The pharynx is sharply set off posteriorly from the esophagus by a well developed mass of high longitudinal folds which marks the beginning of the latter organ. The average measurement of five adult specimens was 19 mm. from the first branchial opening to the end of the pharynx while the greatest width of the pharynx (level of first gill opening) measured 15 mm.

The tubular esophagus is bounded posteriorly by the valvular intestine. Throughout its length the mucosa is folded into high longitudinal folds which run parallel to each other without branching or anastomosis. In an average of five adult specimens the esophagus measured 25 mm. in total length and approximately 7 mm. in diameter.

The valvular intestine (spiral gut) begins anteriorly at the point where the common bile duct enters the digestive tract. The valve extends counterclockwise for two and one-half turns to the region where the most anterior point of the rectal gland is embedded. Throughout the length of the first turn and to a point midway on the second turn the intestinal mucosa, including the valvular surface, is lined by numerous papillae. Beyond this point to the end of the valvular intestine, the mucosa of the outer wall, but not the valvular surface, is developed into a series of parallel folds which run circularly across the long axis of the digestive tract. The mucosa of the spiral valve is covered on both sides by numerous papillae throughout its entire length. Measurements on five adult specimens gave averages as follows: length of the valvular intestine, 80 mm.; diameter at the widest point, 22 mm. The first turn of the spiral, resembling a cone with its apex pointed anteriorly, measured 35 mm. The second turn, also resembling a cone, oriented like the first, averaged 32 mm. long while the remaining half turn averaged 13 mm.

The large intestine begins immediately behind the valvular intestine and ends at the anus. The inner wall of the large intestine is thrown into high longitudinal folds which cover the ducts of the rectal glands. Measurements on five adult specimens gave averages as follows: total length of large intestine, 44 mm.; diameter, 7 mm. at widest region (anterior), 5 mm. at narrowest region (posterior).

Embedded in each fold of the first 15 mm. of the large intestine is one of the eleven rectal glands, each with its own duct occupying the next 18 mm. of intestinal length and emptying separately, but at the same level of the intestine, approximately 9 mm. from the anus.

The anus is anterior to the urogenital opening which in turn is just anterior to the two pairs of claspers on the male fish. The chimaeroid fish, H. colliei, does not possess a cloaca, as the exit of the digestive tract is clearly apart and distinct from that of the urogenital tract in both male and female fishes.

Microscopic anatomy

1. Buccal wall

Histologically the buccal wall can be divided into two layers; the mucosa and submucosa. The mucosa is nearly smooth with only an occasional low ridge seen in cross section. This layer makes up about one fourth to one fifth the total thickness of the buccal wall.

The epithelium consists of a basal row of columnar cells followed by several rows of cuboidal cells with a surface layer of cuboidal cells in some areas and squamous cells in others, the average number of cell layers being between 10 and 13. Sparsely scattered, large unicellular mucous glands are found in this region. A basement membrane of collagenous material is present making up a well defined horizontal line in cross-section.

Directly under the basement membrane lies a stratum compactum of dense collagenous fibers, which may be regarded as a very firm tunica propria. There are extravasated leucocytes in this region and branched melanocytes tend to be concentrated immediately under the epithelium. The collagenous fibers are mainly oriented in horizontal layers, parallel to the epithelium, about half of them at right angles to the others. These are traversed at short intervals by small bundles of perpendicular fibers which extend from the basement membrane to the deeper layers of the submucosa. Numerous sections of blood capillaries appear directly beneath the basement membrane.

The submucosa of the buccal wall is made up of loosely organized irregular connective tissue mostly comprised of collagenous and elastic fibers, and containing many pigment cells and tissue leucocytes. Small blood vessels, lymph vessels and nerve trunks permeate this region. An encapsulated mass of hemopoietic tissue lies embedded in the submucosa of the roof of the mouth, anteriorly. In its posterior region the buccal wall has added to its submucosa a deep connective tissue layer of a more dense consistency. This layer is composed of a mixture of closely set but irregularly disposed fine collagenous and elastic fibers. The submucosa takes up about one half to three fourths of the total width of the buccal wall layers.

2. Pharyngeal wall

The microscopic anatomy of the pharyngeal wall is closely similar to that of the buccal wall, consisting of two main regions; mucosa and submucosa. The epithelium contains stratified cuboidal cells, 10 to 14 cell layers thick, the cells at the surface possessing a basically appressed nucleus and a cuticular border. A few scattered, large unicellular mucous glands are present and a basement membrane is evident. The epithelium makes up one fifth to one tenth of the total thickness of the pharyngeal wall.

Directly under the basement membrane lies a dense layer of coarse collagenous fibers containing scattered pigment cells. The fibers are mainly horizontal in disposition, as in the buccal wall, and coarser and looser in organization near the submucosa. This layer makes up three tenths to one tenth of the total thickness of the pharyngeal wall.

The submucosa is made up of loose irregularly organized connective tissue comprised mainly of collagenous and elastic fibers and pigment cells. Numerous blood vessels and nerves traverse this region, lymph vessels are also found. Thymus tissue, occurring in patches, is embedded within the submucosa of the pharynx. The submucosa takes up about one half to four fifths of the total width of the pharyngeal wall layers.

3. Esophagus

The esophagus can be separated into four layers: mucosa, submucosa, muscularis externa, and serosa. The epithelium is typical stratified cuboidal, eleven to fifteen cell layers thick, the surface cells similar to those of the pharynx. A condensation of collagenous material against the epithelium constitutes a basement membrane. This layer accounts for one twelfth to one seventh of the total width of the esophageal wall.

The submucosa is comprised largely of loose irregular connective tissue. Pigment cells are numerous, often forming partial investments of blood vessels and nerve trunks. Abundant sinus-like blood vessels, lymph vessels, and nerves also traverse this region. A thin layer of circular smooth muscle cells is situated at the bottom of the submucosa, directly adjoining the inner layer of the muscularis externa, and is best developed in the caudal portion of the esophagus. This layer is one half to three fourths of the total thickness of the esophageal wall. The longitudinal folds of the inner surface of the esophagus involve both mucosa and submucosa, constituting primary folds.

The muscularis externa is two-layered and entirely composed of striated fibers. The inner layer is organized into fascicles of longitudinal fibers separated by connective tissue continuous with the submucosa and forming a thin layer between the longitudinal and outer circular fascicles of the muscle layer. Pigment cells and small blood vessels can be seen in cross section in this separating connective tissue layer. The muscularis externa is one third to one half the total width of the wall of the esophagus.

The serosa is readily divisible into an inner connective tissue layer with coarse collagenous fibers of considerable magnitude, and a bounding epithelium composed of a single layer of cuboidal cells. There are many large myelinated nerve trunks and small blood vessels traversing this region. The serosa makes up one fifteenth to one twenty-fifth of the total thickness of the esophageal wall.

4. Valvular intestine

Microscopically the valvular intestine shows four major layers; mucosa, submucosa, muscularis, and serosa. The epithelium is of tall simple columnar cells with numerous goblet cells throughout. A cuticular border is present giving the epithelium the superficial appearance of being ciliated. Infiltrated lymphocytes are common between the epithelial cells, and most numerous near the base of the epithelium. Occasional granular leucocytes are also found, having migrated into the epithelium from the underlying proprial tissue where they may frequently be seen. A number of mitotic figures are present in the epithelial layer. The epithelium makes up one twentieth to one tenth the total width of the wall of the valvular intestine. A basement membrane of collagenous material is present.

Immediately under the basement membrane lies a proprial layer of connective tissue, not sharply defined from the submucosa except for the relative absence of coarse collagenous fibers. This layer contains abundant capillary blood and lymph sinuses. Scattered smooth muscle fibers extend upward into this region from the inner circular layer of the muscularis externa, but a distinct muscularis mucosae is not formed. Extravasated leucocytes and lymphocytes are common. The mucosa, including this proprial connective tissue is thrown into closely set papillae which, however, are displaced by circular folds in the lower half of the valvular intestine, as described in a previous section. The mucosa makes up one tenth to one fifth the total width of the valvular intestine wall.

The submucosa, continuous with the proprial region above, is made up of irregularly disposed connective tissue including elastic and coarse collagenous fibers. A rich supply of blood and lymph vessels is carried in this zone, together with small non-myelinated nerve trunks. The submucosal width is one fourth to one eighth that of the entire valvular intestine wall.

The well-developed muscularis externa consists of an inner circular smooth muscle layer and an outer longitudinal one. The inner layer, as noted above, sends fibers into the proprial folds of the mucosa. A scanty amount of collagenous fibers separates the two layers. The muscularis externa takes up three eighths to one third the total width of the valvular intestine wall.

The serosa, on the outer wall, is composed of a wide connective tissue layer containing coarse collagenous fibers and a bounding epithelium of simple cuboidal cells. The connective tissue carries numerous blood vessels and nerve trunks, both myelinated and non-myelinated. Elastic fibers are conspicuous in the outermost zone of the serosal connective tissue. Pigment cells are scattered throughout this layer. The serosa is one fourth to one seventh as wide as the entire valvular intestine wall.

The spiral valve represents essentially a primary fold of the internal wall, involving mucosa, submucosa, and smooth muscle tissue from the circular layer of the muscularis externa. The surface of the spiral valve is developed, like that of the outer intestinal wall, into papillae. The muscle tissue, however, contrary to its disposition in the outer wall, is developed into a distinct muscularis mucosae divisible into two well-defined layers, perpendicular to each other, inner circular and outer longitudinal in disposition. The submucosal core of the spiral valve carries blood vessels and nerves, as in the outer wall.

5. Large intestine

The wall of the large intestine shows the usual division into mucosa, submucosa, muscularis externa and serosa. Its interior wall is thrown into longitudinal primary folds, involving the mucosal and submucosal portions. The mucosal epithelium is of stratified cuboidal type, mostly eight to ten cell layers thick, with a surface made up of a conspicuous single layer of mucous cells. The nucleus of these mucous cells is closely appressed against the base of the cell, and the free margin shows a striated border. The cells immediately beneath frequently show considerable compression, even approaching squamous character. Large goblet cells are not infrequent within the epithelium. In the lower fourth of the large intestine (below entrance of rectal gland ducts), the top layer of mucous cells is less well developed and goblet cells are few, except near the anal junction.

The epithelium is infiltrated with occasional lymphocytes and granular leucocytes. Occasional mitotic figures appear in the deeper layers. The epithelium represents one tenth to one seventeenth of the total width of the large intestine wall.

Immediately under the epithelium is a dense layer of collagenous fibers running mostly parallel to the epithelium. Extravasated leucocytes and lymphocytes are found in this region. This layer is about as thick as the epithelium.

The submucosa, continuous with the above region, is made up of loose irregularly organized connective tissue composed mainly of collagenous fibers and a lesser amount of elastic fibers. Extravasated leucocytes are present and the layer is traversed by abundant small blood and lymph vessels as well as small nerve trunks. Bundles of longitudinal smooth muscle fibers lie deeply embedded in the submucosa of the primary folds. The prominent rectal glands and their ducts, which also are situated in the submucosa, will be separately described below. In width, the submucosa constitutes two thirds to three fourths the total width of the large intestinal wall in the region containing the rectal glands, and one fifth to one fourth the total width of the wall posterior to the rectal glands.

The muscularis externa is made up of two main layers of smooth muscle; a wide inner circular layer and a more compact outer longitudinal layer. The circular layer is considerably interspersed by connective tissue, giving it a loosely constructed appearance, and is further separated from the longitudinal layer by a zone of connective tissue carrying blood vessels and nerves. Coarse elastic fibers traverse the circular muscle layer perpendicularly, extending radially from the submucosa to the serosa, and investing the bundles of longitudinal muscle, as seen in cross section. This layer makes up one half to three eighths the total width of the large intestine wall.

The serosa is composed of a thin layer of thick collagenous fibers and a border epithelium of simple cuboidal cells. The serosa is one eighth to one tenth as wide as the entire large intestine wall.

The entero-integumental junction is characterized by a decrease in the height of the stratified cuboidal epithelium, going from about ten to about four cell layers in thickness, and a displacement of the submucosa by a coarsely fibrous corium.

The rectal glands, consisting of eleven separate units, each with its own duct emptying separately into the large intestine, lies embedded in the submucosa. Each unit is essentially a compound tubular gland, divisible into lobules. A cross-section of the large intestine will show several of these lobules, including secretory tubules and ducts. The submucosal connective tissue is lightly compacted about and between the lobules to form capsular tissue, and extends into the lobules to form delicate strands of intertubular connective tissue and an investment of the ducts.

The secretory tubules are lined by simple cuboidal epithelium. The simple epithelium of the ducts consists of tall cells containing numerous goblet cells. The ducts are uniform in construction throughout their length and, at the point where they empty into the large intestine, a sharp demarkation between the simple columnar epithelium of the ducts and the stratified cuboidal epithelium of the intestine wall exists.

DISCUSSION

The chimaeroids are regarded by Dean as a highly modified group descended from selachian ancestors during the Devonian period, from evidence supplied by embryological and paleontological studies (16, p.150-156). The two closest living relatives of the Holocephali are, therefore, the Elasmobranchii and the Osteichthyes, both of them selachian derivatives. By comparing the anatomy of the digestive tract of the three groups it may perhaps be possible to make further speculations regarding their relationships.

Adaptive modifications of the alimentary tract to the nature of food or feeding habits of fishes is another factor requiring consideration and has been the subject of many recent studies. Such studies include those of Blake (8;9) on two predaceous fish, _Centropristes striatus_ and _Prionotus carolinus_; Rogick (33) on the herbivorous minnow, _Campostoma anomalum_; Jacobsen (19) on the rat-tail, _Coelorhynchus carminatus_; Curry (14) on the common carp, _Cyprinus carpio communis_; Chan (11) on the deep-water gurnard, _Peristedion longispatha_; and Al-Hussaini (1;2;3;4;5) on the anatomy and histology of the digestive tracts of numerous marine and fresh-water teleosts.

The histology of the digestive tract of _Torpedo_ _ocellata_ was described by Krause (22, p.729-736) and that of other elasmobranchs by Pernkopf, Lehner, and Jacobshagen (31;20). A partial description of the digestive tract of the elasmobranchs is given by Kendall (21, p.190-194).

The intestine of fishes shows many variations and adaptations but in the vast majority of Osteichthyes and in the elasmobranchs the mouth is followed in succession by a pharynx, esophagus, stomach, intestine, and a rectum.

Mucus-secreting cells are found in the mouth of all fishes while in the bony fishes there are also taste buds. Placoid scales occur in the mouth and pharynx of the elasmobranchs. The mouth possesses no salivary glands in fishes as it does in the terrestrial vertebrates.

The internal walls of the pharynx are perforated by branchial clefts in all fishes and externally these clefts are covered by an operculum in bony fishes, by a flap of skin in chimaeroids, and are exposed in elasmobranchs. The same generalizations made concerning the glands and special structures of the mouth hold true for the inner wall of the pharynx. In the elasmobranchs, spiracles open into this region.

The esophogeal walls contain thymus tissue and hemopoietic tissue in the elasmobranchs, thymus tissue in _H_. _colliei_, and neither in teleosts. Unicellular mucous glands abound in all three groups, but multicellular glands are not reported.

No stomach is present in _H_. _colliei_ nor is one present in a large number of higher teleosts. In those teleosts having a stomach, this is always accompanied by blind tube-like sacs, the pyloric caeca. These may be very numerous or few in number. All elasmobranchs studied possess a stomach but no pyloric caeca. In the grey mullet, and in the hickory shad a true gizzard is developed (29, p.169). In fishes possessing a spiral valve a duodenum is usually present between the stomach and the valvular intestine, but no duodenum is present in _H_. _colliei_.

In many carnivorous teleosts the intestine is straight or thrown into one or two simple loops, but in herbivorous and bottom-feeding teleosts it is exceedingly long and coiled. As reviewed below, some teleosts and all ganoids possess a weakly developed valvular intestine.

The spiral valve reaches its maximum development in the elasmobranchs. The number of turns varies greatly in different species, from forty-five in _Alopias_, the thresher shark, to four in _Prionace_, the cub shark (15, p.140). A spiral valve is found in the sturgeons (Acipenser), bichirs (Polypterus), lung-fishes (Dipneusti), bow-fins (Amia), and vestiges of a spiral valve are found in some salmonids (31). A spiral valve is reported to be present in the teleosts Chirocentrus and Gymnarchus (17), but is absent in all the higher teleosts. H. colliei has a poorly developed spiral valve of two and one half turns as previously described. Histologically, the valvular intestine of H. colliei differs from that of Torpedo ocellata in that the longitudinal muscle layer of the outer wall is much better developed in H. colliei. The muscularis mucosae is present in both the outer wall and in the wall of the valve proper in T. ocellata (22, p.729-736) but is present only in the wall of the valve in H. colliei.

In the elasmobranchs and lung-fishes the rectum opens into a cloaca, which also receives ducts from the reproductive organs and kidneys but in the chimaeroids and all the remaining Osteichthyes it opens by the anus, which lies in front of the excretory and reproductive openings. The embedded rectal glands and ducts in the submucosa of H. colliei comprise the only marked histological feature absent in other fishes.

The rectal gland is present only in elasmobranchs and chimaeroids but in elasmobranchs it is always an extrinsic organ surrounded by a fibromuscular capsule, whereas in *H. colliei* it is a complex of eleven separate glands embedded within the large intestinal wall. The parenchymal cells of both types are closely similar.

An attempt to correlate the structure of the alimentary canal with the feeding habits of fishes must be tempered with a consideration of how much the differences between distantly related species can be attributed to inherited phylogenetic factors and how much can be attributed to adaptive modifications. In a study of the histology of the digestive tract of the three closely related species, the mirror carp, *Cyprinus carpio*, the roach, *Rutilus rutilus*, and the gudgeon, *Gobio gobio*, the first being mainly herbivorous, the second omnivorous, and the third mainly carnivorous, Al-Hussaini (1) found very little difference in structure except for slight differences in numbers of taste buds and in intestinal length, but not in absorptive area when related to the weight of the fish. All three fishes were found to be stomachless.

The mouth of *H. colliei* is ventral and subterminal probably indicating that much of its food is gathered off the bottom. The dental plates, previously described, seem well adapted for shearing or cracking hard objects such as molluscs or sea urchins, reported to be a part of their diet (16, p.1-21;23).

The relatively short, straight intestine of H. colliei suggests a mainly carnivorous feeding habit but the data on the food habits of this fish indicate that it is in the main omnivorous (23).

From the digestive tract data gathered in this study, H. colliei must be considered, from an anatomical standpoint, much modified in relation to the elasmobranchs. The modifications include a reduction of the spiral valve, embedded rectal gland, presence of an anus, absence of a stomach and duodenum, and absence of any scales in the oral or pharyngeal wall. Nonetheless, they are more closely related in general features to the elasmobranchs and ganoids than to the teleosts. The similarities which it bears to the teleosts (absence of stomach, reduction of spiral valve, absence of cloaca) may be considered secondarily developed characteristics and do not establish H. colliei as a transitional form but more as an example of convergent development with the teleosts which suggests an early split between the ancestral elasmobranchs and ancestral chimaeroid forms.

SUMMARY AND CONCLUSIONS

1. The digestive tract of *H. colliei* was studied both macroscopically and microscopically.

2. The digestive tract was divided into five regions anatomically: the buccal cavity, pharynx, esophagus, valvular intestine and large intestine.

a. The buccal mucosa is composed of stratified cuboidal epithelium containing large unicellular mucous glands and is underlain by a stratum compactum and a submucosa of loose irregular connective tissue.

b. The pharyngeal wall is identical to the buccal wall except that patches of thymus tissue are embedded in the submucosa.

c. The wall of the esophagus is composed of a mucosa of stratified cuboidal epithelium. Underlying the mucosa is a submucosa of loose irregular connective tissue, a muscularis externa entirely of striated fibers organized into inner longitudinal and outer circular layers and a serosa.

d. The mucosa of the valvular intestine consists of a simple columnar epithelium and an underlying tunica propria. Beneath this layer is a submucosa of loose irregular connective tissue, a muscularis externa of inner circular and outer longitudinal smooth muscle layers and a serosa. The spiral valve, essentially a primary fold of the valvular intestinal wall, possesses the above described mucosa, submucosa, and in addition, a distinct muscularis mucosa is present.

e. The large intestinal wall features a mucosa of stratified cuboidal epithelium containing mucous cells, a submucosa of loose irregular connective tissue, a muscularis externa composed of a wide inner circular layer and a more compact outer longitudinal layer of smooth muscle and a serosa.

f. Rectal glands, consisting of eleven separate units embedded in the submucosa of the large intestine are described.

3. By comparing the digestive tract of H. colliei with those of teleosts, ganoids, and elasmobranchs it is concluded that the chimaeroids are probably a highly modified group which has long been separated from primitive selachian stock.

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APPENDIX

EXPLANATION OF PLATES

Plate I

Figure 1. Digestive tract, pancreas (white) and spleen (dark).

Figure 2. Buccal cavity, pharynx and esophagus.

Plate II

Figure 1. Longitudinal section of the buccal roof showing large hemopoetic organ (dark mass). 180x.

Figure 2. Epithelium of buccal wall showing large unicellular mucous glands. 525x.

Plate III

Figure 1. Longitudinal section of pharyngeal roof showing patches of thymus tissue in the submucosa. 180x.

Figure 2. Cross section of esophagus showing high longitudinal folds. 15.5x.

Plate IV

Figure 1. Cross section of the esophageal wall showing mucosa, submucosa and muscularis externa. 630x.

Figure 2. Valvular intestine.

Plate V

Figure 1. Cross section of valvular intestine showing the relationship between the spiral valve and the outer wall. 14.3x.

Figure 2. Valvular intestine, large intestine and anus.

Plate VI

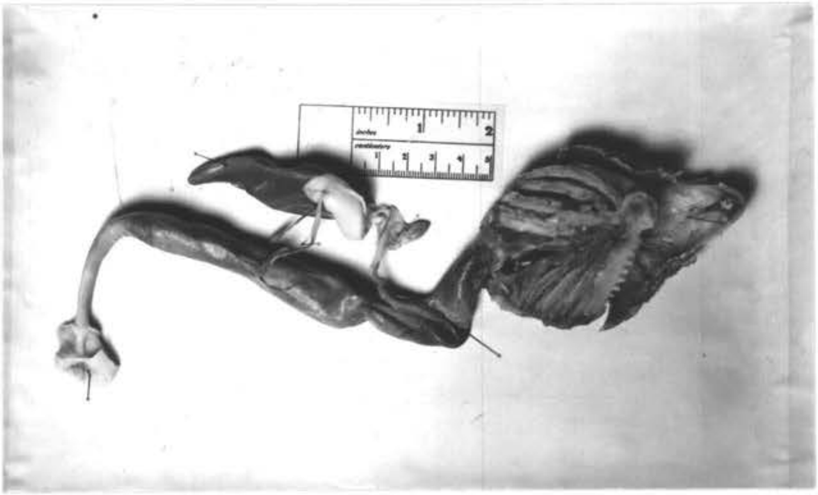
Figure 1. Cross section anteriorly of the large intestine showing rectal glands embedded in the submucosa. 9.2x.

Figure 2. Cross section posteriorly of the large intestine showing rectal glands and ducts. 9.2x.

Plate VII

Figure 1. Rectal glands.

Figure 2. Cross section of rectal glands and duct. 180x.



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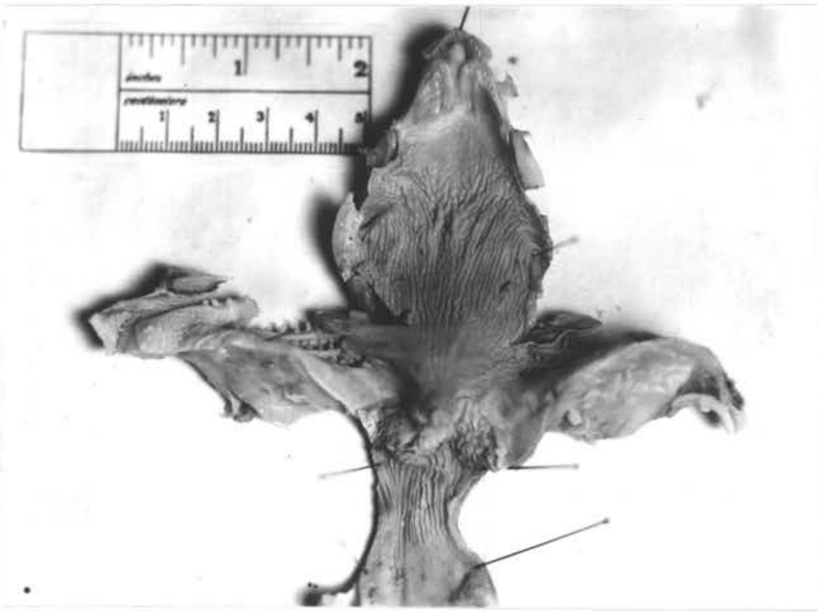

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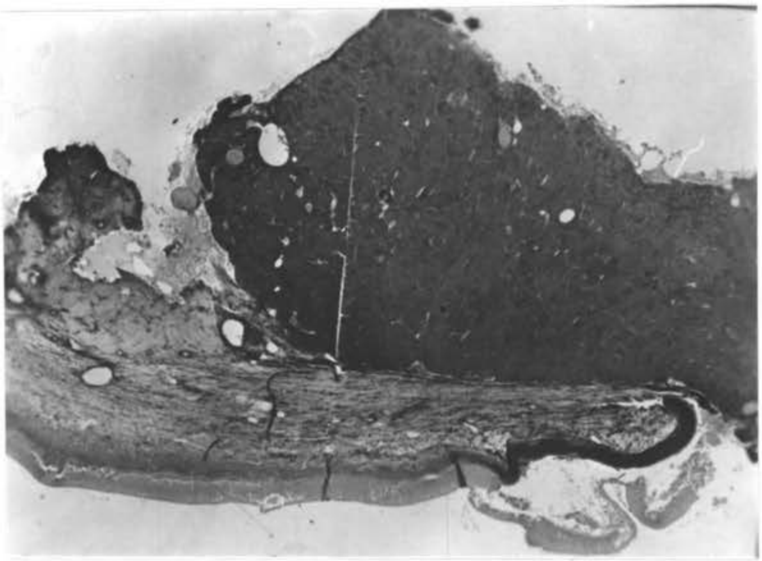

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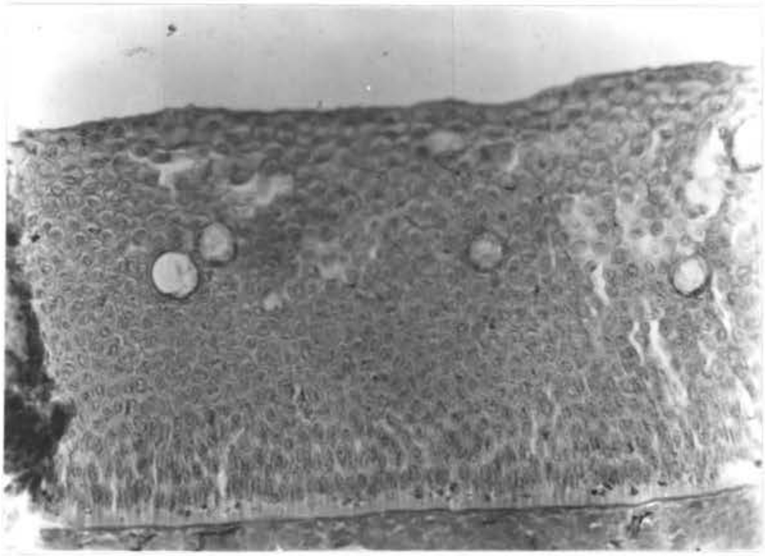

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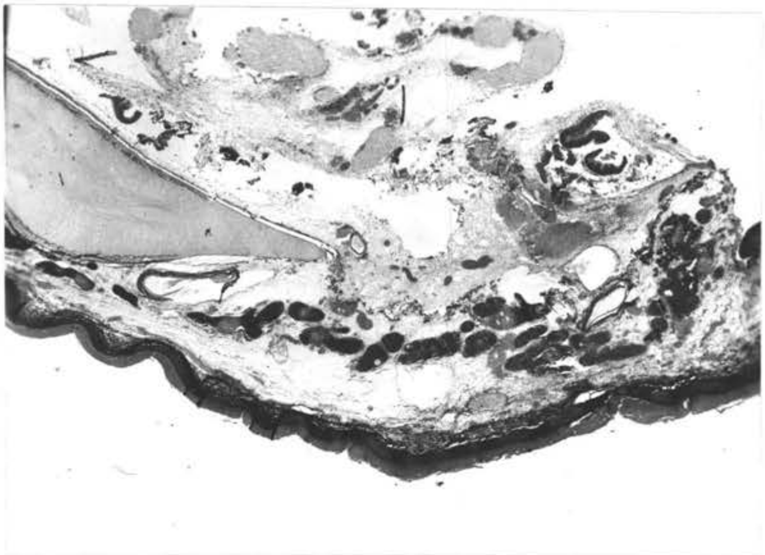

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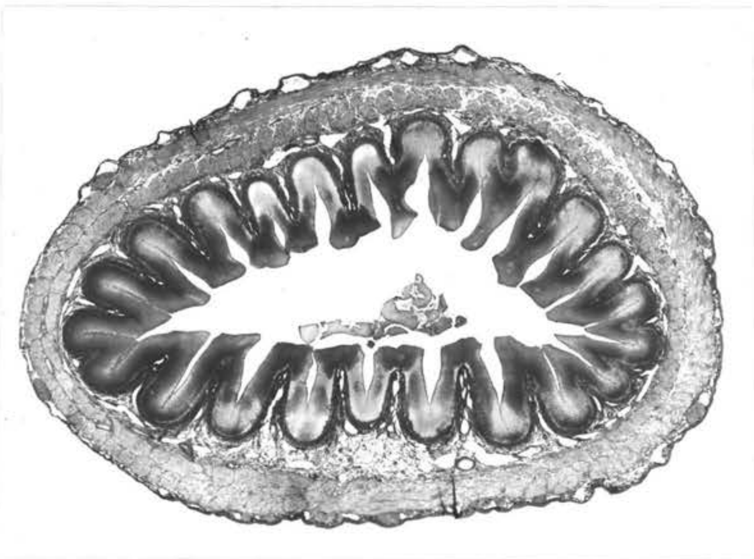

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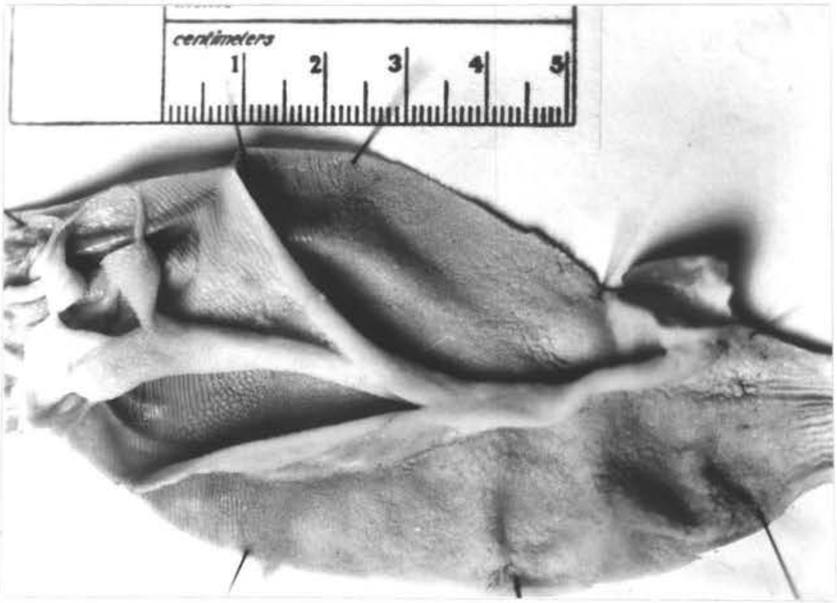

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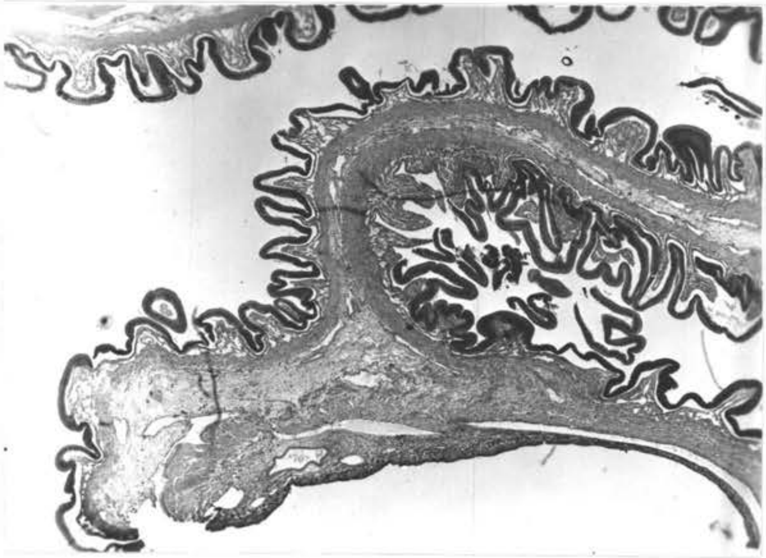

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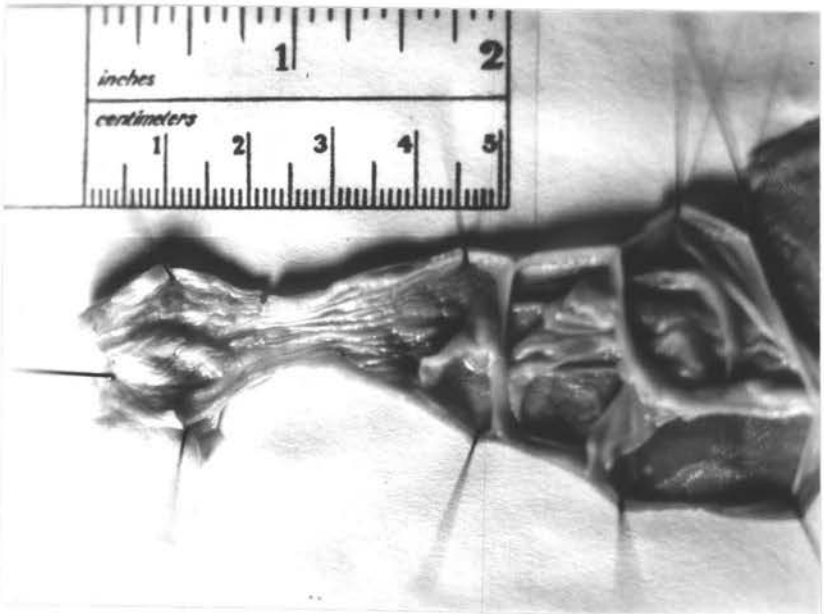

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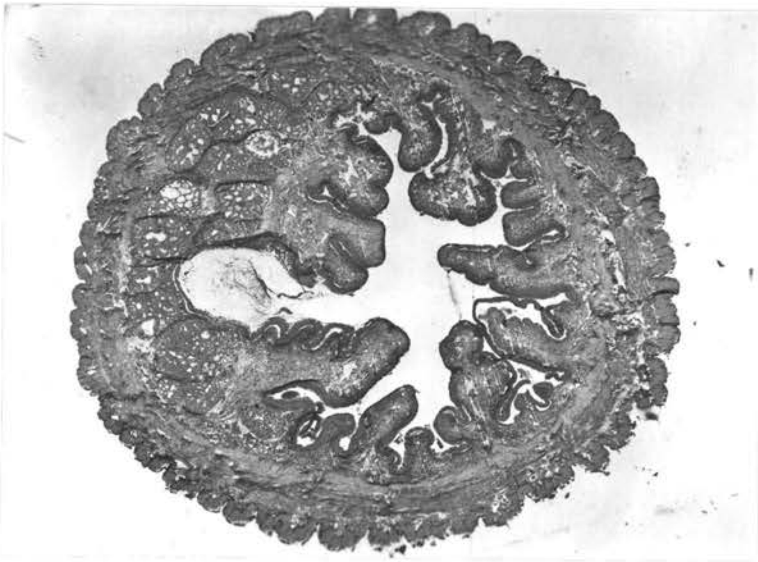

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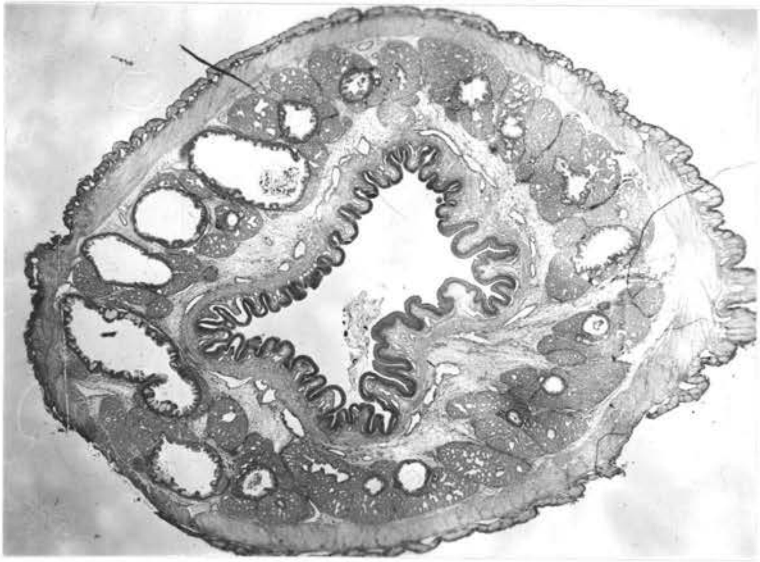

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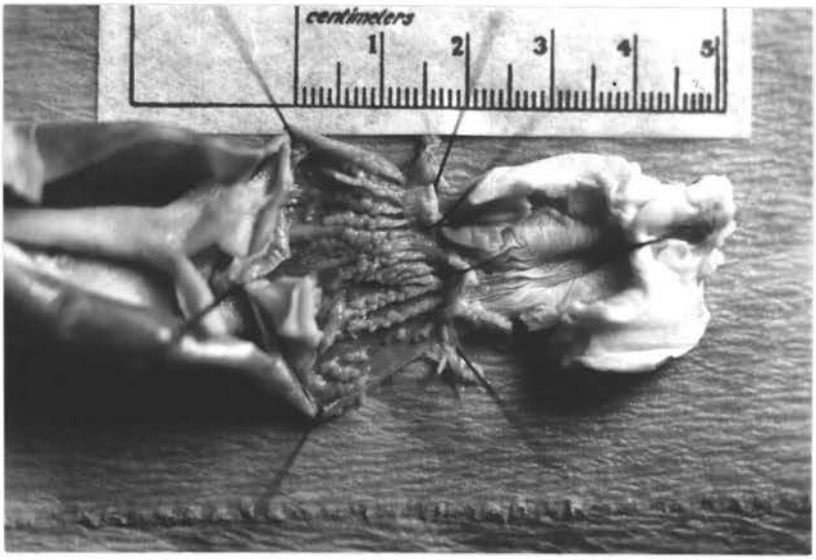

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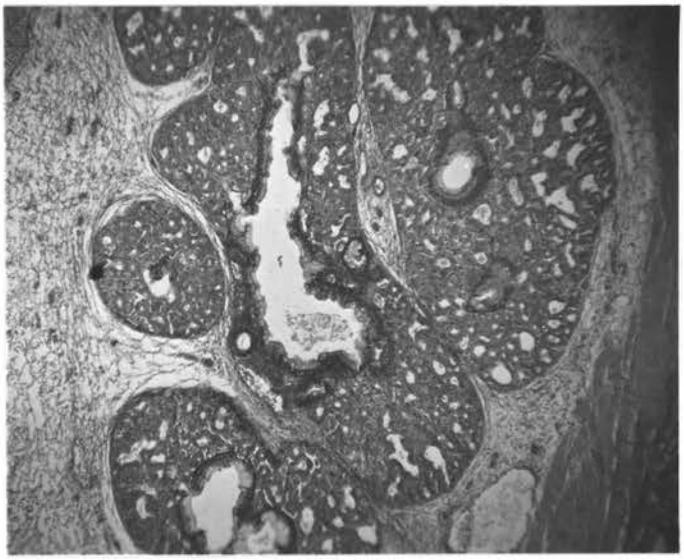

Figure 2