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THE GROSS AND MICROSCOPIC ANATOMY OF THE DIGESTIVE TRACT OF THE OYSTER CRASSOSTREA VIRGINICA (GMELIN)[1]

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Abstract

The gross and microscopic anatomy of the digestive tract of *Crassostrea virginica* (Gmelin), the common oyster of commerce of the North Atlantic Coast, is described. The dorsoventrally compressed mouth bounded by two pairs of labial palps leads into a crescentic oesophagus, thence to the anterior chamber of the stomach from which a complex caecum extends into anteriorly and posteriorly directed spiral appendices. The posterior chamber of the stomach bears a chondroid gastric shield and leads into an elongated chamber which is incompletely divided by two typhlosoles into a style-sac and mid-gut. The intestine is divisible into ascending, median, and descending limbs, the latter merging into the rectum which terminates on the dorsal surface of the adductor muscle. Extensively branched tubular digestive diverticula exit from the stomach by a series of ducts along the margin of the caecum and the posterior stomach. The complete digestive tract is lined by a simple columnar epithelium which is ciliated throughout with the exception of the upper lip or fused external palps, the lower side of the gastric shield in the posterior stomach, and the tubules of the digestive diverticula. Mucous secreting and eosinophilic epithelial cells occur in varying numbers along the course of the tract. Phagocytes are present between the lining epithelial cells, among the peripheral collagenous and muscle fibers, as well as in the lumen of the tract. The gastric shield is shown to be intimately attached to the underlying epithelium by a central clip as well as by minute cytoplasmic processes. The anatomical relationships are compared with various lamellibranchs including the Chilean oyster, *Ostrea chilensis* Philippi; the European oyster, *Ostrea edulis* L.; and the Portuguese oyster, *Gryphea angulata* Lamarck.

Introduction

Crassostrea virginica (Gmelin), the Atlantic coast oyster of commerce, occurs intermittently in coves, bays, and estuaries, and at the mouths of tidal rivers along the eastern seaboard of North America from the south shore of the Gulf of St. Lawrence to the Gulf of Mexico. Although Clark (1920 (6)) has made the statement that the oyster is the best known marine animal in the world, both physiological and pathological investigations have been seriously curtailed by the inadequacy of descriptive data relative to its gross and microscopic anatomy. Brooks (1880 (4)) in a brief account of the development of the oyster *Crassostrea (Ostrea) virginica* described the visceral mass as comprising a folded oesophagus, an irregular stomach surrounded by a dark greenish "liver", and a convoluted intestine. Ryder (1880 (26)) subsequently outlined the course of the digestive tract of the same species referring to the internal foldings of the stomach, the course of the intestine, and the extent of the "liver". Dahmen (1923 (7)) gave a comprehensive account of the gross structure of the tract of *Ostrea chilensis*

Philippi and also referred to its histology.   In an introduction to a physio-
logical study of *Ostrea edulis* L., Yonge (1926 (33)) described the gross ana-
tomical relationships of the tract briefly and the microscopic anatomy in
somewhat more detail.   Leenhardt (1926 (17)) dealt largely with the histolog-
ical structure of the tract of the Portuguese oyster, *Gryphea angulata* Lamarck
(*Crassostrea angulata* Gunter, (1950 (14)), and made only minor references
to gross anatomical relationships.   The present study of the digestive tract
of *Crassostrea virginica* was accordingly undertaken because of the paucity
of data on both the gross and microscopic anatomy of the oyster and of this
species in particular.

Materials and Methods

All oysters used in this investigation were obtained from Malpeque Bay,
Prince Edward Island, Canada.   Initial dissections were carried out on fresh
specimens as well as following preservation and hardening in 5% formalin.
The gross anatomical relationships of the lumen of the tract were determined
from casts made by injecting alkaline latex or vinylite resin through the mouth
and the anus of fresh specimens and subsequently removing the surrounding
tissues.

For histological studies, the relative merits of a number of the more common
fixatives were determined and, of these, Davidson's solution of the following
formula proved most efficacious:

formalin (analytical reagent 35%)	20 parts
glycerin	10 parts
alcohol, 95%	30 parts
glacial acetic acid	10 parts
water (sea water where available)	30 parts

After fixation for 24 hours, specimens were stored in a solution of the same
formula minus the glacial acetic acid.   Following dehydration, toluol was
employed for clearing and Tissuemat of melting point 60° to 62° C. for imbed-
ding.   Sections were cut at 5 to 10 μ and stained with Erhlich's haematoxylin
and Triosin (Galigher, 1934 (12)), iron haematoxylin, Mallory's triple stain,
Van Gieson's picrofuchsin, and cresyl echt violet.

Newly-set spat from less than 1 mm. to 10 mm. in length were fixed in
Bouin's fluid and cleared in creosote or clove oil with or without prior staining
in alum-cochineal.   Serial sections cut at 10 μ were counterstained with
light green.

Gross Anatomy of the Digestive Tract

Terminology

The terminology of Pelseneer (Nelson, 1938 (23)) with regard to the axes
of symmetry of the oyster will be followed in this paper.   Accordingly the
principal axis of the oyster lies in a line drawn through the mouth and the
anus.   The hinge is anterodorsal, the palps and forward portions of the gills
project ventrad, while the hinder portions of the gills extend both ventrad
and posteriorly.

General Anatomical Relationships

The right valve of *Crassostrea virginica* is flattened and usually uppermost in naturally-setting spat, while the left valve is cupped toward the hinge to accommodate the visceral mass. Removal of the right valve exposes the right lobe of the mantle, whose thickened and darkly pigmented free margin bears minute tentacles. The single adductor muscle is located slightly posterior to a line bisecting the principal axis and somewhat nearer the dorsal than the ventral margins of the valves. The crescentic posterodorsal division of the muscle is composed of smooth fibres, while the anterior "catch" division consists of striated fibers (Yonge, 1926 (33)). On the removal of the right lobe of the mantle (Fig. 1), the visceral mass, the gills, and the pericardial cavity are exposed. The visceral mass is ovoid anteriorly and forks posteriorly. The ventral branch is triangular with its apex extending to the mid-level of the adductor muscle. It comprises a posterior diverticulum of the stomach, the so-called style-sac, fused lengthwise with the first segment of the intestine or the mid-gut, as well as the ascending or recurrent limb of the intestine. The cylindrical dorsal branch of the visceral mass encloses the rectum, which terminates on the dorsal margin of the adductor muscle. The ventral anterior margin of the visceral mass is surmounted by two pairs of labial palps whose posteriorly-directed free ends overlap the anterior margins of the gill plates.

Labial Palps and Mouth

The labial palps are roughly triangular plates with an acute apex directed posteriorly (Figs. 1 and 2). Their ventral margins are somewhat crescentic while the dorsal margins are straight and fused anteriorly to the ventral surface of the visceral mass. The outer pair are slightly larger than the inner pair and, except at the anterior roots, are entirely free from the inner palps. The lateral surfaces of the external palps and the medial surfaces of the internal palps are smooth or plane. The adjacent medial surfaces of the external palps and the lateral surfaces of the internal palps are coarsely fluted with ridges directed obliquely towards the mouth opening. The latter takes the form of a dorsoventrally compressed slit at the outer margin of the valve-hinge extremity of the body. Ryder (1880 (26)) described it as appearing between the upper median angles of the palps. The outer pair of palps extend anteriorly and dorsally around the mouth where they fuse in the form of a hood or upper lip. The inner palps are united with each other along their mid-dorsal line for one-half or more of their length and their fused anterior ends are elevated as a fleshy ridge or lower lip. Dahmen (1923 (7)) and Yonge (1926 (33)) have also shown, for O. chilensis and O. edulis respectively, that unlike the majority of lamellibranchs, these species have the inner and outer palps of the two sides fused in the region of the mouth. In addition, however, in the latter species the outer palps are united for one-fourth of their length so that the mouth is entirely enclosed.

Mouth Cavity and the Oesophagus

The mouth opening leads into an elongated dorsoventrally flattened mouth cavity (Fig. 19). Ryder (1880 (26)) noted that "the mouth is so wide the animal can scarcely be said to have an oesophagus". Leenhardt (1926 (17)) described an elongated passageway between the oral opening and the anterior oesophageal orifice in *G. angulata* and suggested its analogy to a pharynx. The presence of this passageway would appear to be a characteristic of the genus *Crassostrea*, since in *O. chilensis* (Dahmen, 1923 (7)) and *O. edulis* (Yonge, 1926 (33)) the mouth leads directly into a short oesophagus. In *C. virginica* the oesophagus arches posterodorsally at an angle of approximately 45 degrees to the long axis of the palps. It measures approximately one-fifth of the maximum anterior–posterior length of the visceral mass and enters the anterior chamber of the stomach at the junction of the latter with the caecum (Figs. 3, 4, 5).

Stomach

The stomach (Figs. 3, 4, 5, 21, 22) is a saccular organ centrally located in the posterior two-thirds of the ovoid portion of the visceral mass. It is completely surrounded by the greenish-brown tubules of the digestive diverticula. The stomach proper is divisible into a smaller anterior chamber grading into a somewhat larger posterior chamber. The anterior chamber appears as an enlargement at the base of the oesophagus. An extensive complex outpouching or caecum arises from its left ventral surface, and takes the form of an oblique channel, with spirally directed anterior and posterior limbs or appendices. The anterior appendix is smaller than the posterior appendix and projects dorsad along the base of the oesophagus (Fig. 4). It comprises one and one-quarter to one and one-half turns which follow a counterclockwise direction. The large posterior appendix appears bandlike

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FIG. 1. Gross anatomical relationships of *C. virginica*, as viewed with the right valve and the right mantle removed. The visceral mass is heavily outlined. A.M., adductor muscle; G.P., gill plates; L.MA., left mantle; L.P., left labial palps; L.V., left valve; P.C., pericardial cavity; V.M., visceral mass.
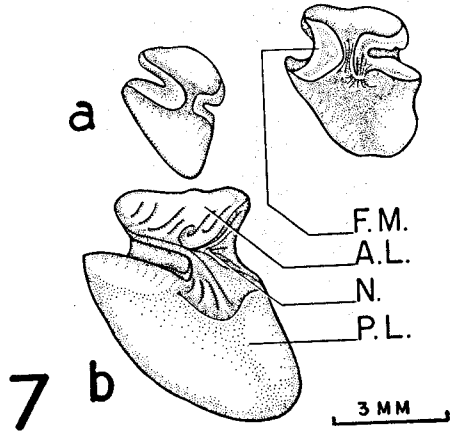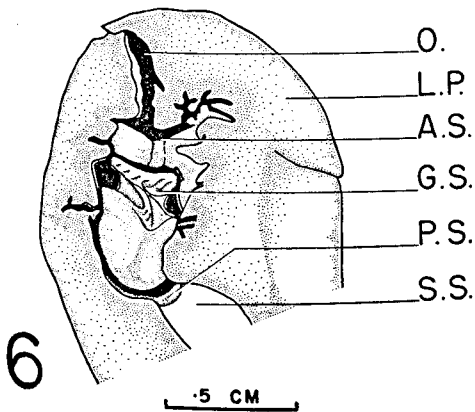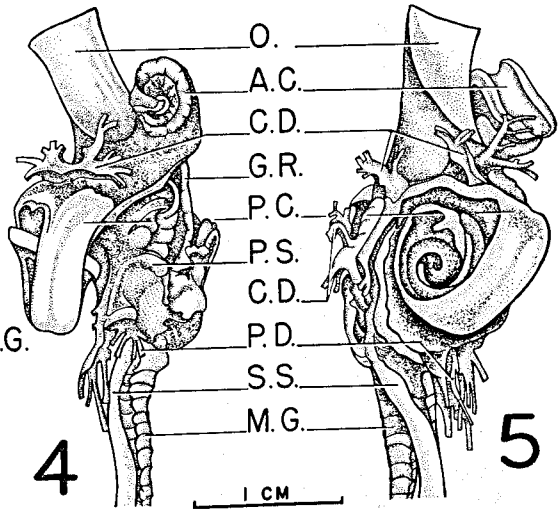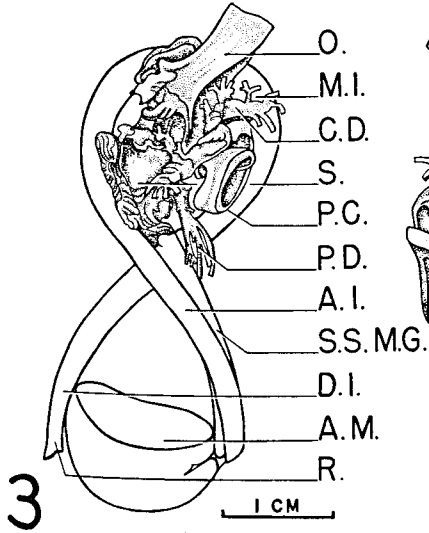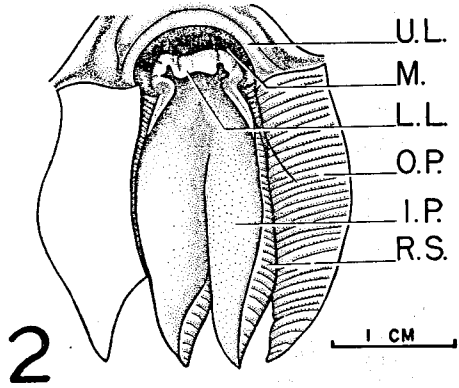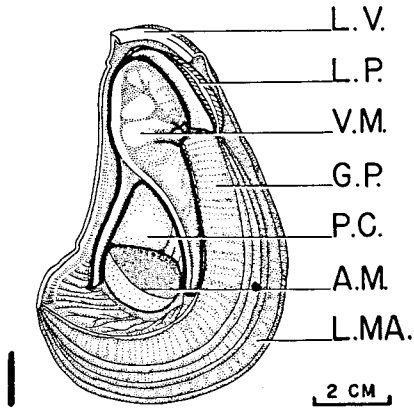
FIG. 2. Mouth opening from the anteroventral aspect, with the inner and outer labial palps spread laterally. I.P., inner labial palp (left); L.L., lower lip; M., mouth; O.P., outer labial palp (left); R.S., ridged surfaces; U.L., upper lip.

FIG. 3. Latex mold of the lumen of the digestive tract, exclusive of the tubules of the digestive diverticula, viewed from the right lateral aspect. A.I., ascending limb intestine; A.M., adductor muscle; C.D., caecal ducts of digestive diverticula; D.I., descending limb intestine; M.I., median limb intestine; O., oesophagus; P.C., pericardial cavity; P.D., posterior gastric ducts of digestive diverticula; R., rectum; S., stomach; S.S.M.G., style-sac and mid-gut.

FIGS. 4 and 5. Latex mold of the lumina of the oesophagus and stomach viewed from the left lateral aspect (Fig. 4) and the left ventral aspect (Fig. 5). A.C., anterior appendix of caecum; C.D., caecal ducts of digestive diverticula; G.R., gastric ridges for attachment gastric shield; M.G., mid-gut; O., oesophagus; P.C., posterior appendix of caecum; P.D., posterior gastric ducts of digestive diverticula; P.S., posterior chamber of stomach; S.S., style-sac.

FIG. 6. Dissection of the stomach with the right wall removed to show the internal ridges and gastric shield in situ. A.S., anterior chamber of stomach; G.S., gastric shield; L.P., labial palps; O., oesophagus; P.S., posterior chamber of stomach; S.S., style-sac.

FIG. 7. Typical gastric shields; (*a*) left lateral aspects, (*b*) medial aspect. A.L., anterior lobe; F.M., flexed margins forming clip; N., neck; P.L., posterior lobe.

1

L. V.
L. P.
V. M.
G. P.
P. C.
A. M.
L. MA.

2 CM

2

U. L.
M.
L. L.
O. P.
I. P.
R. S.

1 CM

3

O.
M. I.
C. D.
S.
P. C.
P. D.
A. I.
S. S. M. G.
D. I.
A. M.
R.

1 CM

4

O.
A. C.
C. D.
G. R.
P. C.
P. S.
C. D.
P. D.
S. S.
M. G.

1 CM

5

6

O.
L. P.
A. S.
G. S.
P. S.
S. S.

·5 CM

7

a

b

F. M.
A. L.
N.
P. L.

3 MM

and is directed ventrally and toward the right of the stomach. It consists of one and one-quarter turns which extend in a clockwise direction. The peripheral walls of the appendices are invaginated as typhlosoles, while the walls adjoining the anterior stomach are flattened and approximate each other.

Ryder (1880 (26)) described the stomach of *C. virginica* as an organ with prominent transversely directed internal folds, two of which lie in a ventral position and take the form of inward projecting lobes "which are themselves lobulated", and presumably correspond to the caecum and its appendices. Dahmen (1923 (7)) indicated that the stomach of *O. chilensis* is divisible into an anterior dorsal and a wide posterior chamber, the left side of which extends into anterior and posterior blind sacs. Yonge (1926 (33)) illustrated the stomach of *O. edulis* as a short compact organ, the internal walls of which are thrown into a series of ridges. A food-sorting caecum extends from the left posteriorly beneath the floor of the stomach and is connected by a deep groove with the opening of the mid-gut. Such a caecum is a much less complex structure than that of *C. virginica*. Leenhardt (1926 (17)) in describing *G. angulata* has followed the terminology of other authors such as Sabatier (1887 (27)) and Thiele (1886 (29)) for lamellibranchs, where the term "utricular stomach" corresponds to the anterior and posterior chambers of the stomach of *C. virginica*. He refers briefly to a "diverticulum stomach" which arises on the anterior, ventral surface of the utricular stomach and which probably is homologous with the caecum of *C. virginica*.

The internal surface of the anterior chamber of the stomach exhibits considerable irregularity and possesses numerous ridges. It is separated from the posterior chamber by a broad fold or ridge, which projects into the lumen (Fig. 6). This ridge is most prominent along the mid-ventral wall and would appear to serve as a means of directing food particles posteriorly through a narrowed channel.

An extensive area of the left ventral wall of the posterior chamber of the stomach is covered by a translucent gastric shield (Figs. 6 and 7). The latter consists of two main lobes or divisions which are joined by a narrow neck region. The anterior division is elliptical in outline and its shorter axis is directed anteroposteriorly. The posterior lobe is two to three times larger than the anterior lobe, and is roughly a quadrant with one radius serving as the ventral margin and the other radius as the anterior margin. The margins of the neck region, and the adjoining margins of both the anterior and posterior lobes are flexed, forming a clip arrangement which fits onto a corresponding elevation of the left wall of the stomach. The marginal flection extending along the anterior radius is considerably more prominent than the ventral one. The gastric shield bears a longitudinal crest or ridge which projects dorsally into the lumen of the stomach. It is most evident in the anterior lobe and becomes progressively reduced in the posterior lobe. The anterior lobe in addition bears a number of irregular prominences or teeth.

L.V.
M.I.
M.
L.L.P.
R.L.P.
A.I.
D.D.
M.G.
H.
S.S.
A.M.,ST.
A.M.,S.
R.
L.MA.
G.P.

I MM

8

D.D.
A.I.
M.G.
D.I.
P.C.
S.S.
A.M.

D.D.
A.I.
S.S.M.G.
M.G.
D.I.
P.C.
S.S.
A.M.
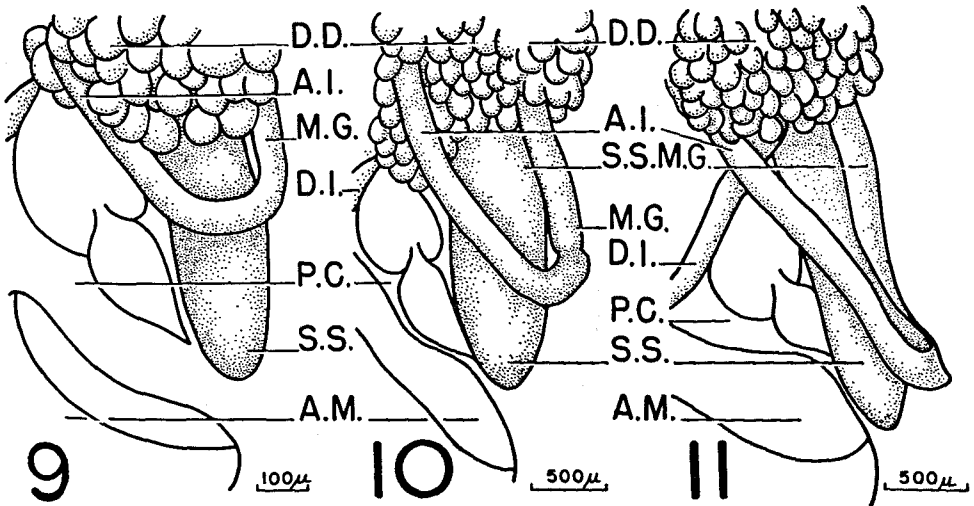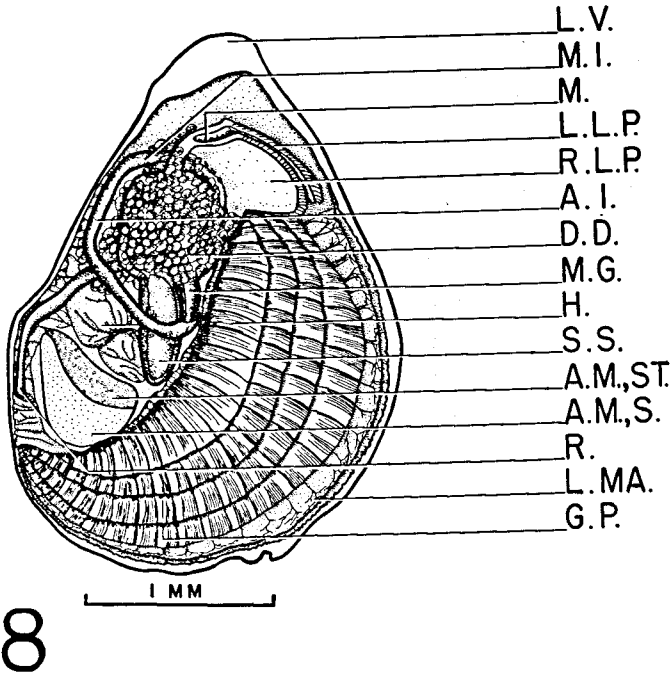
9   100μ   10   500μ   11   500μ

FIG. 8. Camera lucida drawing of cleared specimen of 3 mm. oyster spat viewed from right lateral aspect. A.I., ascending limb intestine; A.M.,S., adductor muscle, smooth; A.M.,ST., adductor muscle, striated; D.D., digestive diverticula; G.P., gill plates; H., heart; L.L.P., left labial palps; L.MA., left mantle; L.V., left valve; M., mouth; M.G., mid-gut; M.I., median limb intestine; R., rectum; R.L.P., right labial palp; S.S., style-sac.

FIGS. 9, 10, and 11. Camera lucida drawings showing relationship of style-sac and mid-gut of 3 mm., 7 mm., and 9 mm. oyster spat respectively, viewed from the right lateral aspect. A.I., ascending limb intestine; A.M., adductor muscle; D.D. digestive diverticula; D.I., descending limb intestine; M.G., mid-gut; P.C., pericardial cavity; S.S., style-sac; S.S.M.G., style-sac and mid-gut.

Nelson (1918 (22)) first coined the term "gastric shield" for the platelike structure of cartilaginous consistency at the point of contact between the anterior end of the style and the epithelium of the posterior stomach. For *C. virginica* he described it as a trilobular structure with the smallest of the three lobes concave on one surface forming a bowl-like depression possibly corresponding to the gastric clip arrangement as described here. The posterior lobe of the shield in the Malpeque Bay specimens is undivided, or marked only by a slight indentation of the posterior margin similar to that illustrated by Yonge (1926 (33)) for *O. edulis*.

Style-sac and Mid-gut

Just caudad to the gastric shield the posterior stomach leads into an elongated outpouching (Fig. 2), which occupies most of the ventral arm of the visceral mass. At the anterior end, two lateral valvular folds project into the lumen of the outpouching and continue posteriorly as the smaller or right and the larger or left typhlosoles, which incompletely divide the passageway into two parallel channels (Fig. 25). The mid-gut comprises the ventral channel and the style-sac lies somewhat dorsal to it. In cross section the lumen of the style-sac usually appears larger than that of the mid-gut, and irregularly circular to oval in outline in contrast to the somewhat laterally compressed mid-gut. Both typhlosoles show considerable variation, but the right one usually appears as a relatively low broad fold, while the left is somewhat more conical. These typhlosoles correspond to those of *O. chilensis* (Dahmen, 1923 (7)) and *O. edulis* (Yonge, 1926 (33)), but are somewhat less prominent than those of other lamellibranchs including *Anodonta* (Nelson, 1918 (22)), *Mya* (Edmondson, 1920 (8)), and *Ensis* (Graham, 1930 (13)). The lumina of the style-sac and the mid-gut enter a common posterior chamber at the mid-level of the adductor muscle.

Sabatier (1887 (27)) in describing *Mytilus edulis* first termed the style-sac and mid-gut a "tubular stomach". Purdie (1887 (25)) demonstrated that the "pyloric appendix" in *Mytilus latus* comprised the crystalline-style caecum and the direct intestine, which were partially separated by two overhanging longitudinal ridges. Dahmen (1923 (7)) referred to this portion of the tract in *O. chilensis* as a stomach–intestine while Leenhardt (1926 (17)) using the term "estomac tubulaire" for *G. angulata* stated that it included a caecum or "canal cylindro-conique" separated from a parallel channel by two ridges. Nelson (1918 (22)) also described this region of the digestive tract for a number of lamellibranchs, including *C. virginica*, as consisting of two tubes incompletely separated by typhlosoles, and Yonge (1926 (33)) corroborated this for *O. edulis*.

The rodlike crystalline style is enclosed in the groove of the style-sac and extends forward to the surface of the gastric shield in the posterior chamber of the stomach. It is composed of gelatinous layers enclosing a central fluid (Fig. 22). The style was first described in detail for *C. virginica* by Nelson (1918 (22)) and does not appear to differ from that of *O. chilensis* (Dahmen, 1923 (7)), *O. edulis* (Yonge, 1926 (33)), or *G. angulata* (Leenhardt, 1926 (17)).
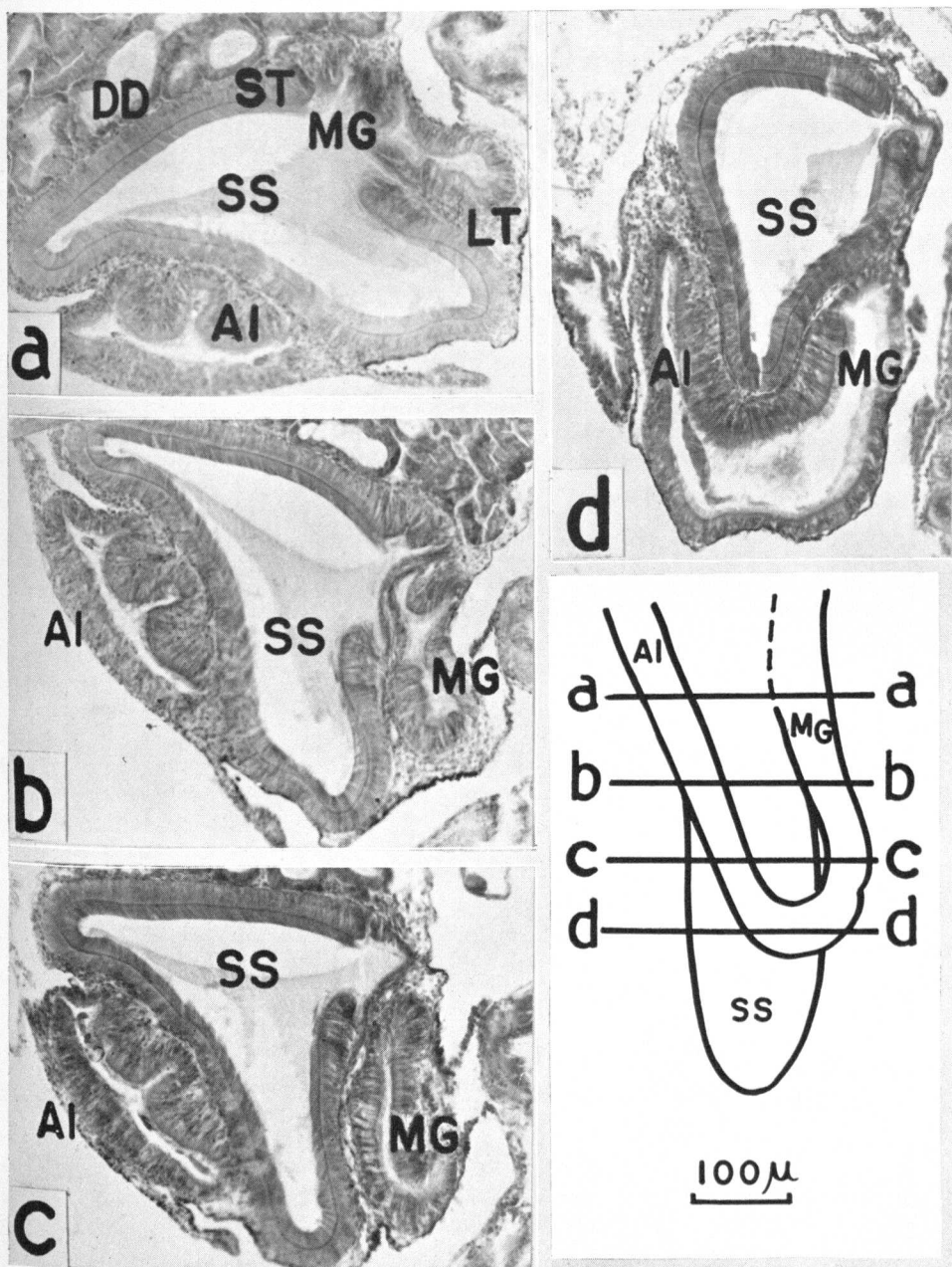
PLATE I

FIG. 12. Photomicrographs of cross sections of style-sac, mid-gut, and ascending limb of intestine of a 5 mm. oyster spat at levels as indicated by horizontal lines on diagrammatic outline. Alum cochineal and light green, 7 μ.

(a) Fused style-sac and mid-gut.
(b) Adjacent walls of style-sac and mid-gut degenerating prior to fusion.
(c) Style-sac and mid-gut discreet, ventral wall of style-sac grooved and non-ciliated.
(d) Style-sac with mid-gut looping over right surface.

A.I., ascending limb intestine; D.D., digestive diverticula; L.T., larger typhlosole (left); M.G., mid-gut; S.S., style-sac; S.T., smaller typhlosole (right).

Intestine—Ascending, Median, and Descending Limbs and Rectum

From the common chamber at the posterior end of the style-sac and mid-gut the intestine can conveniently be divided into ascending or recurrent, median or vertical, and descending limbs, and the rectum. The ascending limb passes anteriorly by an abrupt flexure from its origin at the common posterior chamber of the style-sac and mid-gut (Fig. 3). It exhibits many variations in spatial relationship with reference to the style-sac and mid-gut. Most frequently it
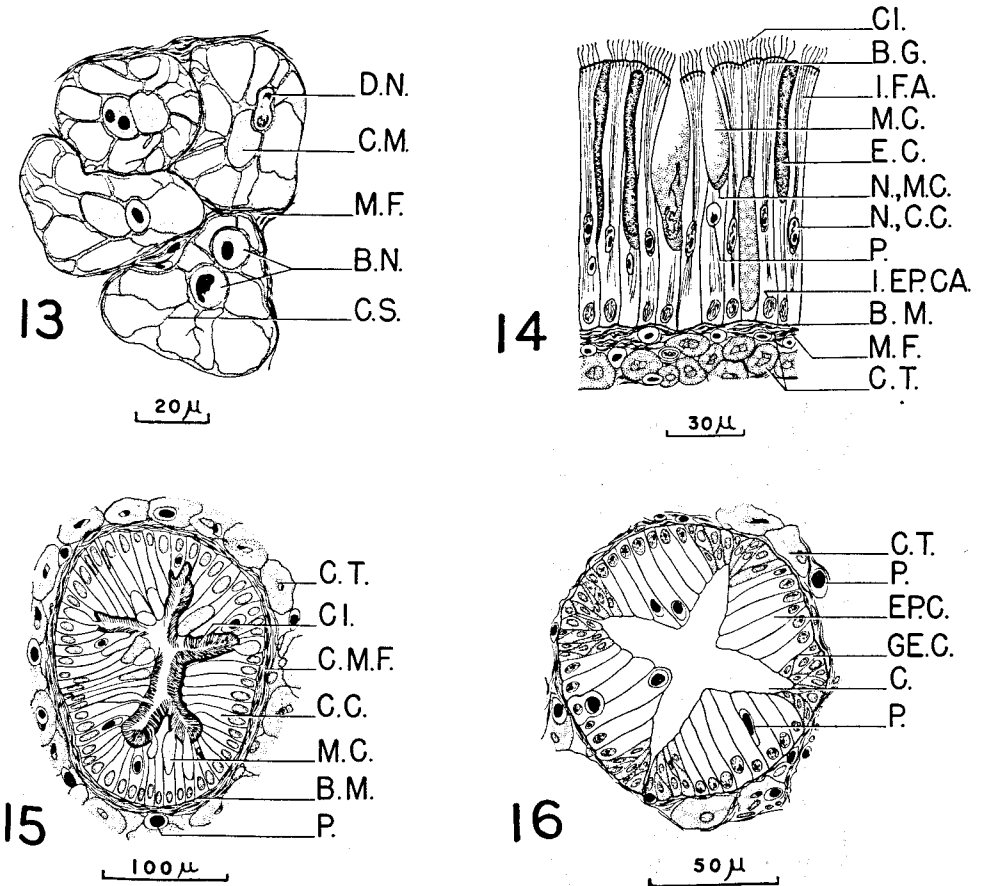
Camera lucida drawings (semidiagrammatic) of histological sections of the digestive tract of *Crassostrea virginica*

FIG. 13. Typical Leydig cells or Langer's vesicles. B.N., binucleate cell; C.M., cytoplasmic mass; C.S., cytoplasmic strands; D.N., dividing nucleus; M.F., muscle fibers.

FIG. 14. Characteristic ciliated epithelium from style-sac. B.G., basal granule; B.M., basement membrane; CI., cilia; C.T., connective tissue (collagenous fibers and Leydig cells); E.C., eosinophile; I.EP.CA., intraepithelial canal; I.F.A., intrafibrillar apparatus; M.C., mucous cell; M.F., smooth muscle fibers; N., C.C., nucleus of ciliated epithelial cell; N., M.C., nucleus of mucous cell; P., phagocyte.

FIG. 15. Transverse section of typical large duct of digestive diverticula. B.M., basement membrane; C.C., ciliated epithelial cell with heavy cuticular border (Cell Type I); CI., cilia; C.M.F., circular muscle fibers; C.T., connective tissue (collagenous fibers and Leydig cells); M.C., mucous cell; P., phagocyte.

FIG. 16. Transverse section of typical tubule of digestive diverticula. C., crypt; C.T., connective tissue; EP.C., secretory (and absorptive) epithelial cell; GE.C., generative cell; P., phagocyte.

passes forward on the right ventral surface of the latter for some distance before flexing obliquely anterior to the pericardial cavity. Less frequently the flexure is more abrupt and it is parallel to the dorsal surface of the style-sac and mid-gut, and sometimes it forms the dorsal limb of a large U with the style-sac and mid-gut as the ventral limb. It subsequently follows the curvature of the dorsal surface of the ovoid visceral mass lying somewhat peripheral to the digestive diverticula.

The median or vertical limb of the intestine follows a crescentic course on the anterior surface of the ovoid visceral mass, passing to the left of the oesophagus. As the descending limb it curves posteriorly along the ventral surface of the ovoid visceral mass, and crossing obliquely to the left, anterior to the style-sac, mid-gut, and the ascending limb, it borders the dorsal margin of the pericardial sac. Aside from a slight decrease in diameter, the descending limb passes without gross demarcation into the rectum. The latter terminates dorsal to the smooth division of the adductor muscle to which it is firmly attached by connective tissue. Its posterior tip is mounted on a connective tissue papilla although the immediate anal region is free.

The course of the intestine is essentially similar to that of *O. chilensis* (Dahmen, 1930 (7)), *O. edulis* (Yonge, 1926 (33)), and *G. angulata* (Leenhardt, 1926 (17)) although it is apparently relatively longer and with less abrupt flexures than in the last species.

Digestive Diverticula

The digestive diverticula consist of irregular brownish-green lobules, which together with the oesophagus and stomach constitute the ovoid visceral mass. These lobules, bound together by an interlobular connective tissue stroma, are exposed on removal of the mantle. They consist of ducts and tubules which fill all the interspaces about the digestive tract proper.

The ducts by which the digestive diverticula communicate with the stomach occur in two main groups: the caecal ducts and the posterior gastric ducts. The caecal ducts may be conveniently divided into four groups (Figs. 4, 5), the most anterior of which represents the fusion of two large ducts. The apertures of these ducts are located along the anterior margin of the caecum. The posterior ducts, comprising two major groups, communicate with the posterior chamber of the stomach on the left side. Dahmen (1923 (7)) described six major ducts in *O. chilensis*, four of which open along the caecum, the remainder into the right and left sides of the stomach proper. Yonge (1926 (33)) indicated the presence of two large ducts opening on each side of the stomach in *O. edulis*, and Leenhardt (1926 (17)) found that several canals open into the "utriculaire" stomach in *G. angulata*.

Typhlosoles of the Intestine

At the posterior termination of the style-sac and mid-gut channels, the larger (left) and the smaller (right) typhlosoles (Fig. 25) unite into a single typhlosole with a median groove. This typhlosole, which comprises about one-half of the wall of the gut, continues throughout the remainder of the

digestive tract to within a short distance of the anus. In the ascending limb
it is deeply grooved and occupies the left wall. With the flection of the intes-
tine into the median limb it forms the anterior wall, while in the descending
limb and rectum it comprises the right wall.

The external contours of the intestine and the surface of the typhlosole
appear smooth and rounded when large quantities of food are present in the
lumen. If there is little or no food or mucous, characteristic constrictions
and dilatations in the opposite wall of the intestine are impinged on the
typhlosole. These are evident throughout the entire tract with the exception
of the anterior portion of the ascending limb and the median limb, both of
which are somewhat deeply imbedded in the dense mass of the digestive
diverticula.

Development of the Tract Following Setting

Development of the digestive tract in the larva of *C. Virginica* has been
described by Brooks (1880 (4)), Stafford (1913 (28)), and Chestnut (1949 (5)).
These descriptions, however, do not include accounts of the metamorphosis
of the tract from the spat to the adult condition. The stomach is evident in
early larval stages as an anterior enlargement of the semicircular tract. At
the time of "setting" the style-sac is a blind posteriorly directed diverticulum
of the stomach (Fig. 8). The mid-gut originates from the stomach slightly
to the right and ventral to the base of the style-sac. It forms a loop on the
right surface of the latter sac. The dorsal limb of the loop traverses the left
surface of the stomach as the anlage of the ascending limb of the intestine.
At the level of the base of the oesophagus it curves posteriorly, as the descend-
ing limb of the intestine and the rectum, to terminate on the dorsal surface of
the adductor muscle. Subsequently the ventral wall of the style-sac and the
closely approximating dorsal wall of the mid-gut become fused to one another
(Figs. 9–12). This line of fusion is marked in the style-sac by a longitudinal
groove of low sparsely ciliated epithelial cells. An initial thinning of the
adjacent walls of both the style-sac and mid-gut is accompanied by a degen-
eration of the cilia and finally of the epithelial cells themselves, until only
the basement membranes remain to be ruptured. This rupturing begins
anteriorly and proceeds posteriorly. The smaller and larger typhlosoles
extending the length of the style-sac and mid-gut are thus indicative of the
right and left fused margins of the two channels. Fusion begins when the
spat are between 3 and 5 mm. in length and appears to be complete in the
majority of 10 mm. spat. The style-sac and mid-gut are thus a combined
gastric and intestinal channel, as shown for *O. chilensis* (Dahmen, 1923 (7))
and for *O. edulis* by Yonge (1926 (33)) and Erdmann (1935 (10)), rather than
simply a tubular stomach as Leenhardt (1926 (17)) has indicated in *G. angulata*.

Microscopic Anatomy of the Digestive Tract

The viscera of the oyster are bound together and supported by connective
tissue consisting of Leydig cells alternately known as Langer's vesicles (Fig.
13), and delicate collagenous fibers. Leydig cells have been described for a

number of the molluscs (Bronn, 1935 (3)).   In *C. virginica* (Fig. 13) they are multiangular and usually slightly elongated.   Each cell possesses one or more vesicular nuclei which lie toward the periphery of a centrally-located mass of finely granular cytoplasm.   Delicate cytoplasmic strands radiate from the central mass to the margin of the cell where they unite to form a thin border adjacent to the cell membrane.   These cells are arranged at random except around blood vessels where the long axes radiate from the encircling collagenous fibers; and in the subepithelial and collagenous layers of the digestive tract and of the mantle.   In the latter they form a circular layer with the long axes parallel to the lumen of the tract and the margin of the mantle respectively.   Dahmen (1923 (7)) found the interspaces between the cytoplasmic strands to contain a clear fluid or very finely granular material. Bargeton (1941 (1)) indicated their importance in the storage of glycogen. In *C. virginica* these cells exhibit a seasonal variation in size.   In early summer prior to spawning, they appear flattened, presumably owing to glycogen depletion and the pressure of the enlarging and permeating gonad.   There is no marked change in the long axes, but the short axes are now reduced to from 20 to 40 μ.   In late summer sometime after spawning, their long axes measure from 40 to 70 μ and their shorter axes from 35 to 60 μ.

The simple columnar epithelial lining layer of the digestive tract (Fig. 14) rests upon a homogenous basement membrane and is separated from the Leydig cell stroma by a somewhat dense, circularly arranged layer of delicate collagenous fibers.   A few smooth muscle fibers, circularly and occasionally longitudinally disposed, usually permeate the periphery of the collagenous layer and partially or completely separate it from the underlying Leydig cells. The muscle fibres are sometimes fusiform, but occasionally appear to have blunt ends, a condition which may be partially attributed to the plane of section.   The epithelium is ciliated throughout with the exception of the upper lip (fused external palps) where cilia are only sporadically present, the tubules of the digestive diverticula, and the lower side of the gastric shield in the posterior chamber of the stomach.   The height of the epithelium varies from one region to another, as does the nature of the cilia.   The cytoplasm is finely granular and the nuclei are large, oval in shape, and usually located from the middle to the base of the cell.   The chromatin is sparse and tends to collect in coarse granules.   One or more nucleoli are present near the nuclear membrane.   An internal fibrillar apparatus appears to arise near the basement membrane in the form of elongated rods or fine fibrils.   These fibrils converge as they pass toward the nucleus and thence spread in the form of a fan to merge into the basal granules near the free surface before penetrating the cuticle.   There is considerable variation in the ease with which the internal fibrillar apparatus can be differentiated in different parts of the tract.   Gutheil (1911 (15), 1912 (16)) described this apparatus in *Anodonta cellensis*, but did not observe it basal to the nucleus although Ellermann (1899 (9)) suggested that the fibrils extended toward the bases of the epithelial cells in the snail *Helix pomatia*.   Mackintosh (1925 (20))

has indicated a similar internal fibrillar apparatus in *Crepidula fornicata* as has Yonge (1926 (33)) for *O. edulis*, and Leenhardt (1926 (17)) for *G. angulata*: A series of "intra-epithelial" canals in the basal third of the cells are similar to those demonstrated by Mackintosh (1925 (20)) and Yonge (1926 (33)). It is suggested that these canals lend tensile strength to the epithelium since they are filled with a densely-staining stringy or albuminous substance and penetrate the bases of the cells.

Secretory epithelial cells of the goblet type are interspersed amongst the ciliated cells. Their proportions and numbers vary from one region of the tract to another (Fig. 14). Some of these are actively secreting mucous cells, while others are apparently regenerating cells. Coarsely vesicular mucous granules or droplets are grouped as ovoid to spindle-shaped masses which extend variable distances from the free border toward the bases of the cells. The granules stain weakly with basic dyes although in early stages before taking on a vesicular character, they stain more intensely. The densely-staining nucleus is oval or crescentic in shape depending upon the volume of secretion. It is located in a position somewhat eccentric to the basal margin of the ovoid mass of secretion. The cytoplasm is finely granular and similar to that of the ciliated cells. Leenhardt (1926 (17)) first described the so-called eosinophilic cell in *G. angulata*. It is an elongated cell, laden with coarse granules, which may extend throughout most of the length of the cell, and cause it to be distended to a greater or lesser extent especially toward the free margin. Cells of this type can be recognized in the digestive epithelium of *C. virginica*. The granules can be stained with both iron and acid hematoxylin and also intensely with acid dyes, such as eosin. The densely-staining nucleus is spherical or oval in shape and located in finely granular cytoplasm toward the base of the cell. Nelson (1955 (24)) has suggested that these may represent a secretory phase of the mucous cell. Validity is loaned to this hypothesis in that there is sometimes considerable difficulty in distinguishing these cells from mucous cells, and wherever mucous cells are abundant, eosinophiles are sparsely represented. Dahmen (1923 (7)) and Yonge (1926 (33)) for *O. chilensis* and *O. edulis* respectively refer to only one type of secretory cell, the "mucous" gland, which occurs in various regions of the digestive tract. The nuclei appear to be identical with those of the ciliated cells. They fail to distinguish any cells which correspond to the eosinophiles of *G. angulata* (Leenhardt, 1926 (17)).

Wandering phagocytic cells from 7 to 10 μ in diameter occur in variable numbers in the lumen, among the epithelial cells and in the surrounding connective tissues of the entire digestive tract. Their small spherical nuclei are 4 to 5 μ in diameter and the chromatin occurs as fine densely-staining granules. The cytoplasm stains faintly with acid dyes. In fixed preparations they frequently exhibit numerous blunt pseudopodia. Some investigators refer to these cells as amoeboid cells or amoebocytes (Yonge, 1926 (33)), while others term them leucocytes (Mackin, 1951 (19)). Gutheil (1912 (16)) showed for *Anodonta* and Yonge (1923 (31)) for *Mya* sp. that large particles

of food can be phagocytized by them and hence they may play an important role in assimilation.

Table I gives a résumé of the specific characteristics of the lining epithelium and extraepithelial tunics of the digestive tract of *C. virginica*. The following descriptions will accordingly deal largely with certain distinguishing features of the various regions.

Labial Palps (Figs. 17, 18)

Each fleshy labial palp is composed of a core of connective tissue surmounted by simple columnar epithelium resting on a homogeneous basement membrane. The connective tissue consists of Leydig cells with some collagenous fibers, the latter, along with longitudinally arranged smooth muscle fibers, being largely concentrated as a layer beneath the basement membrane. The smooth surfaces of the palps, i.e. the lateral faces of the external palps and the medial faces of the internal palps, are bordered by a sparsely ciliated low columnar epithelium with or without a thin cuticle. Both mucous and eosinophilic cells may be interspersed amongst the ciliated cells. The adjacent surfaces of both pairs of palps bear prominent transverse ridges or flutings separated by grooves, and are covered by a heavily ciliated tall columnar epithelium with a distinct cuticle. In longitudinal sections the ridges present an oblique appearance, the proximal walls usually being straight, while the distal walls are characterized by shallow grooves, as Leenhardt (1926 (17)) illustrated for *G. angulata*. Mucous cells tend to be more concentrated at the bases of the furrows and become progressively reduced in numbers toward the summits of the folds. Yonge (1926 (33)) has shown in *O. edulis*, however, that unicellular mucous glands are almost exclusively confined to the vicinity of the summits of the folds. Phagocytes between the epithelial cells and longitudinally arranged muscle fibers under the epithelium of the furrows are also present in *O. edulis*.

Mouth Cavity and Oesophagus (Figs. 19, 20, 30)

In the region of the upper lip formed by the fused external palps the epithelium is low columnar and non-ciliated or irregularly ciliated. The free surfaces of many of the cells bear irregular, rounded, cytoplasmic projections. Most of the cells are of the mucous type, but interspersed among them are prominent eosinophilic cells. The epithelium rests upon a basement membrane which in turn is separated from the adjacent Leydig cells by a layer of collagenous fibers through which are interspersed a few longitudinally arranged smooth muscle cells. The ciliated epithelium forming the covering of the lower lip (fused internal palps) and the lining of the oral cavity is tall columnar with cilia decreasing in length from the entrance toward the oesophagus. Mucous cells are prominent, but are never distended to the extent of those of the upper lip. Dahmen (1923 (7)) found in *O. chilensis* that the mouth opening and oesophagus show a tall, cuticulated epithelium, upon which cilia could be demonstrated in only a few instances. Yonge (1926 (33)) observed that the epithelium of the mouth of *O. edulis* is continuous with

TABLE I

HISTOLOGICAL CHARACTERISTICS OF THE DIGESTIVE TRACT OF *Crassostrea virginica* (GMELIN)

(from specimens 8–10 cm. in length)

Division of tract	Epithelium						Extraepithelial tunics		
	Height of cell, μ	Length of cilia, μ	Cuticle	Mucous cells	Eosinophilic cells	Phagocytes	Basement membrane	Collag. conn. tissue	Smooth muscle
Palps									
Ridged surface	40–50	10–15	++	++	++	++	++	++	++
Smooth surface	20–30	5–7	±	+					
Mouth									
Upper lip (fused external palps)	25–30	0–10	+++	++	+	++++	++++	++++	++++
Lower lip (fused internal palps)	50–55	15–25	+++	++	–		+++	+++	+
Roof	50–55	10–20	++	+	–	++++			
Floor	50–55	10–20	++	++	–				
Oesophagus	75–105	10–15	+	++	+	+	+	+	+
Stomach									
Anterior chamber	55–180	15–20	+++	+++	–	+++	++++	++++	++++
Caecum	20–155	7–15	+++	+++	–	+	++++		
Posterior chamber	45–180	15–25	+	+	–	++++	++		
Gastric shield region	50–230	–		–					
Style-sac, Mid-gut									
Style-sac	65–150	7–25	++	++	++	+++	++	++	++
Mid-gut	55–160	5–20	++	+++		++			
Intestine									
Ascending limb	85–130	5–20	+++	++	+	+++	+	++++	++++
Median limb	65–115	5–12	+++	++	+++	+++	–		
Descending limb	75–110	7–15	+	++++	+++	+++	++		
Rectum	50–125	15–25		+++	+	++++			
Anus	90	10	+	+++	+	++++	+	+	+
Digestive diverticula									
Ducts									
Large caecal and gastric	15–25	8–10	++	++	+++	++	+++	+++	+++
Cell Type I	25–40	4–8	++	++		++			
Cell Type II	10–25	4–6		+		+			
Pretubular									
Tubules									
Secretory cells	10–35	–	–	–	–	++	–	++	?
Generative cells	5–15	–	–	–	–		–		?

NOTE: + signs indicate presence and relative frequency.

that of the grooves between the palps and consists of long, ciliated cells with a few mucous glands, as did Leenhardt (1926 (17)) for *G. angulata*.

The epithelium of the oesophagus is tall, has a prominent cuticle, and bears heavy relatively short cilia, as in *G. angulata* (Leenhardt, 1926 (17)). Mucous cells are numerous and become more abundant toward the stomach, but eosinophilic cells are few. The basement membrane is heavy and lies on a distinct band of collagenous fibers containing a few strands of circularly and longitudinally arranged muscle cells. Phagocytes are scattered throughout the epithelium. Prominent folds may occur in the lateral margins of the oesophagus, which presumably would permit expansion during the passage of food to the stomach. Dahmen (1923 (7)) indicated a high, ciliated epithelium with some mucous cells for *O. chilensis*, as did Yonge (1926 (33)) for *O. edulis* where, however, phagocytes are numerous and "mucous" glands fewer.

Stomach (Figs. 21, 22, 32–34)

The internal surface of the stomach is thrown into irregular ridges separated by furrows. Epithelial cells covering the ridges are much taller than those lining the furrows, and such differences in height partially account for the irregular character of the lumen. With the exception of the gastric shield area of the posterior chamber, the entire epithelial lining is ciliated. Some mucous cells are present but few, if any, eosinophilic cells. In the caecum the epithelium progressively decreases in height from the point of exit from the anterior chamber to the blind terminations of the appendices, with the length of the cilia being correspondingly reduced. Phagocytes are present in large numbers below the prominent basement membrane, between the epithelial cells, and in the lumen. A few smooth muscle cells are arranged irregularly in both a longitudinal and circular direction to form, with collagenous fibers, an extraepithelial tunic. The gastric shield region appears in transverse section to be shaped like an arrowhead (Figs. 22, 23, 24). The epithelium resembles that of the other regions of the stomach except for the apparent lack of cilia. Fine cytoplasmic processes arising from the free borders of some of the cells unite with the overhanging gastric shield and are suggestive of degenerate or modified cilia (Fig. 35). The cells at the apex of the arrowhead (Fig. 36) are very tall, reaching a height of 230 μ, but taper laterally where they become continuous with the cellular lining of the adjacent posterior chamber. The nuclei are slender and situated somewhat nearer the basement membrane than in other regions of the stomach. Neither mucous nor eosinophilic cells appear to be present but numerous phagocytes occur between the epithelial cells. The histological structure of the stomach wall closely resembles that of other described species, *O. chilensis* (Dahmen, 1923 (7)), *G. angulata* (Leenhardt, 1926 (17)), and *O. edulis* (Yonge, 1926 (33)).

The gastric shield is composed of homogeneous layers of a chondroid-like substance (Nelson, 1918 (22)), which stains intensely with acid dyes. The laminated character is most readily exhibited in sections at the apex of the crest or ridge (Figs. 23, 24). The laminae gradually decrease in thickness from the apex to the margins of the shield. The hyaline gastric shields of

Mytilus (List, 1902 (18)) and of *Anodonta* (Gutheil, 1911 (15)) are formed by the fusion of droplets of secretion from the underlying epithelial cells. Although Yonge (1926 (33)) could find no evidence of such secretion in *O. edulis*, nevertheless the shield is joined to the epithelium by fine strands which pass through it and have the appearance of abortive fused cilia arising from basal granules. In *C. virginica*, as indicated above, there are evidences of cytoplasmic connections between the shield and the underlying epithelium and although, during the preparations of sections, such processes are usually severed near the apex, they can be demonstrated near the margins. Dahmen (1923 (7)) and Leenhardt (1926 (17)) consider the gastric shields of *O. chilensis* and *G. angulata* respectively to be products of cellular secretions which have filtered across the border of the epithelial cells to be incorporated with the cilia. The gastric shield could be analogous in certain respects to the peritrophic membrane of insects, which Wigglesworth (1950 (30)) has shown is in some instances composed of concentric lamellae secreted by the underlying epithelial cells of the mid-gut. It may be postulated, therefore, that if the gastric shield of the oyster is chiefly secreted by the epithelial cells beneath the apex, the chondrin would flow laterally, becoming attached to the cilia, which subsequently degenerate. Such a suggestion might account for the failure to observe any central attachment of the shield to the underlying epithelium, whereas the thinner margins invariably adhere by cytoplasmic processes.

Style-sac and Mid-gut (Figs. 25, 37, 38, 39)

The most striking feature of the epithelium lining the style-sac is the density and uniformity of the cilia in contrast to those found in any other region of the digestive tract. The cells are very regularly arranged with large ovoid nuclei. The internal fibrillar apparatus is more prominent than in any other part of the tract. The epithelium comprising the mid-gut wall varies considerably in height and the cilia lack the regularity of arrangement of those in the adjoining style-sac. Phagocytes and mucous cells are somewhat more numerous in the mid-gut wall than in that of the style-sac, (Table I) but eosinophilic cells are sparsely represented in both. In both style-sac and mid-gut the basement membrane is surrounded by a layer of collagenous fibers with sparsely interspersed circularly arranged smooth muscle fibers. Dahmen (1923 (7)), Yonge (1926 (33)), and Leenhardt (1926 (17)) describe no muscle cells around the epithelium in *O. chilensis*, *O. edulis*, and *G. angulata*, but otherwise this division of the tract appears to be essentially the same in these species.

The typhlosoles consist of a core of Leydig cells covered by tall, columnar epithelial cells which grade on one side into those of the style-sac, and on the other into those of the mid-gut. However, the transition from the epithelium of the style-sac to that of the mid-gut is much more abrupt for the smaller or right typhlosole than for the larger or left one and is usually marked by a cleft. The cilia of the smaller typhlosole approximate those of the style-sac in length measuring up to 20 μ while those of the larger typhlosole

range from 10 to 15 μ.   Mucous cells are usually more abundant on the larger typhlosole.

The lumen of the style-sac is occupied by a gelatinous white to yellowish-brown rod, the crystalline style, whose anterior end extends into the posterior chamber of the stomach to rest against the gastric shield.   The central core is fluid while the periphery is firm and consists of several gelatinous strata. In fixed specimens the style usually disintegrates, but occasionally its outer layers may be identified in sections (Figs. 22, 34).   There are diverse opinions regarding the origin of the acellular crystalline style in lamellibranchs.   Its formation has been attributed to the secretory activity of the walls of the "caecum" (Barrois, 1889 (2)) and the "liver" (Mitra, 1901 (21)).   Although many investigators (List, 1902 (18); Nelson, 1918 (22); Edmondson, 1920 (8); Mackintosh, 1925 (20); Graham, 1930 (13)) have suggested that it is secreted by the narrow cells of the minor or right typhlosole, none have been able to offer authentic evidence.   Gutheil (1912 (16)) has described clear secretory granules above the nuclei in the ciliated cells of the style-sac of *Anodonta cellensis.*   Yonge (1926 (32)) demonstrated the presence of droplets of secretion in the style-sac epithelium of part of the minor typhlosole of both *Mytilus edulis* and of *O. edulis* after the injection of iron saccharate, and concluded that these cells of the groove of the style-sac are instrumental in the formation of the style.   Leenhardt (1926 (17)) observed certain haema-toxylin-staining granules in the style-sac ("caecum") of *G. angulata* to which he attributed the secretion of the crystalline style.   There has been no evidence of such specifically staining granules in the epithelium of the style-sac of *C. virginica.*

Intestine—Ascending, Median, and Descending Limbs (Figs. 25, 26, 41, 42)

The intestine is characterized by a prominent typhlosole with a median groove.   The narrow lumen has the form of a double crescent when observed in transverse section.   The epithelial lining exhibits great uniformity through-out all three limbs, the ciliated cells resembling those of the mid-gut adjoining the style-sac.   Mucous cells and eosinophilic cells are both present, with the former increasing in abundance along the course of the tract (Table 1). Phagocytes are numerous among the epithelial cells, below the basement mem-brane, as well as in the lumen of the tract.   The basement membrane of the ascending limb is very broad, but becomes progressively less pronounced as the intestine grades into the rectum.   It rests upon a thin layer of collagenous fibres among which are occasionally interspersed a few smooth muscle fibers, most of which are circularly arranged.

The typhlosole consists of a more or less V-shaped mass of Leydig cells surmounted by epithelial cells which are tallest on either side of the median groove, and becomes lowest at the base of the groove.   On the opposite wall of the gut, the epithelium in the mid-line may project into the median groove of the typhlosole.

Morphologically and histologically, the intestine resembles that described by Dahmen (1923 (7)) for *O. chilensis* and by Yonge (1926 (33)) for *O. edulis* except that in these species muscular tissue has not been demonstrated. Field (1922 (11)) describes circularly arranged muscle fibers in the intestine of *Mytilus edulis* while Leenhardt (1926 (17)) illustrates for *G. angulata* an epithelium comparable to that of *C. virginica*, but does not refer to any muscular cells although the connective tissue layer is prominent. He is in agreement with Sabatier (1887 (27)), who suggested that the connective tissue layer of the intestine of *Mytilus edulis* could be considered as a lymphoid organ because of the large number of amoebocytes present. Such a condition may also hold true for *C. virginica* since these cells are abundant in this region of the tract.

Rectum (Figs. 27, 28, 43, 44)

The rectum resembles the preceding limbs of the intestine with the exception that the typhlosole is more pronounced and the median groove correspondingly deeper. Numerous epithelial folds occur in the lateral walls of the rectum while coarser folds appear in the adjacent typhlosole. The typhlosole gradually disappears near the anal region when the tract assumes a more or less circular outline. Its internal surface is thrown into small folds.

There is a marked increase in the numbers of mucous cells progressively from the median limb of the intestine toward the rectum and anus. Sometimes they may even predominate in numbers over the ciliated cells. Relatively few eosinophilic cells occur in either the rectum or the anal region. Phagocytic cells are numerous throughout the epithelium and beneath the thin basement membrane. There is a definite layer of smooth muscle fibers, circularly arranged, in the region of the anus. Leenhardt (1926 (17)) noted smooth muscle fibers in *G. angulata* which became sufficiently abundant in the anal region as to form a sphincter, but neither Dahmen (1923 (7)) nor Yonge (1926 (33)) refer to them in *O. chilensis* and *O. edulis*.

Digestive Diverticula (Figs. 15, 16, 29, 45, 46, 47)

The digestive diverticula in the oyster are organs of absorption and of intracellular digestion (Yonge, 1926 (32)). The tubules and the ducts of these diverticula are grouped in the form of small lobules indistinctly separated and bound together by interlobular connective tissue composed of Leydig cells with some collagenous fibers. The histological structure of the larger ducts which communicate directly with the caecum and the posterior stomach generally resembles the adjacent region of the stomach. The lumina sometimes appear circular in outline, at other times crescentic or often multiangular. As the primary ducts branch leading toward the secretory tubules, a difference in the height and character of the ciliated epithelium occurs on opposite sides of the wall. On one side the cells are somewhat short and broad with lightly staining nuclei (Cell Type I, Table I). There is a heavy cuticular border and the cilia are relatively long and dense. Cells on the opposite side may be almost double in height, the cuticle is thin, and the cilia

somewhat shorter (Cell Type II, Table I.).   Mucous cells are much more pro-
fuse among the elongated ciliated cells, and eosinophilic cells occasionally occur.
The lumina of the immediate pretubular ducts are generally circular in outline
and the epithelial cells become progressively uniform in height.   Phagocytes
are present in the epithelium, in the lumina, and in the surrounding connective
tissue.   Circularly arranged smooth muscle fibres imbedded in collagenous
connective tissue surround the basement membrane.   The structure of the
duct resembles that described by List (1902 (18)) and Field (1922 (11)) for
the "liver canals" of the digestive diverticula of *Mytilus edulis*.   Dahmen
(1923 (7)) and Yonge (1926 (33)) observed no special variation in the epithel-
ium of the ducts from that of the stomach for *O. chilensis* and *O. edulis*
respectively, but Leenhardt (1926 (17)) recorded an arrangement for *G.
angulata* which is similar to that observed here in *C. virginica*.

The histological structure of the secretory units of the digestive diverticula
is quite different from that of the ducts and a seasonal variation is exhibited.
Yonge (1926 (32)) has described the units as tubules for a large number of
lamellibranchs including *O. edulis*, as did Dahmen (1923 (7)) for *O. chilensis*,
while Leenhardt (1926 (17)) has considered them to be in the form of acini in
G. angulata.   Graphic reconstruction of the units from serial sections indicates
their tubular rather than their acinar character in *C. virginica*.   During the
spring and summer months when the lining epithelium is tall, the lumina of
the tubules appear roughly in the form of a cross or H and less frequently
tripartite.   The non-ciliated epithelium comprising the wall is of two types.
Generative cells located in the crypts formed by the extremities of the cross
are small with large nuclei, each of which possesses a nucleolus.   The cyto-
plasm is somewhat granular and darkly-staining and a basement membrane
is not evident.   Both Yonge (1926 (32)) and Leenhardt (1926 (17)) consider
that these cells are capable of replenishing the absorptive and secretory cells
of the remainder of the tubule.   Cells of the latter type progressively increase
in height from the crypt toward the central lumen and rest on a basement
membrane.   The cytoplasm is coarsely vacuolated and stains very lightly
in comparison with that of the generative cells.   Sometimes engulfed food
particles are evident.   Phagocytes may be present among the epithelial cells.
A thin layer of collagenous connective tissue surrounds each tubule.   During
the winter season (Fig. 47) the lumina of the majority of the tubules become
spherical or somewhat ovoid in outline.   The peripheral borders of the large
coarsely vacuolated cells are quite irregular and some exhibit extensive
degeneration.   There appears to be no change in the generative cells which
occur at the angles of the crypts.

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References

1. BARGETON, M. Les variations saisonnières du tissu conjonctif vésiculeux de l'huître. Bull. biol. France et Belg. **76**, 175–191 (1941).

2. BARROIS, T. Le stylet cristallin des Lamellibranches. Rev. biol. nord France, **5**, 209–226 (1889).

3. BRONN, H. G. Klassen und Ordnungen des Tier-Reichs 3: Mollusca. III Abteilung: Bivalvia, Teil I (F. Haas). 1935.

4. BROOKS, W. K. Development of the American oyster (*Ostrea virginiana* List). App. Rept. Commrs. Fish Maryland. 1–81 (1880).

5. CHESTNUT, A. F. Studies on the digestive processes in *Ostrea virginica*. Doctoral Thesis, Rutgers University. 1949.

6. CLARK, A. H. The Smithsonian Institution, its functions and its future. Science, **63**, 147–157 (1920).

7. DAHMEN, P. Anatomie von *Ostrea chilensis* Philippi. Jena. Z. Naturw. **59**, 575–626 (1923).

8. EDMONDSON, C. H. The reformation of the crystalline style in *Mya arenaria* after extraction. J. Exptl. Zool. **30**, 259–291 (1920).

9. ELLERMANN, W. Über die struktur der Darmepithelzellen von Helix. Anat. Anz. **17**, 590–593 (1899).

10. ERDMANN, W. Untersuchungen über die Lebensgeschichte der Auster. 5. Über die Entwicklung und die Anatomie der ansatzreifen Larve von *Ostrea edulis* mit Bermerkungen über die Lebensgeschichte der Auster. Wiss. Meeres. Helgoland. **19**(6), 1–25 (1935).

11. FIELD, I. A. Biology and economic value of the sea mussel, *Mytilus edulis*. Bull. Bur. Fisheries, Washington, **38**, 127–259 (1922).

12. GALIGHER, A. E. The essentials of practical microtechnique. Albert E. Galigher, Inc., Laboratory of Microtechnique, Berkeley, California. 1934.

13. GRAHAM, A. On the morphology, feeding mechanism, and digestion of *Ensis siliqua* (Schumacher). Trans. Roy. Soc. Edinburgh, **56**, 725–750 (1930).

14. Gunter, G. The generic status of living oysters and the scientific name of the common American species. Am. Midland Naturalist, **43**, 438–449 (1950).

15. GUTHEIL, F. Über Wimperapparat und Mitose von Flimmerzellen. Zool. Anz. **37**, 331–349 (1911).

16. GUTHEIL, F. Über den Darmkanal und die Mitteldarmdrüse von *Anodonta cellensis* (Schröt). Z. wiss. Zoöl. **99**, 444–538 (1912).

17. LEENHARDT, H. Quelques études sur "*Gryphca angulata*". Ann. inst. océanog. (Monaco), **3**, 1–90 (1926).

18. LIST, T. Die Mytiliden des Golfes von Neapel. Fauna u. Flora des Golfes von Neapel u. d. angrenz. Meeresabschnitte, **27**, 253–277 (1902).

19. MACKIN, J. G. Histopathology of infection of *Crassostrea virginica* (Gmelin) by *Dermocystidium marinum*. Bull. Mar. Sci. Gulf Carib. **1**, 72–87 (1951).

20. MACKINTOSH, N. A. The crystalline style in Gastropods. Quart. J. Microscop. Sci. **69**, 317–342 (1925).

21. MITRA, S. B. The crystalline style of Lamellibranchia. Quart. J. Microscop. Sci. **44**, 601–602 (1901).

22. NELSON, T. C. On the origin, nature and function of the crystalline style of Lamellibranchs. J. Morphol. **31**, 53–111 (1918).

23. NELSON, T. C. The feeding mechanism of the oyster. I. On the pallium and the branchial chambers of *Ostrea virginica*, *Ostrea edulis* and *Ostrea angulata*, with comparisons with other species of the genus. J. Morphol. **63**, 1–61 (1938).

24. NELSON, T. C. Personal communication. 1955.

25. PURDIE, A. The anatomy of the common mussels, *Mytilus latus*, *edulis*, and *magellanicus*. Studies in Biol. for New Zealand students. New Zealand Colon. Mus. and Geol. Survey Dept. **14**, 1–45 (1887).

26. RYDER, J. A. On the course of the intestine in the oyster (*Ostrea virginica*). Am. Naturalist, **14**, 674–675 (1880).

27. Sabatier, A.   Anatomie de la Moule commune.   Ann. sci. nat. 5, 1-132 (1887).
28. Stafford, J.   The Canadian oyster.   Commission of Conservation, Ottawa.   1913.
29. Thiele, J.   Die Mundlappen der Lamellibranchiaten.   Z. wiss. Zoöl. 44, 239–272 (1886).
30. Wigglesworth, V. B.   The principles of insect physiology.   Methuen & Co. Ltd., London.   1950.
31. Yonge, C. M.   The mechanism of feeding, digestion, and assimilation in the Lamellibranch Mya. Brit. J. Exptl. Biol. 1, 15-63 (1923).
32. Yonge, C. M.   The digestive diverticula of the Lamellibranchs.   Trans. Roy. Soc. Edinburgh, 54, 703–717 (1926).
33. Yonge, C. M.   The structure and physiology of the organs of feeding and digestion in Ostrea edulis.   J. Marine Biol. Assoc. United Kingdom, 14, 295–386 (1926).

Figs. 17-29.   Photomicrographs of histological sections of the digestive tract of *Crassostrea virginica*.

Fig. 17.   Longitudinal section of the adjacent ridged medial surface of an outer labial palp, and the lateral surface of an inner labial palp.   Ehrlich's haematoxylin and Triosin, 10 μ.   ×50.

Fig. 18.   Longitudinal section of a ridge and adjacent furrows of the lateral surface of an inner labial palp showing the almost straight proximal wall and the grooved distal wall.   Ehrlich's haematoxylin and Triosin, 10 μ.   ×300.

Fig. 19.   Sagittal section showing the relationships of the labial palps, mouth cavity, and oesophagus.   Mallory's triple stain, 10 μ.   ×12.

D.D., digestive diverticula; I.P., inner palp; M., mouth cavity; O., oesophagus; O.P., outer palps.

Fig. 20.   Sagittal section of oral cavity showing low non-ciliated and sparsely ciliated epithelium of upper lip (fused external palps) merging into the typical ciliated columnar epithelium on the roof and floor (right).   Mallory's triple stain, 10 μ.   ×85.

Fig. 21.   Slightly oblique transverse section of stomach region of 5 mm. oyster spat. A.S., anterior chamber of stomach; C., caecum; D.D., digestive diverticula; P.S., posterior stomach.   Alum cochineal and light green.   ×100.

Fig. 22.   Coronal section through the stomach.   ×12.

A.S., anterior chamber of stomach; C., caecum and (anterior appendix); C.S., crystalline style; D.D., digestive diverticula; G.S., gastric shield; P.S., posterior stomach. Ehrlich's haematoxylin and Triosin.

Fig. 23.   Posterior chamber of stomach showing cliplike attachment of gastric shield to underlying epithelium.   Ehrlich's haematoxylin and Triosin, 10 μ.   ×33.

Fig. 24.   Enlarged view of Fig. 23 showing the laminated character of the gastric shield.   ×150.

Fig. 25.   Cross section of the style-sac and mid-gut, and ascending limb of intestine. Ehrlich's haematoxylin and Triosin, 10 μ.   ×20.

A.I., ascending limb of intestine; M.G., mid-gut; S.S., style-sac; L.T., larger or left typhlosole; S.T., smaller or right typhlosole.

Fig. 26.   Transverse section of the descending limb of the intestine showing the prominent typhlosole with the median groove.   Van Gieson's and light green, 10 μ. ×20.

Fig. 27.   Transverse section of the rectum showing pronounced grooved typhlosole. Ehrlich's haematoxylin and Triosin, 10 μ.   ×25.

Fig. 28.   Transverse section of preanal rectum; the typhlosole is disappearing, epithelial folds are present.   Ehrlich's haematoxylin and Triosin.   ×35.

Fig. 29.   Portion of an extensively branched caecal duct of the digestive diverticula with sections of adjacent tubules.   Ehrlich's haematoxylin and Triosin, 10 μ.   ×70.

FIGS. 30–47.   Photomicrographs of histological sections of the digestive tract of *Crassostrea virginica*.

FIG. 30.   Non-ciliated and sparsely ciliated epithelium of the upper lip (fused external palps).   Mallory's triple stain, 10 μ.   ×600.
E.C., eosinophilic cell; L.C., Leydig cell; M.C., mucous cell; P., phagocyte or leucocyte.
FIG. 31.   Ciliated epithelial lining of oesophagus.   Ehrlich's haematoxylin and Triosin, 7 μ.   ×450.
One prominent eosinophilic cell is evident, also numerous mucous cells and phagocytes.
FIG. 32.   Wall of the anterior chamber of stomach.   Ehrlich's haematoxylin and Triosin, 10 μ.   ×250.
The ciliated cells have a prominent cuticular border.   Mucous cells are abundant and phagocytes occur in the lumen and throughout the epithelium and underlying layers.
FIG. 33.   Mid-region of the anterior appendix of the caecum.   Ehrlich's haematoxylin and Triosin, 10 μ.   ×250.
FIG. 34.   Wall of the posterior chamber of stomach.   Ehrlich's haematoxylin and Triosin, 10 μ.   ×225.
Phagocytes are numerous throughout the epithelium.   The cilia are long and the cuticular border is prominent.   Mucous cells are abundant.   C.S., crystalline style.
FIG. 35.   Wall of the posterior chamber of stomach immediately under the apex (neck) of the gastric shield (G.S.).   Ehrlich's haematoxylin and Triosin, 10 μ.   ×225.
The gastric shield has separated from the surface of the epithelial cells during sectioning.   The non-ciliated epithelial cells are the maximum height for the digestive tract.
FIG. 36.   Marginal area of the gastric shield showing the cytoplasmic processes of attachment to the peripheral borders of the cells.   Iron haematoxylin and light green, 7 μ.   ×500.
FIG. 37.   Junction of style-sac and mid-gut.   Ehrlich's haematoxyli nand Triosin, 10 μ.   ×75.
L.T., larger or left typhlosole; M.G., mid-gut; S.S., style-sac; S.T., smaller or right typhlosole.
FIG. 38.   Enlarged view of style-sac on right and adjoining smaller typhlosole of mid-gut on left.   ×225.
FIG. 39.   Longitudinal section through the style-sac showing uniformity of heavily ciliated surface.   Few phagocytes are present.   Ehrlich's haematoxylin and Triosin, 10 μ.   ×200.
FIG. 40.   Typical ciliated epithelium of the style-sac showing internal fibrillar apparatus.   Cresyl echt violet, 7 μ.   ×500.
FIG. 41.   Longitudinal section through the mid-gut showing ciliated epithelial cells and abundant phagocytes.   Ehrlich's haematoxylin and Triosin, 10 μ.   ×200.
FIG. 42.   Transverse section of the ciliated epithelial lining of the ascending limb of intestine.   Ehrlich's haematoxylin and Triosin, 7 μ.   ×225.
Eosinophilic cells are darkly stained.   Mucous cells and phagocytes are numerous.
FIG. 43.   Cross section through the ciliated epithelial lining of the lateral wall and adjacent typhlosole of the rectum.   Phagocytes are present in large numbers.   Ehrlich's haematoxylin and Triosin, 7 μ.   ×225.
FIG. 44.   Coronal section of ciliated epithelial surface of the anal region, showing prominent mucous cells and infiltration of phagocytes.   Ehrlich's haematoxylin and Triosin, 10 μ.   ×225.
FIG. 45.   Transverse section of a large duct of the digestive diverticula with some degenerating tubules from a specimen fixed during the early winter (late November).   Ehrlich's haematoxylin and Triosin, 10 μ.   ×70.
Mucous cells interspersed among the ciliated epithelial cells are abundant in the upper two-thirds of the duct but are rare in the lower third where the cuticle is heavy.
FIG. 46.   Typical tubules of the digestive diverticula with large lightly-staining vacuolated secretory and absorptive cells, and small darkly-staining generative cells.   A section of a small duct to the upper left.   Ehrlich's haematoxylin and Triosin, 10 μ.   ×275.
FIG. 47.   Typical tubules of the digestive diverticula during the winter season, showing the degeneration of the free border of the vacuolated secretory cells.   Ehrlich's haematoxylin and Triosin, 10 μ.   ×275.

PLATE II

PLATE III

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