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The digestive system of the Carolina locust (*Dissosteira carolina* Linn.)

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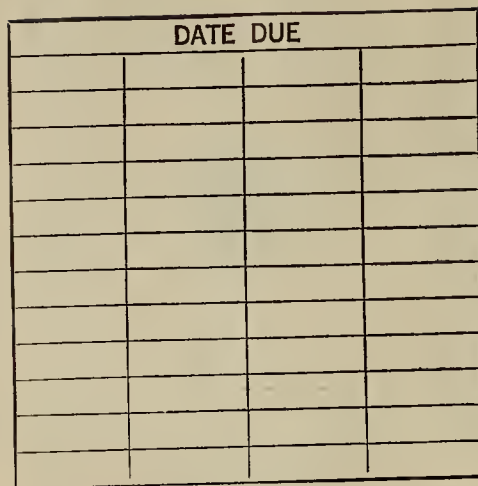
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The Digestive System of the Carolina Locust

(*Dissosteira Carolina* Linn.)

HARRISON M. TIETZ B. Sc.

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THE DIGESTIVE SYSTEM OF THE CAROLINA LOCUST

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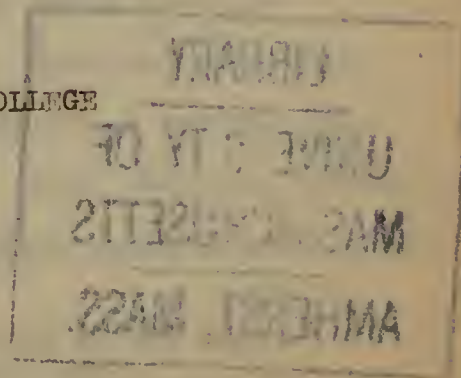
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1922



THE ANATOMY OF THE DIGESTIVE SYSTEM OF THE CAROLINA LOCUST
(*Dissosteira carolina*, Linn.)*

By Harrison M. Tietz.

Introduction.

The typical insect dissected by most students in biology is the Carolina locust or some other common grasshopper. Many laboratory manuals describe the anatomy of these orthopterans in more or less detail but with too few illustrations. This lack of illustrations makes it difficult for the instructor to present the subject and leads to confusion in the minds of the students. It is the aim of this paper to meet this need in part by presenting in its text and figures the results of a detailed study of the alimentary tract of the Carolina locust.

Only one other person, so far as the writer knows, has published a paper on the digestive system of this insect. This article was written by R. E. Snodgrass in 1903 and was issued by the Washington Agricultural College, Pullman Washington. His work, however, fails to show structural details being a mere sketch of the general external characters of the alimentary tract. The article is also not readily accessible.

The present paper forms the third of a series of articles on the anatomy of this insect. In 1917, S. C. Vinal wrote upon the "Respiratory System of the Carolina Locust". This was published in 1919 in the Journal of the New York Entomological Society, Vol. XXVII, 1, p. 19. Later, in 1918, Dr. G. C. Crampton wrote upon the "Thoracic Sclerites of the Grasshopper, *Dissosteira carolina*" which was published

*Contribution from the Entomological Laboratory of the Mass.
Agricultural College, Amherst Mass.

in the Annals of the Entomological Society of America, Vol. XI, p. 347.

In carrying out this work and in the preparation of the material for publication, the writer has received many valuable suggestions from Drs. H. T. Fernald and G. C. Crampton. To Dr. C. L. Bristol he is indebted for the use of the biological laboratory at New York University during the summer of 1922. It gives him great pleasure to acknowledge here his gratitude for their kindness and encouragement.

METHOD OF STUDY AND PREPARATION OF MATERIAL.

In preparing the material for study the procedure was as follows. Specimens were captured in the field and killed in a cyanide jar. As soon as they were dead they were dissected under water. No specimens preserved in alcohol were used. A Spencer binocular with 10x eyepiece and 55, 40, and 25mm. objectives was used in making observations.

Material for histological study was dissected from insects that were still alive but under the influence of ether. The alimentary tract in some cases was dropped into Bouin's fixative without being opened. In others the tract was slit and the contents was brushed out under water. After fixation the usual process was followed and the slides were stained with Delafield's haematoxylin and eosin. The finished slides were examined under a B. & L. compound microscope using a 10x eyepiece with 32, 8, 4, and 1.8mm. objectives. The best sections were those cut 7 to 10 microns thick.

GENERAL CONSIDERATIONS.

On the basis of embryology, the alimentary tract of the Carolina locust can be divided into three regions. The first of these, the fore-gut, is formed by an invagination in the anterior region of the germ band known as the stomodaeum. Later this infolded portion is differentiated into mouth, pharynx, oesophagus, crop, gizzard, and cardiac valve. All these, being ectodermal in origin, are characterized by the deposition of chitin which lines their lumen. Following the fore-gut is the mid-gut formed from endoderm, and producing the stomach (ventriculus) and its gastric caeca. The remainder of the alimentary tract, generally known as the hind-gut, is ectodermal in origin. This portion of the tract, formed by an invagination of the posterior part of the germ band, is known as the proctodaeum, which later forms the pyloric valve, ilium, colon, rectum and anus. The lumen of these portions is also chitinized.

It would be misleading to state that the various portions of the alimentary tract always occupy the same location in the body with reference to the segments. Their location changes for several reasons, (1) the elasticity of the wall of the gut, (2) the loose attachment of the alimentary tract in the body, and (3) the distentions of the various portions of the tract as they are filled with food. All these factors will determine the extent of the various portions of the gut with reference to the body segments. The writer, while making dissections of well fed and ^{also of} starved specimens, noted that in the former individuals that portion of the alimentary tract

to which the gastric caeca were attached lay in the anterior part of the second abdominal segment, due probably to the distention of the crop and gizzard with food material. In the starved specimens, on the other hand, this area of the digestive system lay in the last thoracic segment.

THE MOUTH AND BUCCAL CAVITY.

The buccal cavity forms the most anterior region of the alimentary tract and its posterior wall is, in part, formed by the tongue or hypo-pharynx. This organ is between 3 and 4 mm. long, rather strongly chitinized, and bears upon its surface fine spines which point backward. These spines, which seem to have a gustatory function, arise from small pits. The writer intends, at some future time, to make a histological study of this organ. On the under surface of the tongue near its tip will be found the opening of the common salivary duct. This duct runs for a very short distance ^{backward} towards the posterior attachment of the tongue but, before reaching this region, it divides, one branch passing to the right, and the other to the left ^{side} of the insect. These branches pass into the thorax where they give off smaller branches which connect with the white grape-like clusters of salivary glands. The number and arrangement of these clusters is shown in Fig. 2. These glands are compound alveolar, each alveolus consisting of a mass of glandular cells, irregular in shape, with distinct nuclei. Some seem to be serous cells in which the secretion is scattered throughout the cytoplasm in fine granules. Others appear as mucous cells the secretion being concentrated into a clear glistening drop. In none of the sections could the writer find any indication

of a reservoir for their products.

After the food in the buccal cavity has been thoroughly mixed with the saliva, it then passes into the oesophagus.

THE OESOPHAGUS.

This is a very short, slender tube extending first upward and backward from the buccal cavity; then, at about where it enters the thorax, bending ventrally somewhat and about the middle of the first thoracic segment, joining the crop. The inner surface of the oesophagus is thrown up in longitudinal folds .16 mm. high and is covered with a chitinous coat .024 mm. thick. Beneath these folds we find a layer of columnar epithelial cells. These cells have very large prominent nuclei but very indistinct cell walls. Below the epithelium there is a layer of connective tissue which is very prominent in the central portion of the elevations where it forms the "core". Under the furrows between the ridges, however, it is very scant and seems in some places to be wanting. Next in order come the bands of longitudinal muscle. In a few cases we find a band directly under a fold but such strips are generally confined to portions lying between these elevations. The outermost layer consists of circular muscle to the depth of about .03 mm. and a few strands of longitudinal muscle, the latter joining the tract to the body wall.

The so-called "molasses" glands are supposed by some writers to lie in the oesophagus. In my sections I could see no traces of glandular tissue nor distinct ducts through the

chitinous lining. Under the oil immersion the chitin showed some striations but whether these were pores or merely the lamellate structure of the chitin itself the writer could not say. The chitinous intima throughout the whole alimentary tract presented the same appearance.

THE CROP.

The crop can sometimes be distinguished outwardly from the preceding region by its dilated appearance. If the insect has been well fed before dissection, the crop often stands out distinctly from the oesophagus as a sudden dilation of the alimentary tube, but in poorly fed or starved specimens one portion merges into the other so gradually that the limits of each are not clearly seen. Internally, however, the crop is transversely ridged so that it is not difficult to identify it. These ridges, about thirty in number, are about .28 mm. high and spaced .08 mm. apart. The most anterior and posterior ridges are merely a series of short disconnected folds, and the former do not bear the short chitinous teeth mentioned later on. These teeth are .02 mm. long and are distributed, with the exception just mentioned, along the tops of the ridges in rather even rows, the broader elevations bearing three or four rows, the narrower but a single row. The teeth serve to cut the food into shreds and this seems to be one of the functions of the crop. The ridges may act in such a manner as to retard the quick passage of food into the next region (the gizzard) and so the crop may also serve as a reservoir. A third function of the

crop, according to some investigators, is that of straining out foreign material from the food. This function is supposedly carried on by the teeth but Duport shows that the long teeth found in the crop of Gryllus pennsylvanicus do not prevent the passage of large particles into the stomach. In his article (Psyche Dec. 1918) he states, "Particles of chitin, quartz, and woody tissue found in the proventriculus and mesenteron were fully as large as any found in the crop... The action of the proventriculus might be compared with that of the rollers in a mill; anything caught between them is carried onward. If it is strong enough to resist the breaking power of the rollers it will come out unaltered on the other side, if not it will be crushed." Since the teeth of D. carolina are much smaller and do not project as far into the lumen as those of G. pennsylvanicus, they would be less likely to act as strainers. On the other hand, the rigidity they possess owing to their shortness, combined with the fact that they are extremely sharp, favors the theory that the teeth have a triturating function.

The histological elements in the crop are the same as in the oesophagus. The same layers are present and are in the same order excepting the outer strands of longitudinal muscle which are not present in the crop. The ridges in the crop are transverse instead of longitudinal so we find that their relation to the bands of inner longitudinal muscle is different. In the oesophagus the bands run parallel to the ridges and between them. In the crop they run at right angles to the

ridges. Besides this difference we also find some indication of a thicker layer of circular muscles but this is not marked.

THE GIZZARD.

The external demarcation of the gizzard is not evident for there is but a slight constriction between this portion of the gut and the crop. Posteriorly the outer wall merges into that of the cardiac valve and cannot, therefore, be differentiated from it. Internally the gizzard can be distinguished by the presence of a series of discontinuous folds or ridge-like elevations grouped in longitudinal rows. These rows, about fifty in number, are from .004 to .008 mm. apart and project into the lumen .09 to .1 mm. Many of the elevations bear one or two teeth .008 mm. long.

The histology of the gizzard differs somewhat from that of the oesophagus in the following details. The central portion of each protuberance contains very little connective tissue, the epithelial cells being rather tightly packed together. In the basal portion of each elevation, connective tissue is largely replaced by longitudinal muscle. Another very noticeable difference is the great development of circular muscle which is thicker here than at any other part of the tract.

THE CARDIAC VALVE.

The location of this portion of the tract is indicated externally by a slight constriction just anterior to the point of attachment of the gastric caeca. If a longitudinal section be made through the cardiac valve, it will be seen that this portion of the digestive system is very narrow and projects

into the ventriculus, the latter having a larger diameter to allow for this intrusion. The small lumen of the valve is further reduced by six elevations which appear as "V" shaped structures projecting from the wall of the valve, the broad part of the V being anterior and the point posterior, i.e. near the stomach. The wide end of the V is .5mm. across. Each elevation is 1.4mm. long and the cleft which gives it the V shaped appearance runs about half way to its tip. (See Pl. II., Fig. 7.) These protuberances are 1.3mm. high and bear upon their surfaces fine teeth which become smaller near the apex of the V.

The cellular structure of the cardiac valve is shown in Figs. 23 and 24. The V shaped projections are covered with a chitinous coat .02mm. thick, under which lie the epithelial cells. Below these there is a small amount of connective tissue, and under this we find a thick band of circular muscle.

The bands of longitudinal muscle forming the outer coat of the stomach continue anteriorly until they reach the point of attachment of the gastric caeca. Here some divide and go around on either side of the caeca, uniting on the other side where they form an incomplete outer coat of the cardiac valve. This coat runs for a very short distance ending just below the point where the V like projections begin. The remaining longitudinal fibres may form the outer coat of the caeca.

This portion of the alimentary tract may prevent the food from passing too rapidly from the gizzard into the stomach as well as preventing regurgitation of the food already in the stomach.

THE STOMACH (Ventriculus)

There are two characters that enable one to identify the stomach without cutting into the alimentary tract. These characters are the nature of the stomach wall, and the presence of the gastric caeca. The wall is very thin being not more than .02mm. thick. This character gives it a white translucent appearance which is very noticeable. The gastric caeca, which serve as a second means of identification, mark, at their point of attachment, the anterior limit of the stomach. These organs, sometimes called diverticula or Appendices Ventricularis, are six in number and are paired, each caecum having a single point of attachment to the wall of the stomach from which point there is directed anteriorly a finger-like lobe and posteriorly a pouch. This finger-like lobe is nearly twice as long as the pouch and the latter is sometimes reduced making it still shorter. Both lobes and pouches are blind pockets being closed at their distal ends and open at their proximal ends into the stomach. The openings of the six pairs of caeca are not confluent but are so arranged that a line drawn through their openings would encircle the tract. The longitudinal axes of the caeca run parallel to the longitudinal axis of the alimentary tract.

In D. carolina both the anterior and posterior pouches of each caecum are covered by a layer of smooth longitudinal muscle.

The other cellular layers, however, differ both in structure and arrangement.

In the anterior lobe, beneath the

muscular coat just mentioned, there is a very thin layer of connective tissue though in many places this is not evident. Inside this lies the epithelium which is thrown up into twelve or thirteen longitudinal folds (Fig. 18). These folds project so far into the lumen that they almost divide each pouch into compartments. The epithelial cells are columnar with distinct nuclei situated near their bases, the cytoplasm is densely granular, and the free surfaces of each cell appear ciliated. In the posterior lobe there seems to be no definite arrangement of the cells. Many are irregular in shape, all are closely packed, and they fill the lobe with the exception of a small lumen in the center. The nuclei are very distinct, the cytoplasm is not densely granulated, and none of the cells are ciliated. Although the gastric caeca are outgrowths of the stomach, this latter organ shows histological characters peculiar to itself. Instead of one layer of muscles we find two. The outermost is unstriated and longitudinal. Next to this comes a layer of circular muscle which also appears unstriated. Permeating the rest of the wall of the stomach are strands of connective tissue in which lie imbedded two types of cells. In the first type both the nuclei and cytoplasm stain deeply. The cells are very closely packed together with their cell walls not perceptible. They appear as dome-shaped masses in longitudinal sections and as columns when viewed in cross section. Between these masses there are crypts or nests of nuclei (nidi) which form the second type of cell. Their nuclei stain well but not so

deeply as in the first type. The surrounding cytoplasm remains very clear and unstained. Many of the cells appear polynucleated probably owing to the fact that their cell walls are imperceptible. They have all the appearances of being centers for the generation of new cells needed to replace those destroyed during the process of digestion.

It has been claimed that there is a chitinous intima lining the inner surface of the stomach but the writer could find no evidence of its presence. Instead that portion of the stomach wall next to the lumen was composed of disintegrating cells with here and there scattered nuclei. From the sections studied, the writer is under the impression that the nidi are centers where new cells are constantly being produced and that these cells then migrate towards the lumen where they are broken down during the process of digestion.

THE MALPIGHIAN TUBULES.

It has been mentioned that the attachment of the gastric caeca outwardly marks the anterior boundary of the stomach. For convenience the Malpighian tubules may be considered as marking the posterior limit of the stomach at the point where they are attached to the alimentary tract. It should be remembered, however, that these tubules are proctodaeal in origin and are not therefore part of the stomach. In fact the tubes enter the tract just in front of the pyloric valve.

The Malpighian tubules are threadlike in appearance, about seventy in number, and are pigmented most of their length, though near their points of attachment no color is present. In

the specimens examined the color was a very dark brown and so distributed as to give the tubules the appearance of being either transversely ringed or banded and blotched. The tubes are about .05 mm. in diameter and vary in length, the longer ones measuring ten millimeters or more. They are composed of cells with prominent nuclei but with indistinct cell walls. The cells rest upon a very thin basement membrane and the latter is in close contact with trachioles that wind themselves about the tubules even to their tips. There seems to be no lumen near their points of attachment. At their point of attachment to the gut wall, the Malpighian tubules are grouped in six masses of about twelve tubes each. While the tubes do not coalesce but retain their individuality from their place of insertion to their most distal point, each group has but a single common opening.

THE PYLORIC VALVE

The ilial muscles might force the contents of the ilium back into the stomach were it not for the presence of the pyloric valve. This valve consists of (1) a transverse fold shown in Fig. 8, and (2) somewhat spherical elevations situated just posterior to the fold. When viewed from the inner surface, this fold appears as a ditch cut transversely in the wall of the digestive tube. At the bottom of this ditch we find six cup-shaped depressions. When viewed from the outer surface, these depressions appear as six dome-like elevations .12 mm. high. It is to these protuberances that the Malpighian tubules are attached. These tubes as Miall states have only a secondary connection with the alimentary canal depending as it

would seem upon intercellular communication and not to clearly defined ducts for the passage of waste products into the digestive tract.

The spherical elevations posterior to the fold are of the same structure as that of the ilium to be discussed later on. Anteriorly each elevation is .24 mm. in diameter but posteriorly it is drawn out gradually, becomes narrower, and at the same time slopes down towards the wall of the ilium. Finally its identity is lost for it merges into the many folds of the ilial epithelium. The longitudinal axes of these elevations run parallel with the longitudinal axis of the alimentary tract. They do not normally touch each other being spaced about .4 mm apart. It seems reasonable to suppose, however, that when the circular muscles of the ilial wall contract, thereby reducing the diameter of the lumen, these projections may be brought together, may touch each other and thereby close up the anterior end of the ilium. Such a stoppage would prevent the contents of the ilium from reëntering the stomach.

THE ILIUM.

This is a rather short, straight, tapering tube whose posterior diameter is about one half that of the anterior end. Externally, the limits of the ilium are only roughly indicated. One can consider that portion of the alimentary tract to which the Malpighian^{tubules} are attached as the anterior limit of the ilium. Posteriorly this portion of the digestive system extends to the first constriction behind these tubes.

Internally, the wall of the ilium is thrown up into many longitudinal folds that rise about .32 mm. from its surface. They are connected by similar folds which take a more or less oblique direction. These two types of elevations give to the inner ilial wall a much wrinkled appearance. Since one of the functions of the ilium is absorption, these numerous folds serve to increase the absorptive surface.

The epithelium forming the folds consists of a single layer of cuboidal cells whose free surface is covered with chitin to a depth of .008 mm. The central portion of each fold is loosely filled with connective tissue upon which these cuboidal cells rest. Next comes a thin coat of circular muscle outside of which, and forming the outermost portion of the ilium, there are about six bands of longitudinal muscle.

THE COLON

It is often difficult to recognize the colon without cutting through its wall and examining the internal structure. When the six longitudinal bands of muscles, to be mentioned later on, appear through the wall and when the constrictions between the ilium and colon, and colon and rectum are pronounced, external identification is made much easier.

Internally, however, this portion of the alimentary tract presents unmistakable characters that would prevent its confusion with any other region of the digestive system. The outstanding features are the six longitudinal folds, .24 mm. high, that project into the lumen of the colon.

They are about .2 mm. broad and are placed about .012 mm. apart. The tops of these elevations are not flat but, on the contrary, present under the microscope a rather undulating appearance. These elevations are continuations of the ilial folds.

The histology of the colon is quite similar to that of the ilium with the exception that the chitinous intima in the colon is thicker being .012 mm. in depth. There is also a noticeable increase in the amount of circular muscle. The longitudinal muscles of the colon are merely continuations of the ilial muscles.

THE RECTUM.

The rectum begins just behind the last constriction of the alimentary tract, this constriction marking it off from the colon. From this point it dilates then gradually tapers to the anal opening. In addition to this character, the six bands of longitudinal muscles that appear as dark streaks on the outer rectal wall, also aid in fixing the limit of the rectum although the muscular bands may sometimes be seen on the colon wall as well.

Upon dissection it will be noticed that the six folds in the colon have been continued into the rectum where they have undergone some modifications. In the rectum the folds have been reduced in height to .12 mm., but their width has been increased to .58 mm. at their widest part though they become narrower as the rectum tapers. With an increase in the width of the folds, there is a proportional decrease in their distance apart, each elevation rising within .008 mm. of its neighbor causing the intervening furrows to be very narrow. Lastly, the surface of the rectal folds are fairly smooth and flat.

The musculature of the rectum consists of a thin layer of circular muscle outside of which lie six rows of longitudinal muscles. These longitudinal muscles are placed just opposite the furrows between the rectal folds and are, therefore, external indications of the location of these elevations.

The epithelium of the rectum consists of columnar cells closely packed together whose nuclei and cell walls are well marked. The chitin lining the lumen appears, in all my sections, to be very thin.

At the posterior end of the rectum, all the characters that have just been mentioned are lost or become very indistinct. Finally the rectum opens to the exterior through the anus. The anus marks the posterior limit of the intestine and is situated above the genital opening.

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EXPLANATION OF PLATES

Fig. 1. Sagittal section of the alimentary tract in situ.

Fig. 2. General external view of the alimentary tract
as seen from dorsal surface.

Fig. 3. Longitudinal profile of the alimentary tract
(Vertical and horizontal scales different. Letters refer to the
location of the sections. figured.

Fig. 4. Diagrammatic reconstruction of the oesophagus.

Fig. 5. Diagrammatic reconstruction of the crop.

Fig. 6. Diagrammatic reconstruction of the gizzard.

Fig. 7. Diagrammatic reconstruction of the cardiac valve.

Fig. 8. Diagrammatic reconstruction of the pyloric valve.

Fig. 9. Diagrammatic reconstruction of the colon.

Fig. 10. Diagrammatic reconstruction of the rectum.

Fig. 11. Section through an alveolus of a salivary gland.

Fig. 12. Cross section of oesophagus.

Fig. 13. Longitudinal section of oesophagus.

Fig. 14. Cross section of crop.

Fig. 15. Longitudinal section of crop.

Fig. 16. Cross section of gizzard.

Fig. 17. Longitudinal section of gizzard.

- Fig.18 and 19 Cross section of cardiac valve
- Fig.20 Cross section of cardiac valve at the point where the posterior lobes of the gastric caeca open into the lumen of the stomach.
- Fig.21 Cross section of a Malpighian tubule with trachea
- Fig.22 Longitudinal section of a Malpighian tubule
- Fig.23A Longitudinal section of the cardiac valve
- Fig.23B Epithelial cells from the anterior lobe of gastric caecum showing cilia.
- Fig.24 Longitudinal section of the cardiac valve between the gastric caeca.
- Fig.25 Cross section of the stomach
- Fig.26 Oblique cross section of the stomach.
- Fig.27 Longitudinal section of the stomach.
- Fig.28 Oblique longitudinal section of the stomach.
- Fig.29 Cross section of the pyloric valve.
- Fig.30 Long. " " " " "
- Fig.31 Cross section^{of} ~~an~~ ilium
- Fig.32 Long. " "
- Fig.33 Cross section of the colon
- Fig.34 Long. " " " "
- Fig.35 Cross section of the rectum.
- Fig.36 Long " " " "

ABBREVIATIONS.

A. Hypopharynx	I. Malpighian Tubule
B. Salivary Duct	J. Trachea.
C. Oesophagus	K. Stomach.
D. Crop	L. Ilium
E. Salivary Gland	M. Colon
F. Gizzard	N. Rectum
G. Anterior lobe of Gastric Caecum	O. Anus
H. Posterior " " "	

ci. Cilia
 c.d. Cup-shaped Depressions
 chi. Chitin
 c.m. Circular Muscle
 c.t. Connective Tissue
 c.v. Cardiac Valve
 d. Duct
 d.c. Disintegrating Cells
 epi. Epithelium
 l.m. Longitudinal Muscle
 m. Membrane
 m.c. Mucous Cells.
 n. Nidi
 p.v. Pyloric Valve
 r.g. Rectal Gland.
 s.c. Serous Cells
 t. Teeth
 tr. Trachea
 V V-shaped Islands

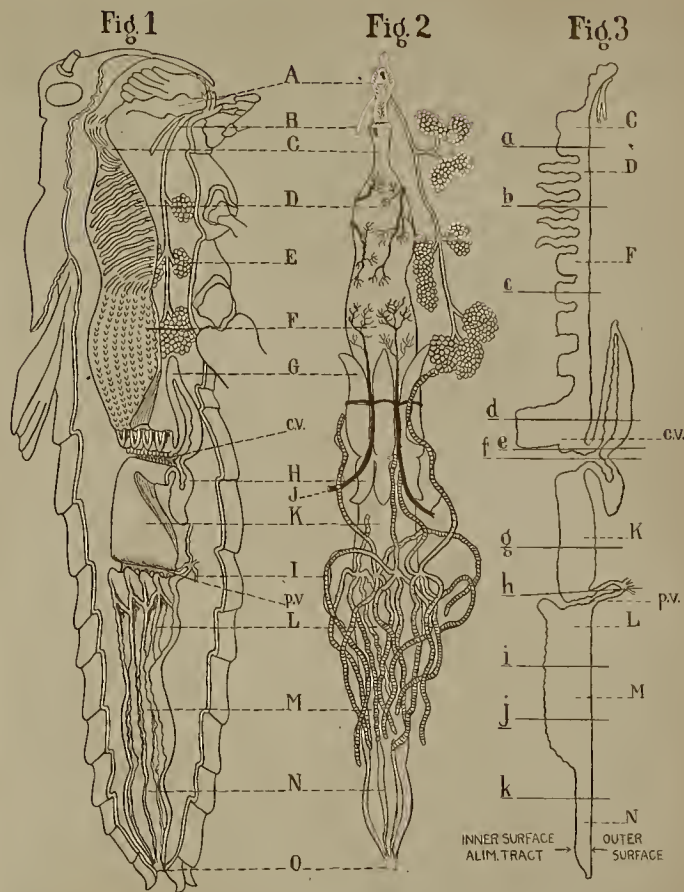


Fig.4



Fig.5



Fig.6



Anterior

Fig.7



Fig.8

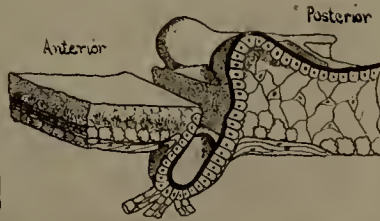


Fig.9



Fig.10



Fig.11

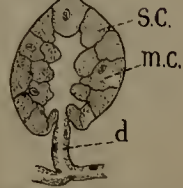


Fig.12

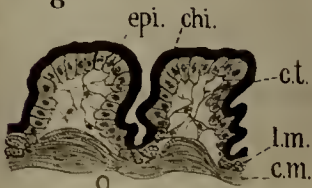


Fig.13



Fig. 14

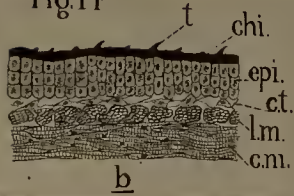


Fig. 15



Fig. 16

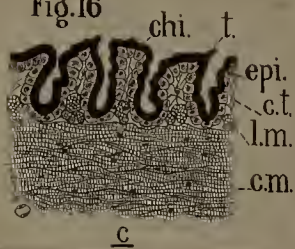


Fig. 17

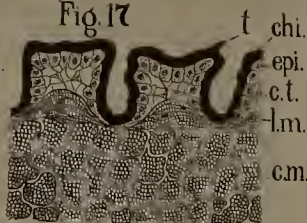


Fig. 18

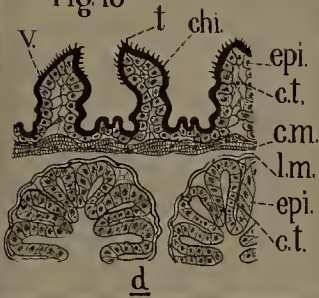


Fig. 19

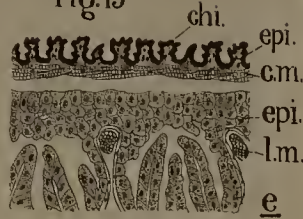


Fig. 21

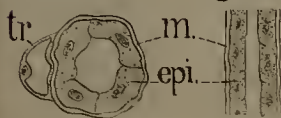


Fig. 22

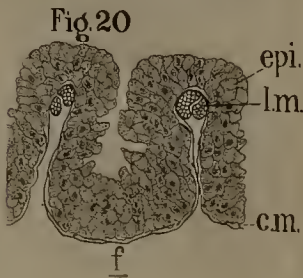


Fig. 23A

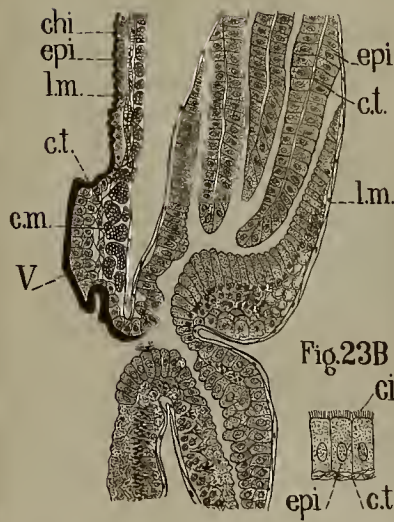


Fig. 23B



Fig. 24

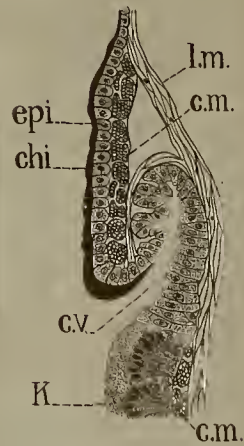


Fig. 25



Fig. 26



Fig. 27



Fig. 28

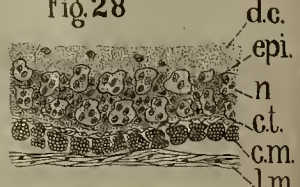


Fig.29

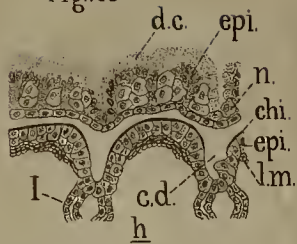


Fig.30



Fig.31

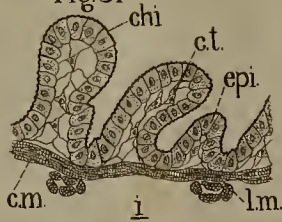


Fig.32

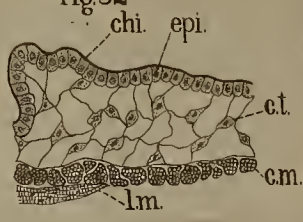


Fig.33

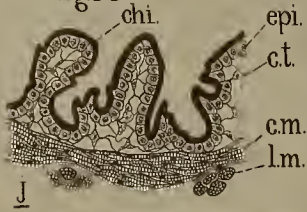


Fig.34

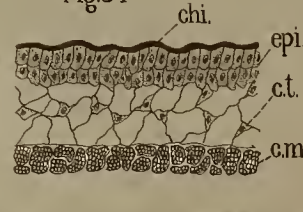


Fig.35

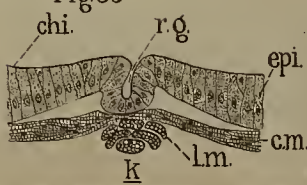


Fig.36



