CHAPTER V

THE DIGESTIVE SYSTEM

The Oral Cavity

THE *mouth* in the Crocodilia is large, as is well known, and may be opened very wide. It is bounded anteriorly and laterally by the teeth of the two jaws; these teeth were described in connection with the skull. The mucous membrane of the roof of the mouth and of the dorsum of the tongue, especially the former, exhibits numerous small papillæ (see page 160), and among these, in the posterior region of the mouth, are the ducts of mucous glands.

The *tongue* extends from just back of the mandibular symphysis to the glottis. It is attached throughout its entire ventral side except for a short distance at its tip, so that it may be elevated and depressed but not protruded. Among the papillæ on its dorsal surface are sense organs, said to be tactile and gustatory corpuscles (see page 165). The posterior margin of the tongue is elevated as a transverse fold that meets a corre-

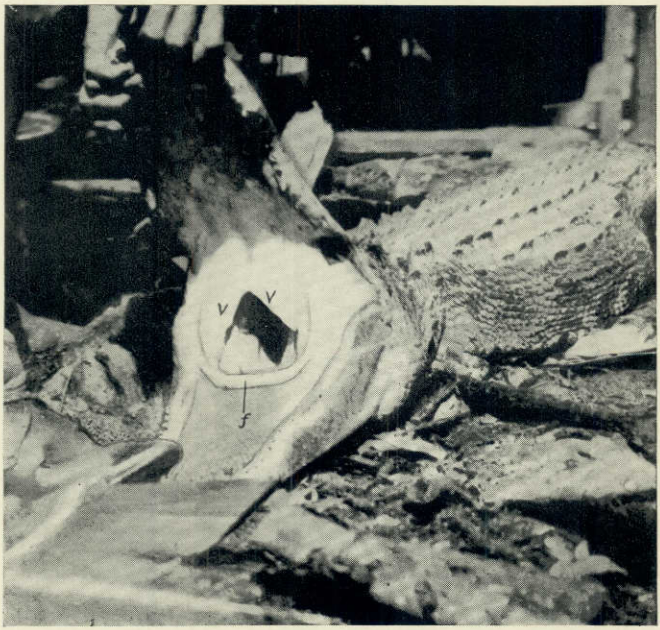

FIG. 33. INTERIOR OF THE MOUTH OF A. MISSISSIPPIENSIS

f, transverse fold at the base of the tongue; *v,v*, velum palatinum.

sponding fold, the *velum palatinum*, from the lower side of the palate and completely shuts off the mouth from the openings of the trachea and gullet (Fig. 33). Into this hinder chamber open the posterior nares, so that the animal can open its mouth under water without getting water into its trachea; or it may, while holding its prey in its mouth, come to the surface to breathe, without danger of letting water into its trachea. The nasal passages, leading from the nostrils to the posterior nares, are, of course, completely inclosed by bone, as described in connection with the skull. Ventral to the larynx and posterior part of the mouth is the large, shield-shaped hyoid apparatus, Fig. 25, h, also described in connection with the skull.

The Œsophagus

The œsophagus, Fig. 34, *e*, is long and of about the same diameter throughout except possibly for a slight enlargement of the anterior region where it leaves the pharynx. The two "olivary enlargements" mentioned by Chaffanjon (15) are not always present, and when seen were found to contain either food or small stones or both.

The outside of the œsophagus is smooth and muscular while the lining is thrown into numerous longitudinal folds that in the empty œsophagus nearly obliterate the lumen; where distended by food or pebbles the longitudinal folds may be almost

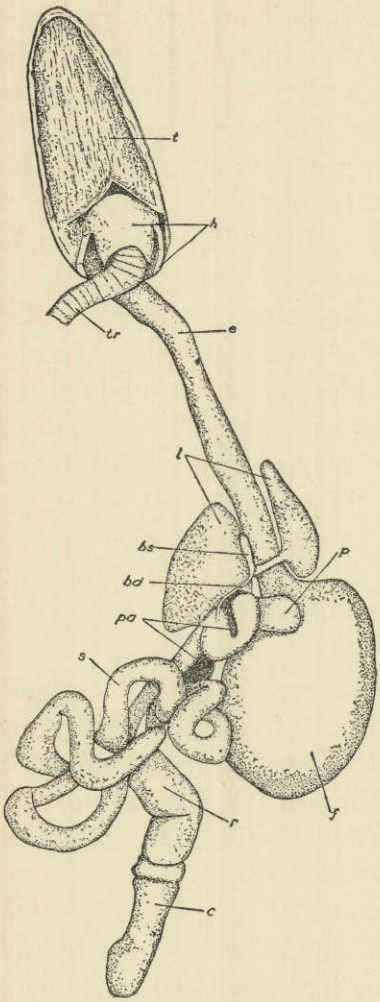

FIG. 34. DIGESTIVE SYSTEM OF A MISSISSIPPIENSIS.

bd, bile duct; *bs*, bile sac; *c*, cloaca; *e*, œsophagus; *f*, larger or fundic region of stomach; *h*, hyoid apparatus; *l*, liver; *p*, smaller or pyloric region of the stomach; *pa*, pancreas; *r*, rectum; *s*, small intestine; *t*, tongue; *tr*, trachea.

obliterated. In a thirty-inch animal the œsophagus is about six inches long, and opens suddenly, but without any apparent valve, into the large chamber of the stomach. The histology of the œsophagus and the other regions of the digestive tract will be described later.

THE STOMACH

The stomach, as is well known, is made up of two distinct parts; that on the animal's left, into which the œsophagus opens, is many times larger than the part from which the small intestine leads. The larger or *fundic region*, Fig. 34, *f*, has, as will be described, very heavy muscular

walls. When empty the lining of this part of the stomach is thrown into a few comparatively large folds, but when greatly distended with food, as it sometimes is, the internal folds are completely obliterated and the muscular layers are stretched until they have scarcely an eighth of their original thickness. In Figure 34 the stomach is considerably distended.

The large region of the stomach frequently contains a number of stones, and for that reason, probably, is sometimes spoken of as the gizzard. In one thirty-inch alligator fourteen pebbles of irregular shape, varying in largest diameter from four to seventeen mm. and aggregating six grams in weight, were found. Voeltzkow (78) says that gastroliths of two to three cm. diameter are found in the stomach of the adult Madagascar crocodile.

Neither the transverse fold nor the smooth, lateral disks (or shields) described by Chaffanjon could be seen in either the empty or in the distended stomach.

The *smaller part* of the stomach, Fig. 34, *p*, lies to the right and somewhat ventrad to the anterior region of the larger part, near the entrance to the œsophagus. It connects by a fairly large opening with the larger part of the stomach, and by a smaller opening with the duodenum. The former opening apparently has no valve, unless it be a slight sphincter muscle; the latter is guarded by

a pair of thickened lips, called by Chaffanjon "semilunar valves."

The walls of the smaller part of the stomach are, as might be expected, much thinner than those of the larger region, but they are proportionately fairly thick and are internally thrown into numerous folds.

The Intestine

In the intestine three regions may be distinguished: a long, considerably coiled small intestine; a wide, nearly straight rectum; and a short, wide cloaca.

The *small intestine*, Fig. 34, *s*, is of moderate and rather uniform diameter, though somewhat thicker near the stomach, and is not coiled so extensively as figured by Chaffanjon. Near the stomach it receives the ducts of the liver and pancreas. The bile duct, Fig. 34, *bd*, is a continuation of an elongated bile sac, *bs*, which lies between the large right and smaller left lobes of the liver, *l*. The two main lobes of the liver, which appear smaller than in reality because of foreshortening in drawing, are connected, across the base of the œsophagus, by a narrow transverse band.

The pancreas, *pa*, which is of fair size, lies partly dorsal to and partly in a narrow loop of the intestine, so that it is not very evident in a ventral view of the animal.

The small intestine has heavy muscular walls whose histological structure will be described elsewhere. It opens abruptly, without any indication of a cæcum, into the large intestine or rectum.

The *rectum*, *r*, is of about twice the diameter of the small intestine, though this, of course, varies with the amount of fecal matter it contains; it is nearly straight and possesses much thinner walls than the small intestine, though this, again, varies with the state of collapse or distention.

At the posterior end of the rectum is a heavy sphincter valve separating that part of the intestine from the cloaca.

The *cloaca*, *c*, is widest anteriorly where it is about as wide as the rectum; it gradually diminishes in diameter caudad, and appears flattened laterally. Its wall has the same general structure as the rectum, as will be described below. The mucous membrane posterior to the openings of the genital ducts is thrown into a more or less complete, ring-like transverse fold (Fig. 55 G.). In some species there may be a second, half-ring-like fold in the dorsal wall caudad to the more complete ring. The cloaca is divided by this fold into a larger anterior portion, g, and a shorter posterior portion, h; in the former the mucous membrane is thrown into a large number of small folds that in places form a network; in the latter the mucous membrane has a hard, thick epithelium, with a smooth surface and only a few longitudinal folds.

The *ureters* open, Fig. 55, *d*, *e*, at a moderate distance from each other, into the anterior region of the cloaca (about where the dorsal and lateral walls of this region come together). The *genital ducts* (oviducts or vasa deferentia), *c*, *f*, on the other hand, open close together through the ventral wall of the posterior half of the cloaca, just in front of the copulatory organ.

Into the cloaca, very near the anus, open two glands of fairly large size that Rathke called *musk glands*. These glands lie outside of the pelvis between the side walls of the cloaca and a large muscle that surrounds this part of the body. They have an oval form and open usually from their anterior end, sometimes just caudad to this, by a short, fairly wide, slit-like opening which has an anteroposterior direction. The walls of the glands are made up of three closely associated layers of connective tissue, the inner one being thrown into folds. Since these layers contain no muscle fibers the secretion of the gland is probably squeezed out by contraction of the circular muscles of the cloaca. Usually the cloacal glands are stretched full by a thick, yellowish mass that smells strongly of musk.

The part of the cloaca caudad to the pelvic opening has a differently arranged musculature from the more anterior region. It consists of two separate pairs of striped muscles that surround the musk glands on the outer side. The first

pair form a fairly broad, moderately thick ring muscle next to the anus that is attached anteriorly to the pubis and posteriorly to the second hæmal process. When these muscles draw together they narrow or completely close the anal slit. The muscles of the other pair are broader but thinner, and extend in a general dorso-ventral direction. Anteriorly, above the cloaca, they are united with each other, but posteriorly they separate and, with the above ring muscle, are inserted on the second hæmal arch. Judging from their attachment they widen the anal opening laterally.

The Histology of the Enteron of the Florida Alligator

It has long been known that the sea lamprey, *Petromyzon marinus*, during the spawning season, when the body is distended with eggs, takes no food, and that the digestive tract during this period shrivels up until it is reduced to a mere thread. This condition doubtless obtains in other forms as well, though it has not been actually observed by the writer elsewhere.

A number of small alligators that were kept alive in the laboratory for a year or more caused the writer to wonder whether any very marked change had taken place in their digestive tracts during the months they took no food.

In captivity, especially if the water in their tank

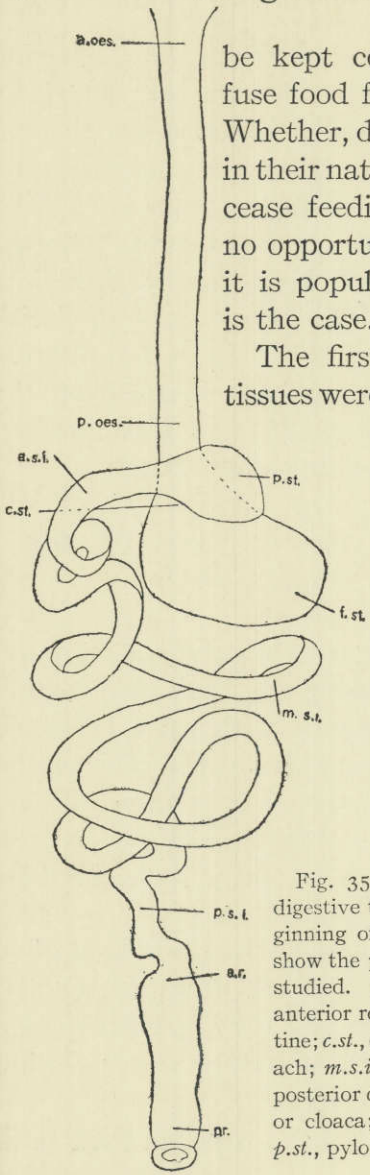

FIG. 35. OUTLINE OF DIGESTIVE TRACT

be kept cold, alligators may refuse food for five or sixth months. Whether, during the winter months, in their native haunts, they entirely cease feeding, the writer has had no opportunity to observe, though it is popularly reported that such is the case.

The first alligator from which tissues were taken was about a year and a half old, and measured eighteen inches in length. It was killed in March after a fast of several months, probably four or five, possibly more, though it was not in the writer's possession for so long a time.

Although carefully

Fig. 35. A diagrammatic outline of the digestive tract of the alligator from the beginning of the œsophagus to the cloaca, to show the planes of the sections that were studied. *a.oes.*, anterior œsophagus; *a.r.*, anterior rectum; *a.s.i.*, anterior small intestine; *c.st.*, cardiac stomach; *f.st.*, fundic stomach; *m.s.i.*, middle small intestine; *p.oes.*, posterior œsophagus; *p.r.*, posterior rectum or cloaca; *p.s.i.*, posterior small intestine; *p.st.*, pyloric stomach.

fixed in the usual fluids, the epithelial structures from this animal were not as clearly defined in most cases as could be desired; this rather unsatisfactory fixation may have been due to some physiological condition characteristic of the period of hibernation. That this was the case seems likely from the better fixation obtained by the same methods in the case of animals killed during the feeding season.

The other animals from which tissues were taken were considerably smaller than the one mentioned above. They were killed early in the fall, after having been fed regularly for about five months upon bits of meat, both raw and cooked.

The Tongue. The covering of the tongue was studied in two regions, near the free end, and towards the base.

A section of the former region, drawn under high power, is shown in Figure 36. It consists of a dense mass of fibrous tissue, *a*, and small scattered cells, overlaid by a stratified epithelium of eight or ten layers. Only a small part of the fibrous base, just beneath the epithelium, is here shown. It is a dense areolar tissue with the elastic fibers apparently predominating.

The epithelium, *e*, consists, as has just been said, of about eight or ten layers of cells, those at the base being generally cuboidal in shape, while towards the surface the cells become more and more flattened until at the surface they form

a thick horny layer, *h*, in which no nuclei can be seen. The cells of the horny layer are flattened into mere fibers, which, at places, are seen projecting from the surface. The boundary between the horny cells and those beneath is quite distinct, though perhaps not quite so sharp as shown in the figure under discussion.

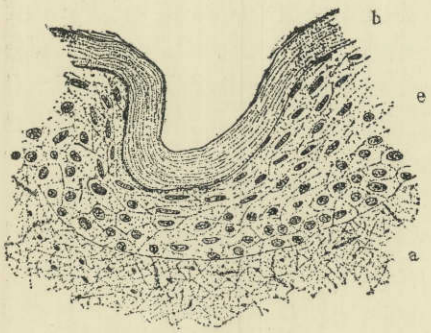

FIG. 36. The covering of the anterior region of the tongue of the hibernating animal, under fairly high magnification; the plane of this section is not shown in Figure 35; *a*, areolar tissue; *e*, epithelium; *h*, horny layer of epithelium.

In a previous paper, the writer noted that the dorsum of the tongue is covered with small, evenly distributed papillæ, easily seen by aid of a hand lens. These so-called papillæ are here seen to be hardly papillæ at all, but small folds or wrinkles, although the epithelium is somewhat thickened at intervals. No glands are to be seen in this region of the tongue.

The only difference between the anterior region of the tongue during hibernation and during the feeding season seems to be in the scaly layer of the epithelium. Instead of the compact, sharply differentiated layer of scaly cells seen in Figure 36,

the anterior region of the tongue during feeding is covered with a layer of rather loose, scaly cells, in most of which the nuclei may be seen. No difference in the amount of sloughing off can be noticed as is the case with the epithelium of the roof of the mouth.

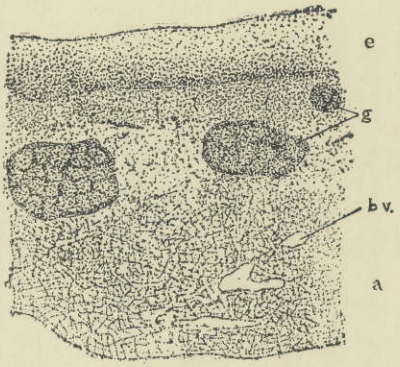

FIG. 37. Covering of the posterior region of the tongue of the hibernating animal showing glands, under low magnification; *a*, areolar tissue; *bv*, blood-vessels; *g*, glands; *e*, epithelium.

Figure 37 represents a section, under very low magnification, of the covering of the base of the tongue. The areolar tissue, *a*, is about the same as in the preceding section, except that it is more compact just under the epithelium than it is in its deeper regions. It seems also more vascular than in the preceding section.

The epithelium, *e*, is of the stratified squamous variety, but consists of many more layers of cells than in the preceding section and is hence several times as thick. While its cells are flattened towards the surface, after the manner of this kind of epithelium, they do not form the definite horny layer described above.

The most marked difference between the two regions of the tongue is the presence, in the posterior or basal region, of numerous glands, *g*, probably mucous- or slime-secreting. They are thickly

FIG. 38. One of the glands from the posterior region of the tongue of the hibernating animal, under high magnification; *a*, areolar tissue; *av*, alveolus.

scattered through the areolar base, close beneath the epithelium. Two large glands and one small one are shown in the figure under discussion. Each gland opens to the surface by an apparently wide duct, but since no good section of such a duct was obtained it is not shown in the figure. Although the rest of the tissue was well preserved

and showed cell structure clearly, it was with difficulty that the details of the glands could be determined.

A high-power drawing of a portion of one of the glands is shown in Figure 38. The large alveolus, *av*, to the left, is from the peripheral region of the gland and is surrounded, on its free side, by the areolar tissue described above. The inter-alveolar spaces, which are somewhat exaggerated in the figure, are filled with fibers which are arranged more or less in layers and hence appears different from the surrounding areolar tissue. The alveoli are circular or elongated in section, and have fairly wide lumina. They are lined with a single layer of columnar or cuboidal cells which are very granular, so that their walls are difficult to determine. Each cell contains, near its base, a very large, usually spherical nucleus. These nuclei stain darkly and give the dark appearance to the glands as seen under low magnification, especially in rather thick sections.

During feeding the epithelium of this region of the tongue consists of fewer layers of cells than during hibernation but is otherwise unchanged from what is described above. The glands consist, at least in all of the material examined, of much fewer alveoli than are shown in Figure 37. One of these glands is shown in Figure 39.

Although no more care was used in fixation than in the corresponding tissue of the hibernating

animal the glands here show their cell details far more clearly than in the former tissue; this may have been partly due to the latter sections being thinner.

The glands are of a compound, tubulo-alveolar type; although numerous sections through ducts were obtained (as in Fig. 39), no details of these ducts could be seen.

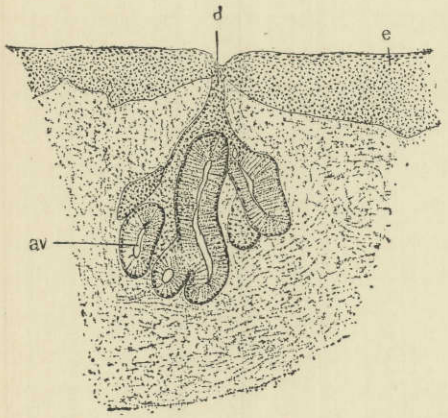

FIG. 39. One of the glands from the posterior region of the tongue of the feeding animal, under somewhat higher magnification than used in Figure 37; *av*, alveolus; *d*, duct of gland; *e*, stratified epithelium.

As noted above, and as may be seen by comparing Figures 37 and 39, the gland during hibernation, at least in the animals studied, consists of many more alveoli than during the feeding season; this, of course, might not prove to be always the case if larger numbers of animals were studied; the difference in the ages of the animals might have caused this difference in the glands. In the material studied the largest glands from the hibernating animals consist of more than twice as many alveoli as the glands in the feeding animals. As seen

under high magnification there is no noticeable difference in the glands at the two seasons.

Rathke has given the name of "Geschmackwärzchen" to the conical projections found on the dorsum of the crocodilian tongue; they are distinguished by their softness and thinner epithelial covering from the cones that, in many of these animals, bear the openings of the mucous glands.

These taste papillæ generally have the form of a truncated cone and often are surrounded by a shallow circular pit, outside of which, in turn, is sometimes a small low wall. They are distributed over the entire dorsum of the tongue, usually at considerable distance from each other in comparison to the size of the tongue, and are not so numerous as the taste papillæ of the Mammalia. Rathke found their absolute number greatest in *A. lucius*.

Rathke mentions other larger and harder projections on the tongue of certain Crocodilia which, though not perforated by a mucous duct, he thinks are of questionable relation to the sense papillæ. They usually have more the form of a flattened than of a truncated cone, and are very numerous in some species.

The Roof of the Mouth. In the paper mentioned above the author notes that the papillæ on the roof of the mouth are evenly distributed and are more distinct than those of the dorsum of the tongue.

One of these papillæ as seen under fairly high magnification is shown in Figure 40.

The areolar tissue, *a*, forming the base of the section is of about the same character as seen in

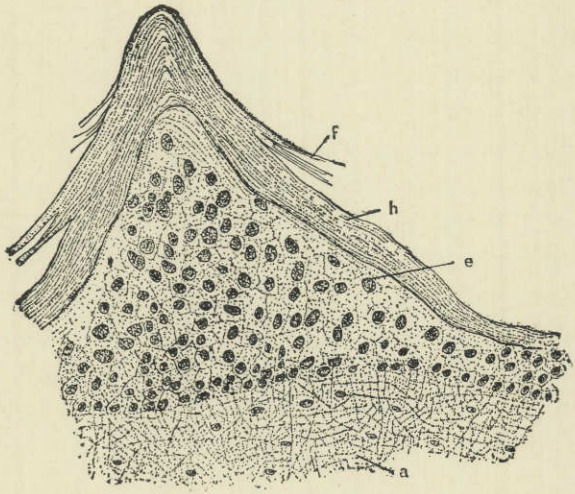

FIG. 40. The covering of the roof of the mouth of the hibernating animal, under fairly high magnification; *a*, areolar tissue; *e*, epithelium; *h*, horny layer; *f*, fibers of horny layer.

the section of the tongue. Less than one tenth of the thickness of the entire areolar base is shown in this section.

The epithelium, *e*, where not thrown into papillæ, has also about the same character as that of the anterior region of the tongue—the same number of cell layers and the same distinct horny layer.

At intervals the thickness of the cellular part of

the epithelium is greatly increased, and at the same time the horny layer is also thickened, to form distinct papillæ like the one shown in the figure. These, as has been said, are comparatively small and have the shape of a blunt cone. The center of the cone is, of course, made up of the cellular epithelium, while the outside is covered with the thickened horny layer from which fibers, *f*, are often seen projecting. Near the apex of the cone the nuclei are larger and more widely scattered than those at the base.

No glands were seen in the roof of the mouth of the hibernating animal, but since the entire roof was not sectioned it is probable that they may exist in some regions; in fact, as noted below, sections through the posterior region of the roof of the mouth of the feeding animal do show numerous glands.

As might be expected there is comparatively little difference between this region of the enteron during hibernation and during the feeding season. The only noticeable difference is in the stratified epithelium; that of the feeding animal not only has less sharp papillæ but has also a much thinner scaly layer of cells. As is seen in the figure of the roof of the mouth during hibernation the scaly cells make up, except on the papillæ, nearly or quite half of the thickness of the epithelium, while in the feeding animal they make up not more than one fourth or one third of the entire epithelium. Very

few cells are seen sloughing off as in Figure 40; possibly the act of feeding keeps the superficial scaly cells rubbed off smooth.

In the extreme posterior region of the roof of the mouth the epithelium consists of a greater number of layers (though the number is very variable) than in the region shown in Figure 40. In this posterior region, as noted above, glands are found. These glands have the same structure as those described in connection with the posterior region of the tongue.

The Œsophagus. Sections of the œsophagus were made from two regions, an anterior, half-inch caudad to the pharnyx, and a posterior region, half-inch cephalad to the opening of the œsophagus into the stomach (Fig. 35).

The general structure of the wall of the œsophagus, as seen under a low magnification, will first be described, after which the minute structure of the epithelium, as seen under high magnification, will be discussed.

In the *anterior region* the usual layers of the vertebrate enteron are present, except, possibly, the muscularis mucosa.

The epithelium, to be described later, is, together with the submucosa, thrown into complicated folds; its closely arranged and darkly stained nuclei cause it to stand out in strong contrast to the other tissues of the section (Fig. 41, *e*).

The submucosa, *sm*, is of considerable thickness.

It is composed of a fairly dense mass of connective tissue, mainly elastic fibers, through which are scattered small blood-vessels, *bv*, and small dark areas, *mb*, that are apparently longitudinal bundles of involuntary muscle fibers. These few and scattered fibers probably represent the muscularis mucosa that is so well developed in the posterior region of the œsophagus.

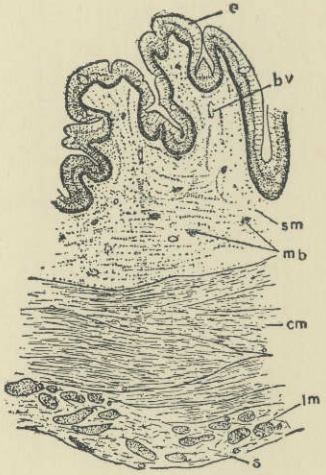

FIG. 41. A transsection through the anterior region of the œsophagus of the hibernating animal under low magnification *bv*, blood-vessels; *mb*, muscle bundles; other letters as in Figure 42.

Outside of the mucosa is a thick circular layer of involuntary muscle fibers, *cm*, the fibers being collected into irregular bundles, between which are narrow spaces filled with connective tissue that contains a few small blood-vessels.

Surrounding the circular layer is a thinner and less clearly defined layer of longitudinal muscle fibers, *lm*. The muscle bundles are more definite than in the circular layer and are separated from each other by a considerable amount of connective tissue with a few small blood-vessels.

The serosa, *s*, is here quite indistinct. It consists of a slightly vascular connective tissue which cannot be distinctly differentiated from the connective tissue of the longitudinal layer.

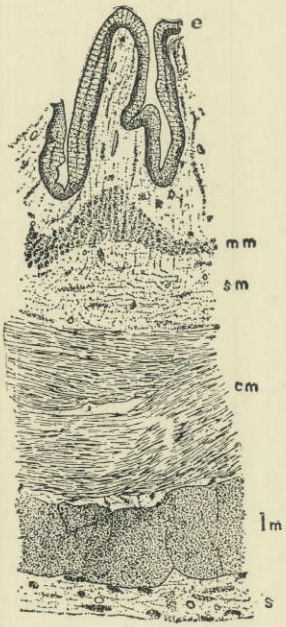

FIG. 42. A transsection through the posterior region of the œsophagus of the hibernating animal, under low magnification; *e*, epithelium; *cm*, circular muscles; *lm*, longitudinal muscles; *mm*, muscularis mucosa; *sm*, submucosa; *s*, serosa.

In the *posterior region* of the œsophagus, as may be seen by comparison of figures 41 and 42, the wall as a whole is about one third thicker than in the anterior region just described, though how much of this difference is due to different degrees of distension or contraction it is hard to say.

The epithelium, *e*, is in the tissue studied thrown into less complicated folds than in the anterior region, and is not so thick.

The submucosa, *sm*, if the entire layer may be so called, has about the same thickness and structure as in the more anterior region; but instead of the small and widely scattered bundles of longitudinal muscle fibers there is a distinct layer of muscle

which may be called the muscularis mucosa, *mm*, lying about midway between the epithelium and the circular muscle layer.

The muscularis mucosa is somewhat variable in thickness and is thrown into folds that correspond to the larger folds of the epithelium and the submucosa; one of these folds is shown in Figure 42. The fibers of the muscularis mucosa are apparently all longitudinal in position.

Outside of the submucosa is a layer of circular muscle fibers, *cm;* it is here somewhat wider and more dense than in the anterior region.

The longitudinal muscle layer (Fig. 42, *lm*) is much wider and more compact than in the anterior region. The fibers are indistinctly divided into large irregular masses as shown in the figure.

The serosa (Fig. 42, *s*) is a varying but fairly thick layer that is quite distinct from the longitudinal muscle layer. It consists of the usual connective tissue groundwork with scattered blood-vessels.

The epithelium, as was said above, is thicker and somewhat more folded in the anterior than in the posterior region, and in the former region is partially ciliated while in the latter cilia are entirely wanting. With these exceptions the epithelium is practically the same in the two regions.

Figure 43 represents the epithelium from the anterior region as seen under high magnification. The outlines of all the cells could not be determined

but if each nucleus represents a cell there are twenty-five or thirty layers of cells. The nuclei are arranged in two dense, irregular groups, one along the base of the epithelium, the other about two thirds of the distance from the base to the free border. The basal nuclei are perhaps slightly larger and more rounded than those of the distal group. Between these two groups are numerous more scattered nuclei; while scattered through the epithelium, except near the free border, are smaller, round nuclei that stain somewhat darker than the rest; these, from their size and appearance, seem possibly to belong to an invisible network of connective tissue that has penetrated the epithelium from the surrounding mucosa.

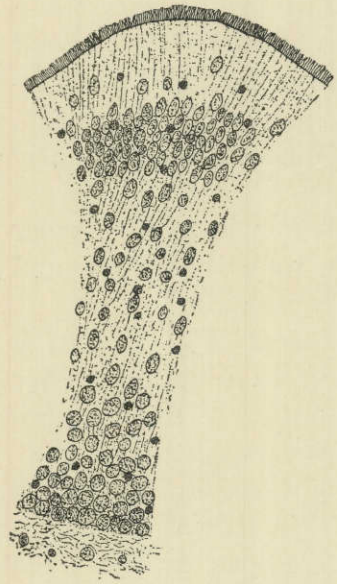

FIG. 43. The epithelium of the anterior region of the œsophagus of the hibernating animal, under high magnification.

The free border of the epithelium consists of long, ciliated, columnar cells in which the cell walls may be easily seen. The cilia are of average length and

even in this anterior region are not everywhere present; possibly they are arranged in bands, but the material at hand was not sufficient to determine this. As was noted above, cilia are wanting in the posterior region.

The only differences noted in the anterior region of the œsophagus between the feeding and the hibernating conditions are in the muscularis mucosa and the epithelium. As was noted above, the muscularis mucosa is practically absent in the hibernating stage, being represented only by a few small, scattered bundles of longitudinal muscle fibers; while in the feeding stage there is a narrow but fairly distinct layer to represent the muscularis mucosa.

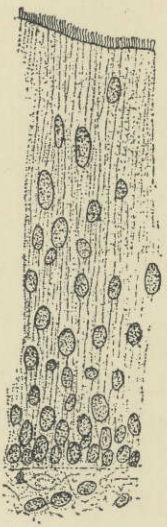

FIG. 44. The epithelium of the anterior region of the œsophagus of the feeding animal, under high magnification.

The difference in the appearance of the epithelium is not striking. The nuclei are somewhat larger in the feeding stage and, instead of being crowded into a basal and a median zone, as noted in the hibernating conditions, they form a dense basal zone, but show no indication of medial zone. From the dense basal zone the nuclei become more scattered towards the free surface and are rarely found closer to the surface than is shown in Figure 44.

The smaller nuclei scattered among the larger ones, noted in connection with the hibernating stage, are not here seen.

As in the hibernating stage cilia are present on some but not all cells of this region.

The only noticeable difference between the feeding and hibernating conditions of the posterior region of the œsophagus is in the epithelium, which, as in the feeding condition of the anterior œsophagus, exhibits but one zone of closely set nuclei, that at the base of the epithelium.

The Stomach. The stomach was sectioned in three regions, as shown in Figure 35: (1) in the cardiac region very near the opening of the œsophagus; (2) in the middle or fundic region; and (3) in the region near the opening of the pylorus. The first two sections are in the first or large region of the stomach; the third section is in the second or small region of the stomach (Fig. 35).

The wall as a whole is thickest in the fundus, being there practically twice as thick as in the pyloric and half again as thick as in the cardiac region. This great thickening is due mainly to a thickening of the middle or oblique layer of muscle, which is here remarkably developed. The mucosa is of nearly uniform thickness in the different regions and will be described later.

Since there is no striking difference beside that of thickness in the general structure of the wall of the

different regions, the pyloric region, as seen under low magnification, will now be described (Fig. 45).

The mucosa, *m*, consists of fairly long glands underlaid by a well-marked muscularis mucosa, *mm*, the latter exhibiting a compact circular layer over a wider but more scattered layer of longitudinal fibers. A considerable amount of fibrous connective tissue lies among the muscle fibers. The circular layer of the muscularis mucosa sends towards the surface numerous strands or septa between the glands; six or eight of these are seen in the figure. These strands are not nearly so numerous in the large region of the stomach. As was said, the outer or longitudinal layer of the muscularis mucosa is wider but less compact than the circular and its bundles of fibers are seen in the figure as a layer of large, scattered dots just beneath the circular layer.

The submucosa, *sm*, is of average thickness and density. In the fundic and cardiac regions it seems to extend between the circular and oblique layers; at any rate, there is a considerable layer of connective tissue between these two muscular layers.

The circular muscular layer, *cm*, is of only moderate thickness and is of rather a loose character. In the pyloric region it is not very distinct from the underlying oblique layer, but in the other regions, as has just been said, it is separated from

the oblique layer by a considerable layer of connective tissue like that of the submucosa.

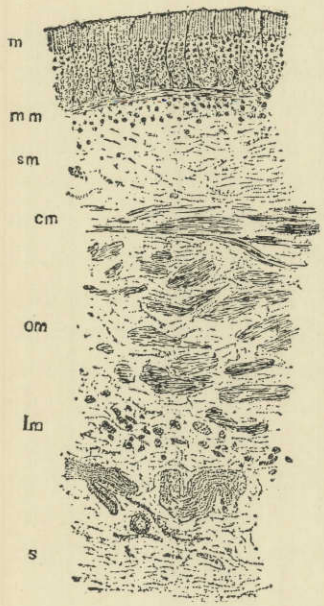

FIG. 45. A transsection through the wall of the pyloric region of the stomach of the feeding animal, under low magnification; *m*, mucosa; *om*, oblique muscles; other letters as in Figure 42.

The oblique layer, *om*, even in this section of the pyloric region is the thickest of the three muscle layers; while in the cardiac, and especially in the fundic, regions it is of great thickness, as was noted above, and is made up of larger bundles with less intervening connective tissue.

The outer or longitudinal muscle layer, *lm*, is comparatively little developed and consists of small rather scattered bundles of muscles with a correspondingly large amount of connective tissue. This connective tissue passes insensibly into that of the surrounding serosa, *s*, a loose, vascular layer of varying thickness and density, shown very thick in Figure 45, but often much thinner.

So far as could be determined, the mucous mem-

brane has the same structure in both anterior and middle regions of the stomach. That of the pyloric or small region, although fixed, stained, et cetera, just as carefully as the rest, did not show cell details sufficiently well to draw; the ducts of the glands in this region are fairly distinct but the deeper parts of the glands have the appearance of series of alveoli or large adipose cells. What the significance of this condition may be the writer is not able to say, but since the structure of this region of the gastric mucous membrane is not clear no attempt will be made to describe its appearance under higher magnification than was employed in the figure above. However, as will be noted below, there is probably no great difference between the pyloric mucosa and that of the other regions of the stomach.

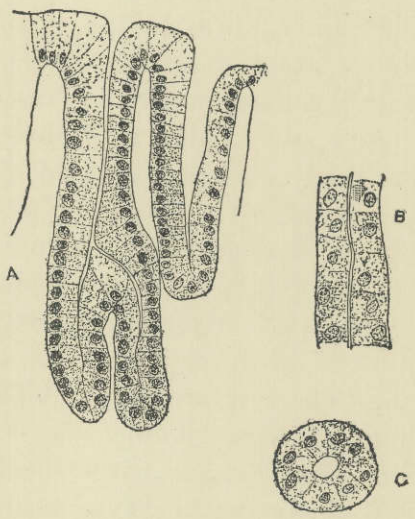

FIG. 46. The glands of the middle or fundic region of the stomach of the hibernating animal, under high magnification; *A*, through duct; *B*, through body of gland; *C*, through fundus of gland.

Figure 46 shows portions of typical glands

from the mucosa of the middle region of the stomach, the posterior border of the large stomach cavity; *A* is a longitudinal section through two ducts where they open to the surface; *B* is a similar section through the body of a gland below the region of the duct; *C* is a transsection through the bottom or fundus of a gland; all are drawn with a camera under the same magnification.

As is seen in Figure 45, under low magnification, the duct is about one third of the entire length of the gland. The lumen of the duct is fairly wide, that of the body of the gland is reduced to a mere slit, while that of the fundus is quite wide.

One, two, or possibly more, glands may open to the surface through one duct, as is shown in Figure 46. There is nothing peculiar about the epithelium of these glands. Near the opening of the duct the cells are of a typical columnar character with finely granular cytoplasm, each with a nucleus at its basal end.

In the deeper parts of the duct the cells become shorter until in the body of the gland (Fig. 46, *B*) they are cuboidal in outline.

The bodies of the glands are so closely packed together that it is difficult to pick out an individual tube that will show details clearly enough to draw with a camera lucida. So far as could be observed all of the cells of this region of the gland are alike.

The bottom or fundus of the gland, as seen in Figure 46, *C*, is somewhat enlarged and has a wide

lumen. The cells are of the same general character as in the more distal parts of the gland except that they are somewhat more columnar or pyramidal than in the body of the gland. The nuclei of the body and fundus are usually somewhat larger and more nearly spherical than in the columnar cells of the duct.

The feeding animals from which tissues were taken were considerably smaller than the hibernating specimen, so that the stomach walls were proportionately thinner; but, so far as could be discovered, there was no difference in structure.

The relative thickness of the entire wall in each of the three regions sectioned was about the same as described above.

As has been said, the mucosa of the pyloric or small region of the stomach from the hibernating animal was so poorly fixed that its structure could not be made out. In the feeding stage the mucosa of this region was as well fixed as any of the other tissues and showed that its structure is essentially like that shown in Figure 46, except that the glands are proportionately not quite so long as in the fundic and cardiac regions, and are somewhat more open — that is, they have wider lumina; their lining cells are all of one kind and are unchanged from what was seen in the hibernating condition.

The Small Intestine. Three regions of the small intestine will be described: (1) an anterior, just

caudad to the stomach; (2) a middle; and (3) a posterior, one half inch cephalad to the rectum or large intestine (Fig. 35).

As might be expected, the general structure of the wall of the intestine is essentially the same in all three regions, the slight differences noticeable being due mainly to variations in the thickness of the various layers.

The middle and posterior regions have about the same diameter, while the diameter of the anterior region is considerably greater, due partly to the greater diameter of the lumen but mainly to the greater thickness of the constituent layers, especially the mucosa. The mucosa is also thrown into more numerous and complicated folds in the anterior than in the middle and posterior regions; the complexity of the mucosa seems to diminish as the intestine is followed caudad. In the anterior region the mucosa may form at least one half of the entire thickness of the wall, while in the posterior region it may form less than one third of the thickness of the intestinal wall. The minute structure of the intestinal epithelium will be described below.

The chief peculiarity of the intestinal wall is the apparent total absence of a submucosa (Fig. 47). As will be described later, the mucosal epithelium is laid upon the usual bed of fibrous and lymphatic tissue, the tunica propria (Fig. 47, *tp*).

At the outer border of the tunica propria, and with no tissue corresponding to a submucosa between it and the circular muscular layer, is a thin and indistinct layer that has the appearance

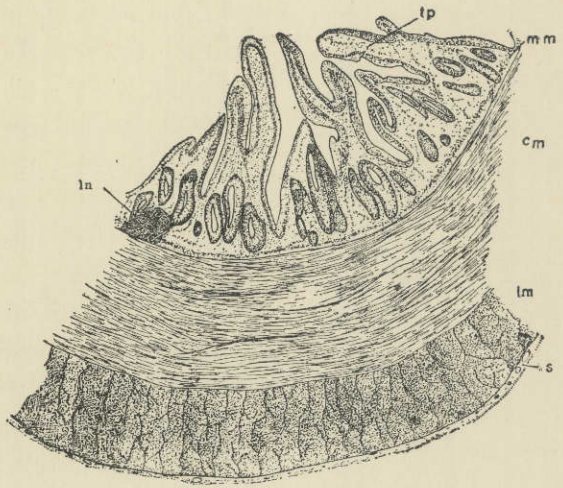

FIG. 47. A transsection of the wall of the anterior region of the small intestine of the hibernating animal, under low magnification; *ln*, lymph node; *tp*, tunica propria; other letters as in Figure 42.

of a longitudinal layer of muscle fibers; this should correspond to the muscularis mucosa (Figs. 47, 48, 49, and 51, *mm*).

The circular, *cm*, and longitudinal, *lm*, muscle layers are compact, and are distinct from the other layers of the wall; the former is approximately twice the thickness of the latter. The relative thickness of all the layers in the three

regions of the intestine may be seen by comparing Figures 47, 48, and 49.

The serosa, *s*, which is of about the same character in the three regions under discussion, is a distinct and fairly dense layer of connective tissue with numerous blood-vessels.

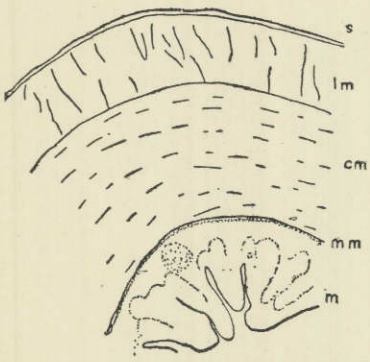

FIG. 48. An outline of a transsection of the wall of the middle region of the small intestine of the hibernating animal, under low magnification; lettering as in Figure 42.

The general appearance of the mucous membrane as a whole is sufficiently clear in the low-power drawing described above, so that all that need be shown under a higher magnification is the epithelium (Fig. 50). The upper part of this figure represents the lower end of one of the intestinal glands cut longitudinally, below which is the end of another gland in transverse section. Between the two sections is the compact tunica propria of lymphatic tissue.

The section from which this particular figure was drawn was in the anterior region, but the corresponding part of a section in either of the other regions would have practically the same appearance.

The epithelium is of the stratified columnar type. The superficial cells are very tall and narrow, with the nuclei generally at or near the bases, though an occasional nucleus may be seen near the free end of a cell. Below the tall columnar cells are four or five rows of nuclei which represent smaller, irregular cells, though the cell walls could not always be determined between the closely packed nuclei. No goblet cells are to be seen at any place.

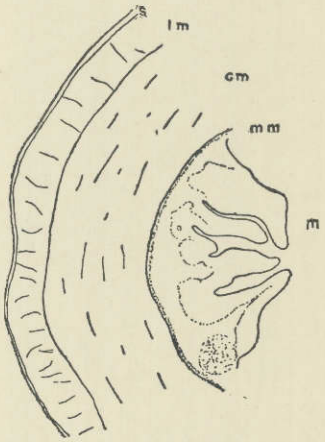

FIG. 49. An outline of a transsection through the wall of the posterior region of the small intestine of the hibernating animal, under low magnification; lettering as in Figure 42.

The relative diameters of the three regions of the small intestine in the feeding condition are about the same as noted for the hibernating stage; that is, the anterior region has the greatest diameter and the other regions are smaller and have about the same average diameter.

The most marked difference between the intestine during hibernation and feeding is in the relative thickness of the mucosa and muscular layers. As described for the hibernating stage, so in the feed-

ing stage, the mucosa is relatively the thickest in the anterior regions and diminishes in thickness caudad; but while, in the hibernating stage, it forms, in the anterior region, as much as half of the entire thickness of the wall, in the feeding condition it forms, in the same region, at least two thirds of the entire wall and in the middle and posterior regions more than half of the wall.

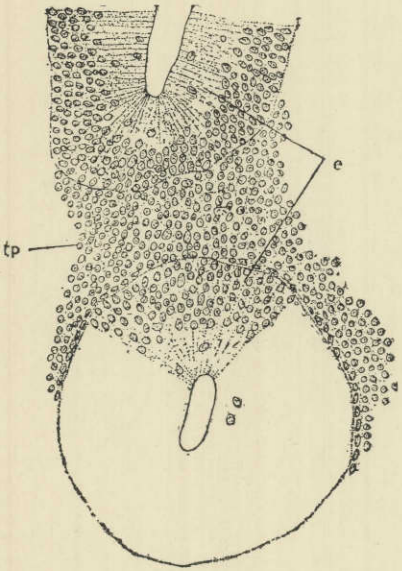

FIG. 50. Part of the mucous membrane of the anterior region of the small intestine of the hibernating animal, under high magnification. The upper part of the figure shows a part of a gland cut longitudinally, the lower part of the figure shows another gland cut transversely; *e*, epithelium; *tp*, tunica propria.

The feeding animals being the smaller, the diameter of the intestine was considerably less than in the hibernating stage; but the actual thickness of the mucosa was practically the same, so that the difference in diameter was due to the difference in the thickness of the muscular and fibrous layers. It is therefore probable that the differences noted above are due rather to the differences in the size

of the animals from which the tissues were taken than to the different conditions of hibernation and feeding. The point to be noticed is that the increase in the diameter of the intestine is due almost if not entirely to an increase in thickness of the connective tissue and muscle layers.

No difference in the complexity of the folds of the mucosa of the two stages can be noticed.

The thickness of the fibro-muscular part of the wall of the intestine varies considerably on different sides of the same region, but it consists of the same layers in about the same relative amounts.

Figure 51 represents in outline the wall of the middle region of the small intestine during feeding.

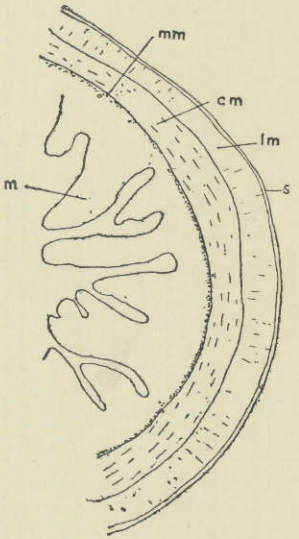

FIG. 51. An outline of a transsection of the wall of the middle region of the small intestine of the feeding animal, under low magnification; *m*, mucosa; other letters as in Figure 42.

The epithelium is of the same thickness in the two stages, and the only difference in its character that can be seen under a high magnification is that, in the middle region at least, the nuclei are not crowded so close together at the basal ends of

the cells as in the hibernating stage but are scattered more towards their free ends.

Altogether, the differences in microscopic struc-

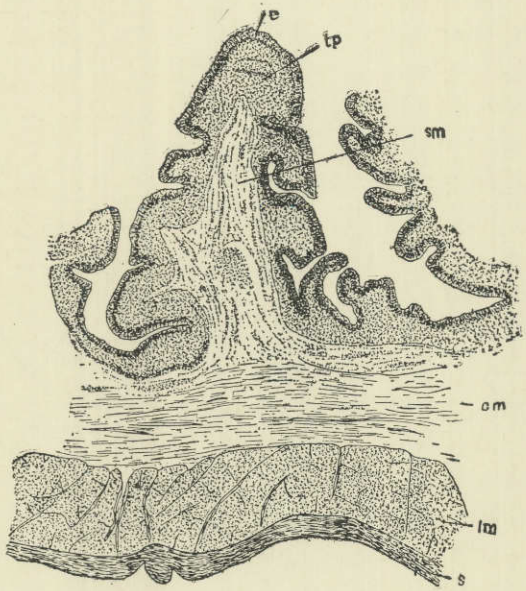

FIG. 52. A transsection of the wall of the anterior region of the rectum or large intestine of the hibernating animal, under low magnification; *tp*, tunica propria; other letters as in Figure 42.

ture between the small intestine of an alligator at the end of the hibernating period and at the end of a period of regular feeding are very slight.

The Large Intestine. The planes of the two sections studied are shown in Figure 35; a low-

power drawing of the posterior region is shown in Figure 52. The anterior and posterior regions of the large intestine do not differ from each other sufficiently to make it worth while to represent both by drawings. Had an entire section through either region been drawn it would be seen that the wall is of very different thickness in different places, as was noted in connection with the small intestine; the posterior section was drawn where the wall was thin.

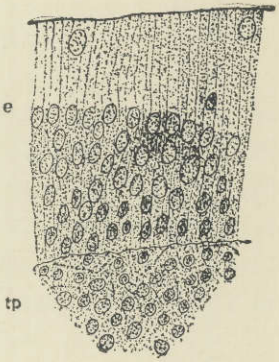

FIG. 53. The epithelium of the anterior region of the rectum of the hibernating animal, under high magnification; *e*, epithelium; *tp*, tunica propria.

It might be supposed that in the feeding season the fecal matter in the posterior region of the rectum would stretch the walls sufficiently to obliterate largely the prominent folds seen in Figure 52, but such does not seem to be the case. The usual layers of the vertebrate intestine are present.

The epithelium, shown under high magnification in Figure 53, is of the same character and thickness throughout, except that as the anal aperture is approached the columnar epithelium changes into the stratified variety. It consists of very tall and narrow columnar cells apparently in one layer, though it is difficult to be sure of this. With an

occasional exception, near the top, all of the nuclei are arranged in a fairly wide zone below the middle of the epithelium. The nuclei are oval in shape and lie so close together that it is difficult, as has been said, to be sure that the cell to which each belongs extends throughout the entire thickness of the epithelium.

Beneath the epithelium (Fig. 52, *e*) is a dense tunica propria, *tp*, underlaid, in turn, by the muscularis mucosa, *mm*, and a submucosa, *sm*, of the usual character, which is thrown into marked folds. The circular, *cm*, and longitudinal, *lm*, layers are of the usual character except that they vary more in thickness, as noted above, and in density than is usually the case.

The serosa, *s*, is comparatively thin and compact in both regions, and varies somewhat in thickness at different places.

The large intestine of the feeding animal was sectioned in the same regions as in the hibernating. As has been said, the feeding animals used were much smaller than the hibernating, so that, as might be expected, the diameter of the large intestine was much less in the former than in the latter. Except for this difference in diameter there was no noticeable difference between the two stages. In the case of the small intestine, it will be remembered, the greater diameter of the intestine of the larger animal was mainly due to the greater thickness of the muscular and connective-

tissue layers and not to any increase in thickness of the mucous membrane. In the large intestine the mucosa varies in thickness in the animals of different size as do the other layers of the wall.

The glandular character of the lining of the large intestine seems to indicate that his region of the intestine must have some digestive or absorptive function and that it does not act merely as a receptacle for fecal matter; this makes it all the more strange that there should not be some change produced in its structure by five or six months of feeding or of fasting.

Summary. The material used in this investigation was taken from young animals at the end of a feeding period of about five months, and towards the end of the hibernating period after fasting for four or five months.

The regions of the enteron that were studied were as follows: the tip and base of the tongue; the anterior and posterior regions of the roof of the mouth; the anterior and posterior regions of the œsophagus; the cardiac, fundic, and pyloric regions of the stomach; the anterior, middle, and posterior regions of the small intestine; the anterior and posterior regions of the large intestine. Since the work was started at the end of the hibernating period, the tissues of that period were studied and drawn first.

The only difference between the structure of the tip of the tongue during hibernation and during

the feeding season is that the scaly epithelium with which it is covered is somewhat thicker and more compact in the former than in the latter condition, though even this difference may have been due to differences in the ages of the animals used. The base of the tongue differs from the tip in having a thicker epithelium and in having compound tubulo-alveolar glands. These glands in the hibernating animal have many more alveoli than in the feeding animal, though this, again, may have been due to the difference in age.

The lining of the roof of the mouth is essentially the same as that of the tongue. The glands are found only in the posterior region. The slight differences in thə papillæ here found may easily be due to the difference in age.

The œsophagus shows the usual layers for that region. Its epithelium is partly ciliated in the anterior part. The muscularis mucosa is very scant in the anterior region. The only difference between the two stages is that in the feeding the muscularis mucosa in the anterior region is much more strongly developed than in the hibernating stage; and in the former the nuclei of the epithelium are not arranged in two zones as in the latter.

The stomach has the usual layers, and has essentially the same structure in the three regions studied, except that the wall in the fundic region is much the thickest, due mainly to the great

thickness of the middle muscle layer. Only one kind of cell is found in the gastric glands. No difference is to be noted between the hibernating and feeding conditions.

The chief peculiarity of the small intestine is the apparent entire absence of the submucosa. Goblet cells are also wanting. The greater diameter of the anterior region is due both to the greater diameter of the lumen and to the greater thickness of the walls. The middle and posterior regions have about the same diameter, though the mucosa becomes thinner and less complicated caudad. There is practically no difference between the hibernating and feeding stages.

The anterior and posterior regions of the large intestine have essentially the same structure. No difference can be seen between the hibernating and feeding conditions.