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by Roscoe W Wells

A THESIS Submitted to the Graduate Committee in partial fulfillment of the requirements for the
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Montana State University
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A STUDY OF THE ANATOMY AND HISTOLOGY OF
THE DIGESTIVE TRACT OF *TABANUS ATRATUS* Fabricius.

A contribution from the Entomological
Laboratory of Montana State College.
By R. W. Wells.

Introduction

In spite of the importance of many species of Tabanidae as parasites of horses and cattle, as pests of man and as possible agents in the transmission of certain diseases, very little has been published dealing with their internal anatomy. This lack of literature is especially noticeable concerning American species.. The most valuable work on the subject to date is that of Patton and Craig (Text book of Medical Entomology), which concerns species native to India.

The present paper is a result of a study of the anatomy and histology of the digestive tract of *Tabanus atratus* Fabricius and is submitted as a part of the requirements for the Degree of Master of Science.

The specimens used in this study were obtained from a southern biological supply firm. They were preserved in formalin-alcohol.

The digestive tract of *Tabanus atratus* consists of the basipharynx, the oesophageal pump, the oesophagus, the proventriculus, the ventriculus, the pyloric valve, the ileum, the Malphigian tubes, the colon, the rectum, and the salivary glands.

Basipharynx

The basipharynx (Pl.1, figs. 1 and 2, bph) is a tube, the anterior half of which is collapsible and fits into the posterior half. When collapsed and seen from the front (fig.2) it is spatula-shaped and is anteriorly concave and posteriorly convex. Dorsally it empties into the cesophageal pump (fig.1, oep); ventrally it is continuous with the labrum-epipharynx (lep) and with the labium-hypopharynx (lhp). The anterior, concave wall is flexible and by the contraction of a set of horizontal muscles (bm), which are attached to the front of the head capsule below the anterior arms of the tentorium, may be pulled away from the posterior wall, thus forming a hollow tube. This creates a suction, which, during the act of feeding, draws the blood into the cavity of the basipharynx. Dorsally the lateral edges are prolonged on each side of the cesophageal pump into horns or cornua (fig.1, h). Muscle tendons (fig. 1, ht) extend from each of these to the dorsal portion of the head capsule and together with muscles (fig.3, hl) joining the lateral part of each cornua to the corresponding anterior arm of the tentorium, hold the basipharynx in place.

Cesophageal Pump

The cesophageal pump (fig.1, oep), a dipper-shaped structure, fits between the cornua of the basipharynx and, during the act of feeding receives the food from the latter. Ventrally its flexible wall converges to a slit (fig.3, s) through which it communicates with the basipharynx. This converging wall is completely encased by an anterior

and a posterior series of horizontal, semi-circular muscles, which are attached to the cornua (fig.1, wm). The dorsal portion of the posterior series is covered by another series of semi-circular muscles (fig.1, cm), which are oblique. These are attached to the chitin on both sides of the oesophageal pump immediately above the muscles which they cover.

The dorsal wall of the oesophageal pump is a flexible, chitinous diaphragm to which is attached a strong, vertical muscle (oepm). This muscle joins the head capsule above, and by contracting the diaphragm upward, greatly enlarging the cavity of the oesophageal pump. This creates suction and the food is thus drawn from the basipharynx into the cavity of the pump. Opposed to the vertical muscle is one (tm) which extends obliquely upward from the tentorium and attaches to the anterior wall.

Posteriorly the pump is continued as a narrowing tube between the oesophageal ganglia. Four muscles are attached to its distal end, just posterior to the ganglia (g). These attach to the occiput and, in conjunction with those previously mentioned, control the action of the pump.

Patton and Craig (Text book of Medical Entomology p. 26 and plate 5, fig.1, ph) discuss the oesophageal pump as the pharynx, and the basipharynx as the buccal cavity. The former terms were used by Peterson (The Head-Capsule and Mouth Parts of Diptera, 1916, p.51) and have been adopted by the writer because they seem to more adequately express the homologies concerned.

The Oesophagus

The oesophagus (Pl.1, fig.1, oe) communicates with the oesophageal pump immediately behind the oesophageal ganglia (gg) and continues as a tube of even caliber through the cervical region and into the thorax where the crop immediately diverges from it ventrally. Just posterior to where the crop diverges, the oesophagus joins the anterior, basal portion of the proventriculus (pv) and does not make a dorsal bend as in the housefly.

The wall of the oesophagus (Pl.III, fig.7) consists of a basement membrane (bm), a pavement epithelium (ep), a chitinous intima (ch), a layer of circular muscles (cm), and an outer layer of longitudinal muscles (lm). The wall of the tube when empty has several longitudinal folds. The cells of the epithelium are flat with large nuclei. Where the crop diverges from the oesophagus, the number of circular muscles (cm) is greatly increased (fig.7). This thick coat of muscles extends a short distance along the duct of the crop and probably aids the crop in its function.

Crop

The crop duct continues posteriorly, ventral to the proventriculus and the salivary glands, to the third segment of the abdomen where, ventral to the ventriculus, it widens abruptly, forming a bilobed sack, the crop (Pl.I, fig.5, cr). The crop and crop duct when dissected appear to have a double wall. The outer wall (Pl.III, fig.7)

is a separate layer of striated muscle fibers (ml). The inner wall is membranous tissue containing large nuclei.

In cross section the wall of the crop (Pl.III, fig.1) consists of a nucleated membrane (mem), a chitinous intima (ch) and an outer layer of longitudinal muscles (lm). When sectioned nearer the neck of the crop (fig.2) there appears to be a set of circular muscles (cm) outside of the longitudinal muscles.

Patton and Craig (p.103) describe a dorsal crop, which they say diverges dorsally from the anterior end of the proventriculus and extends posteriorly into the abdomen. In the specimens examined during the present study the only part found to be analogous to such a structure is the aorta (Pl.I, fig.1, ao) leading into the head. The author has traced it anteriorly, parallel to the oesophagus, to a point where it turns upward just posterior to the brain. Its posterior portion lies dorsal to the alimentary canal and joins the pulsating vesicle, or heart, in the abdomen..

Proventriculus

The proventriculus (Pl.I, fig.5, pv) extends from the anterior part of the thorax into the first segment of the abdomen. Anteriorly it widens into two lateral processes (apr), which extend obliquely forward and upward. Each of these taper to a small diameter near the wall of the first thoracic segment, to which they are attached by small muscles. Posterior to this widening, the proventriculus

continues through the thorax, gradually diminishing in diameter. Its wall is beset with globular protrusions (Pl.II, fig.4, ev) which are pouch-like evaginations of the wall.

The wall itself is composed of a basement membrane (Pl.II, fig.7, bm) a cubical epithelium (ep), and an intima which stains with eosin. Encircling the lumen in the anterior end of the proventriculus, where it joins the oesophagus, is a thickening of the epithelium (Pl.III, fig.7, vth), composed of columnar cells. These cells are thick distally and narrow basally, throwing the epithelium into folds, which have a leaf-like appearance in longitudinal sections. Encircling the proventriculus at this region are a great number of circular muscles (cm), which serve to draw the folds together in a valve-like structure. Outside of the basement membrane of the proventriculus is a nucleated membrane (Pl.II, fig.7, nmem), and outside this a network of muscles which cannot be distinguished as separate circular and longitudinal layers. Exterior to this network of muscles is a nucleated membrane (rm) bearing on its outer surface chitinous ridges, which are thickened distally.

The author regards the valvular thickenings (Pl.III, fig.7, vth), previously described, as homologous to a cardiac valve and as the anterior end of the mesodeum or midgut. The term proventriculus is used here merely to indicate an anterior region of the ventriculus or mesodeum. The term is applied in Orthoptera and Coleoptera to a portion of the stomodeum anterior to the cardiac valve, lined with chitinous

teeth or ridges and provided with strong circular muscles. What is termed the proventriculus in this paper is lined by an intima, as described, which stains with eosin, as does the chitinous intima in no other part of the digestive tract. This intima becomes thinner posteriorly and, near where the alimentary canal enters the abdomen, it discontinues. In this region the evaginations are in longitudinal rows. The evaginations diminish in size and the longitudinal elevations continue as longitudinal folds and the cells of the epithelium become more and more columnar, typifying those of the villi of the ventriculus, which are described later.

Ventriculus

The ventriculus (Pl. I, fig. 5, v) is an ellipsoidally ovate structure lying ventrally in the abdomen. Its anterior end tapers into an elongated portion which joins the proventriculus. Posteriorly, it tapers abruptly and joins the hind gut a little anterior to the pyloric valve. Its walls are thrown into longitudinal folds and indentures which are sub-divided into what Patton and Craig called villi (vil). These project into the lumen.

The walls are composed of a basement membrane (bm), an epithelium and circular (cm) and an outer (lm) longitudinal layer of muscles. The cells of the epithelium are columnar. In the villi the cells are distally blunt and basally narrowed producing in section a leaf-like appearance. The nuclei stain very deeply. Many vacoules (vac) appear in the distal end of the cells of the villi. In the lumen

appear deeply stained globules. Some of these are joined to the cells of the villi and undoubtedly are digestive secretions in the process of being constricted off and liberated in the lumen.

Pyloric Valve

The pyloric valve (Pl.II, fig.2, plv) and Pl.I, fig.5, plv) consists of a constriction of the anterior end of the proctodeum or hind gut and a forward protrusion of the wall of the ileum (Pl.I, fig.5 and Pl.II, fig.2) over the constriction. The walls of the valve originate from the proctodeum and join the walls of the ventriculus a little anterior to the constriction (Pl.II, fig.2, x). They consist of a basement membrane, a pavement epithelium, a chitinous intima (ch), a layer of circular (cm) and a layer of longitudinal (lm) muscles. The circular muscles at the constriction of the valve are very numerous.

Ileum

The ileum is an oval, pouch-shaped, distensible structure, (Pl.I, fig.5, il) having, when empty, deep longitudinal folds. The anterior end is narrowed into a neck extending anterior to the constriction of the pyloric valve. Its walls (Pl.II, fig.1) consist of a chitinous intima (ch), an epithelium (ep), a basement membrane (nm), circular muscles (cm) constricting the epithelium and an external layer of longitudinal muscles (lm). The epithelium, the cell walls of which are indistinct, is thick in the intervals between the circular muscles and thin at the points of constriction. The chitinous intima is modified

into circular, acute, processes, which are directed posteriorly and probably aid in expelling the contents of the ileum. Some of these chitinous processes appear to be pectinate, with minute teeth or barbs.

Malpighian Tubes

The Malpighian tubes (Pl.I, fig.5, mt), four in number, join the ileum in the region of the pyloric valve. They are of comparatively even diameter except proximally, where they taper somewhat before entering the ileum. In length, they equal approximately three times the length of the abdomen. They are richly supplied with tracheae, from which they are difficult to untangle. Winding in all directions, they reach practically every part of the abdomen (none having been found extending into the thorax). Under the dissecting microscope (Pl.II, fig.5) they are seen to have an epithelium of large, flat cells of the pavement type, which surround the lumen in a single layer. The nuclei (n) appear as large, colorless areas within the cells. In stained preparations the wall is found to consist of a thick basement membrane (bm), an epithelium (ep) of large cells with deeply stained nuclei (n), and a chitinous intima (ch) surrounding the lumen. At the basal end of the tubes where they taper before entering the ileum, the cells of the epithelium are much smaller and the deeply stained nuclei correspondingly much more numerous.

Colon

The colon (Pl.I, fig.5, co) after extending posteriorly a short distance from the ileum, turns abruptly upward to the left, curves

anteriorly a short distance, then ventrally and posteriorly to the rectum (r). It is of fairly constant diameter and, when empty, its walls are somewhat folded. The wall consists of a basement membrane (Pl.III, fig.4, bm), an epithelium of cuboidal cells (ep), a chitinous intima (ch) and the usual layers of circular (cm) and longitudinal muscles (lm). The chitinous intima is not modified as in the ileum. The cells of the epithelium are of nearly uniform size and shape (fig.4), being externally rounded and internally flattened. At its anterior end where it joins the rectum, the number of circular muscles is greatly increased.

Rectum

Anteriorly the rectum (Pl.I, fig.4) begins as a tube much like the colon, then widens into a cone-shaped region, the apex of which is posterior. This cone-shaped region owes its shape to six wedge-shaped structures called papillae (or glands) which project into the lumen with their apices directed posteriorly. They have a basal expansion (Pl.III, fig.5. lp) or lip which protrudes as an oval prominence beyond the rectal wall. Tracheae (Pl.I, fig.4, tr) enter the glands along a median groove in this prominence.

The wall of the rectum (Pl.III, fig.5) consists of a basement membrane (bm), a pavement epithelium (ep), a chitinous intima (ch), an internal layer of circular, and an external layer of longitudinal muscles.

A large group of circular muscles serve as a sphincter at the anterior end of the rectum and another at the posterior end, where it is

constricted to form the anus.

The walls of the papillae (Pl.III, fig.5) consists of an epithelium (ep) of large columnar cells and a chitinous intima with many perforations (pf) around which the chitin projects into spinose processes. The interior of a papilla is lined with a nucleated, plasmodium-like membrane (Plm) which is slightly separated from the epithelium and communicates with the latter through tubes formed by the tissues of the membrane.

Into the cavity thus formed several tracheae enter and their minute branches reach the cells of the epithelium through the tubes just described.

Salivary Glands

Two tubular salivary glands (Pl.I, fig.5, sg) lie parallel to the proventriculus, and extend into the third abdominal segment. Their diameter, greatest near the posterior end, gradually diminishes anteriorly. Near the anterior end of the thorax they bend ventrally, and join into a small duct under the nerve cord. This duct extends anteriorly through the cervical region into the head, still ventral to the nerve cord and bends downward, widening into a club-shaped reservoir (Pl.I, fig.1, srv). This reservoir empties into a trough-shaped chitinous salivary pump (sp), which has a dorsal, flexible wall. A set of finely divided muscles (sm), attached obliquely from the basi-pharynx, dilate this flexible wall of the pump, creating suction, which draws the salivary fluid into it from the reservoir.

The pump narrows into a tube, which penetrates the entire length of the labium hypopharynx (lhp), where the saliva is discharged at its distal end.

Explanation of Plates

Abbreviations Used.

a.	anus
ao.	aorta
apr.	anterior process of proventriculus
ar.	anterior end of the rectum
bm.	basement membrane
bph.	basipharynx
c.	nerve cord
ch.	chitinous intima
cm.	circular muscle
co.	colon
cr.	crop
ep.	epithelium
ev.	evagination
g.	ganglion
gl.	globules in lumen of ventriculus
hl.	muscle between cornu and tentorium
ht.	tendon from cornu
il.	ileum
int.	intima of proventriculus
lep.	labrum epipharynx
lhp.	labium hypopharynx
lm.	longitudinal muscle

lu.	lumen
mem.	membrane
ml.	muscular layer
mt.	Malphigian tube
n.	nucleus
nmem	nuclear membrane
oe.	oesophageal pump
oepm.	muscle of the oesophageal pump
op.	oval process on rectum
pf.	perforations on rectal papillae
plm.	plasmodial membrane
plv.	pyloric valve
pv.	proventriculus
r.	rectum
rg.	rectal papilla
rm.	ridged membrane
sg.	salivary gland
sm.	muscles of salivary pump
sp.	salivary pump
sphm.	sphinctor muscle
srv.	salivary reservoir
t.	tentorium
tm.	tentorial muscle
tr.	trachea
v.	ventriculus

vac. vacuole
vil. villus
vth. valvular thickening
wm. well muscle of oesophageal pump
x. end of chitinous intima where ventriculus
joins the hind gut.

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Plate I

- Fig. 1. View of a portion of the internal anatomy of the head with part of left side of the head capsule removed.
- Fig. 2. Front view of oesophageal pump and basipharynx.
- Fig. 3. Front view with front part of oesophageal pump cut away.
- Fig. 4. Rectum.
- Fig. 5. Dorsal view of alimentary tract with crop out of normal position.

Plate II

- Fig. 1. A portion of a longitudinal section of the wall of the ileum.
- Fig. 2. Longitudinal section of the pyloric valve and a portion of the ileum.
- Fig. 3. A portion of a longitudinal section of the wall of the ventriculus.
- Fig. 4. A lateral view of a portion of the proventriculus.
- Fig. 5. A view of a portion of a Malphigian tube under magnification.
- Fig. 6. A cross section of a Malphigian tube.

Plate II, Continued

- Fig. 7. A portion of a longitudinal section of the proventriculus.

Plate III.

- Fig. 1. A portion of a cross section of the crop.
- Fig. 2. A portion of a cross section near the neck of the crop.
- Fig. 3. A longitudinal section of the anterior end of the rectum.
- Fig. 4. A portion of a longitudinal section of the colon.
- Fig. 5. A longitudinal section of a rectal papilla and of a portion of the rectal wall.
- Fig. 6. A cross section of a salivary gland.
- Fig. 7. A longitudinal section of the posterior end of the oesophagus, of the anterior end of the crop duct, and of the anterior end of the proventriculus.

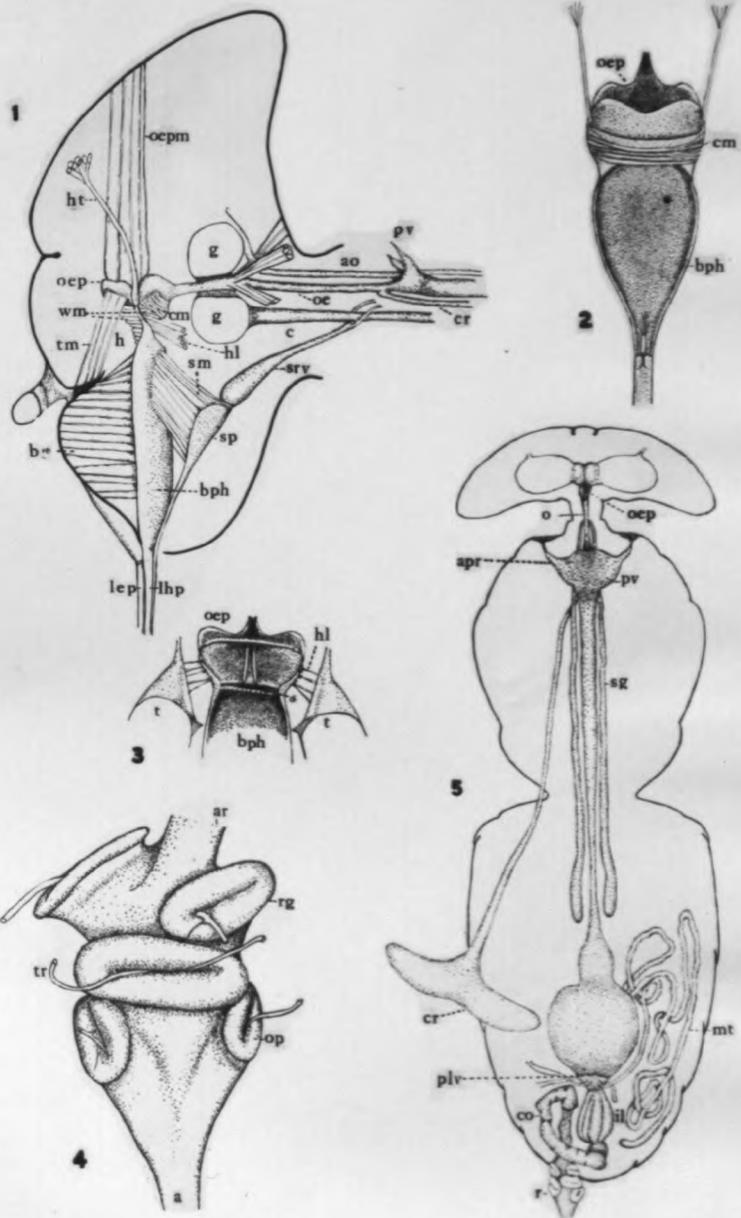


Plate I

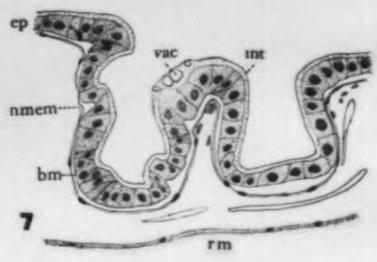
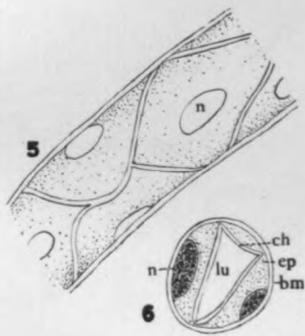
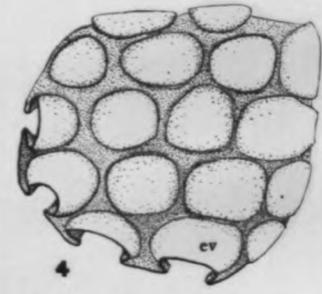
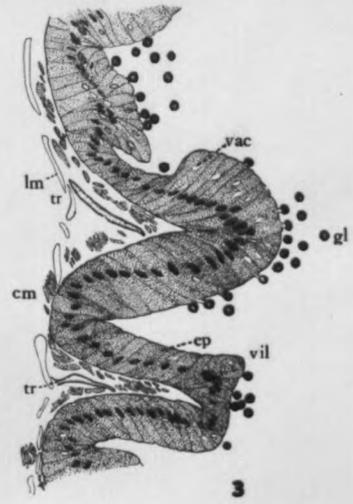
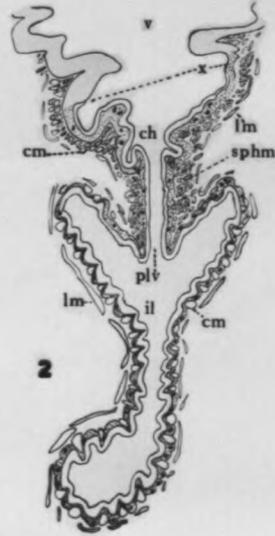
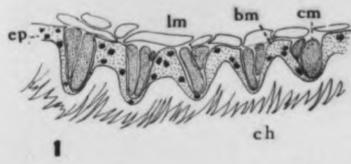


Plate II

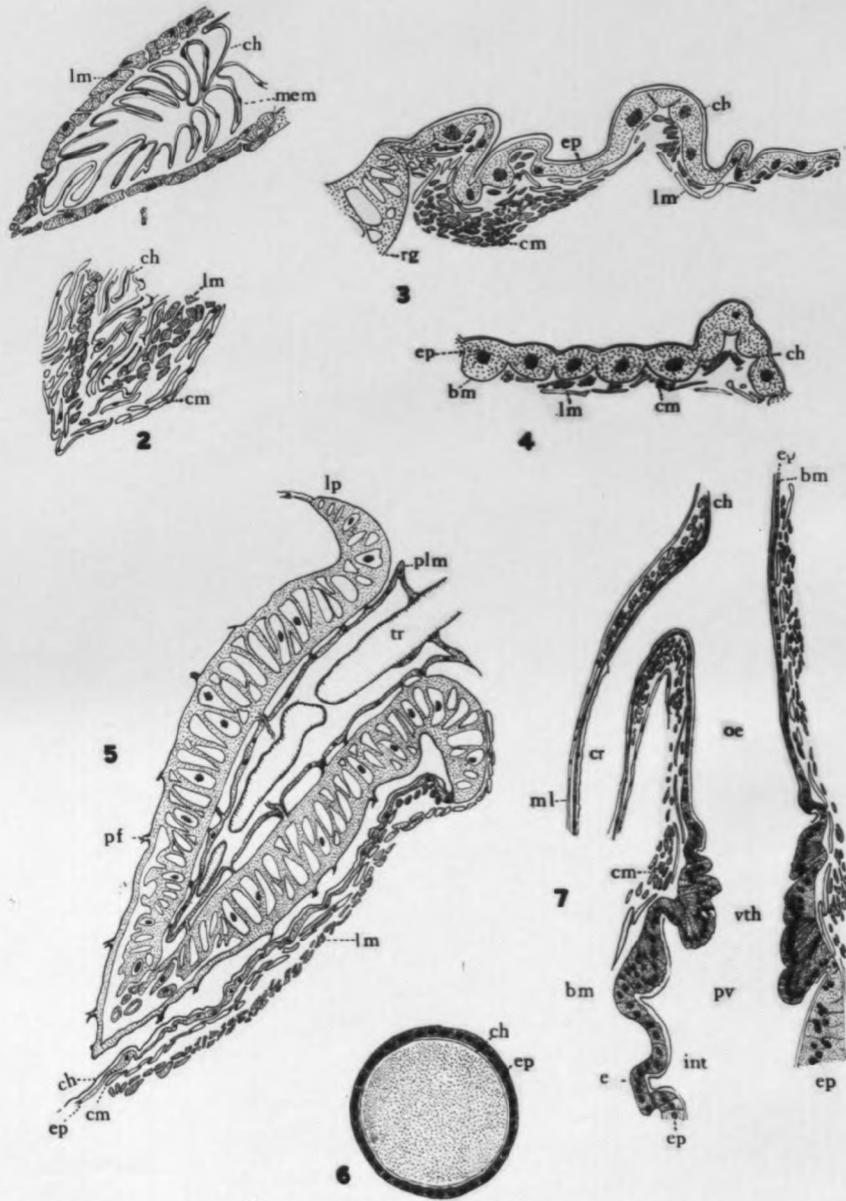


Plate III

