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THE HISTOLOGY OF THE DIGESTIVE TRACT OF THE CLUSTER FLY, *POLLENIA RUDIS*

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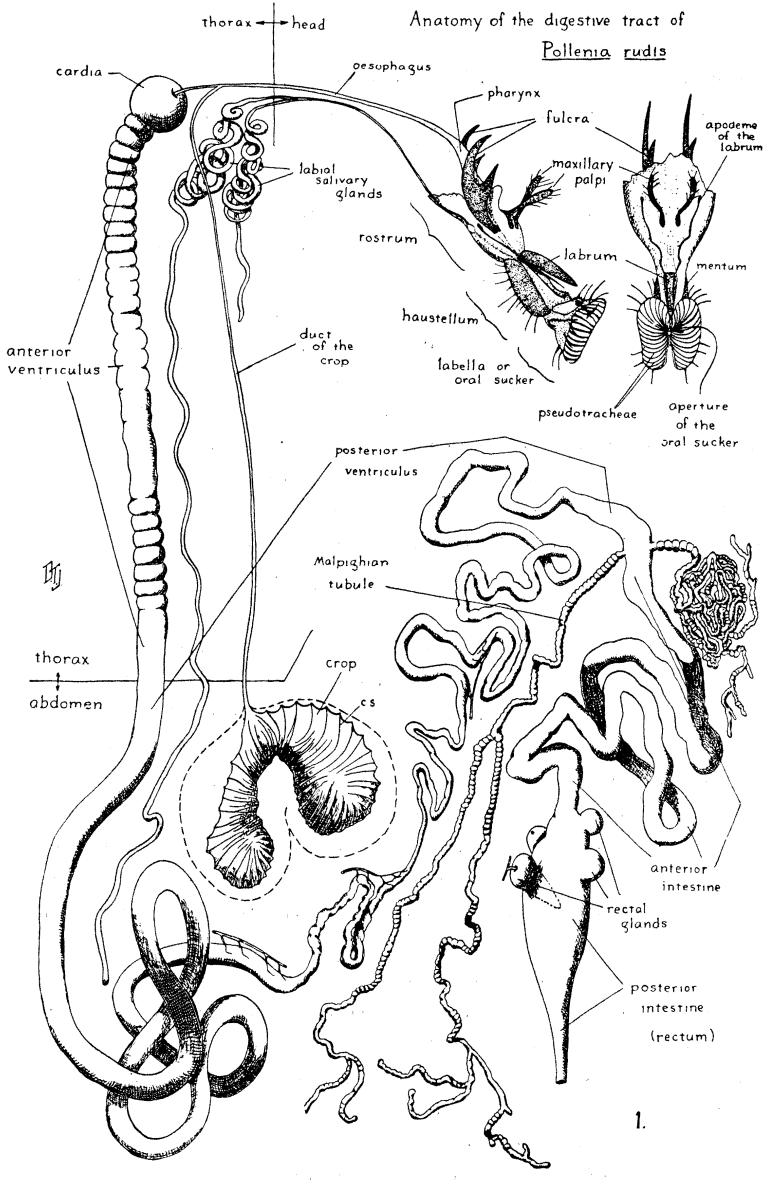
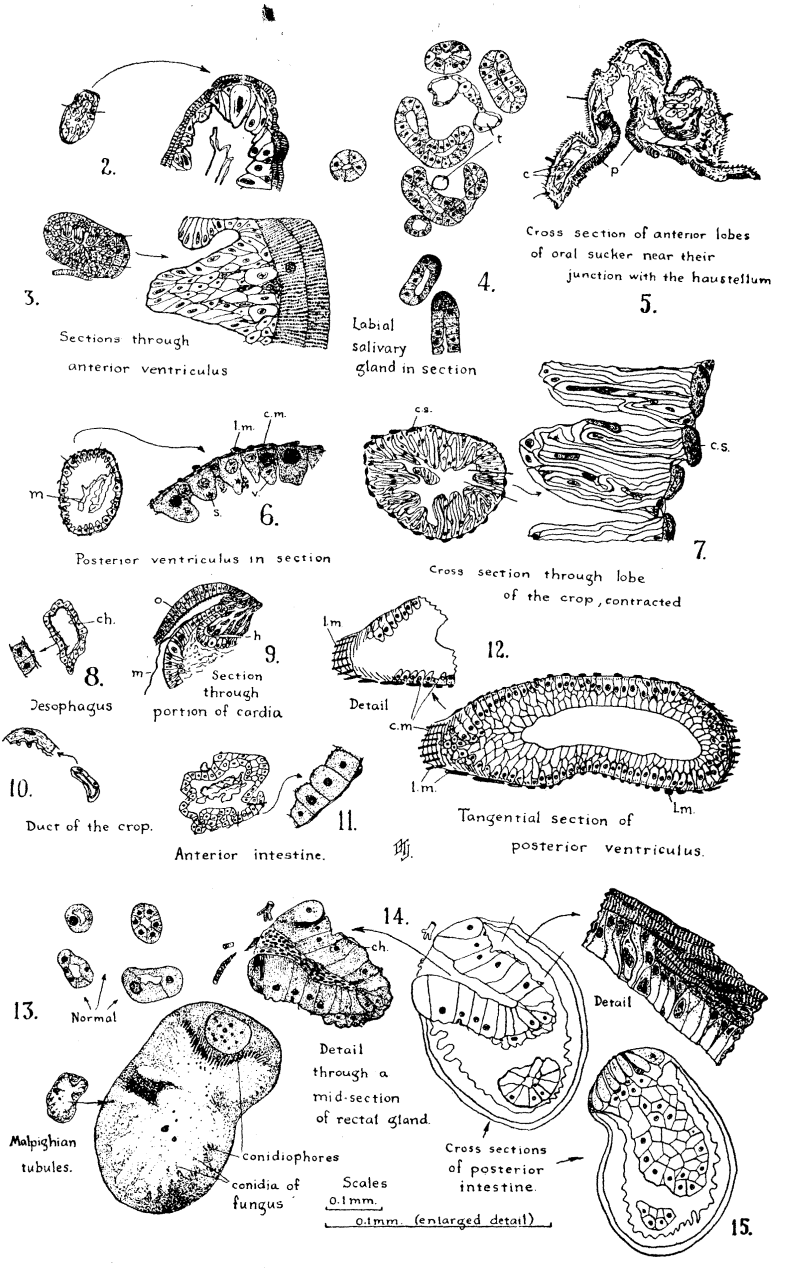
Pollenia rudis (Fabricius), the cluster fly, is a common household pest in Iowa in the fall, winter, and early spring. This house fly is readily distinguished from *Musca domestica* L. by its thoracic pubescence of fine crinkled golden hairs, its sluggish, almost tame habits, and its parasitizing woodland earthworms of the genus *Helodrilus* (De Coursey 1927) instead of breeding in horse manure. The flies were readily available indoors at Ames throughout the winter, as they emerged a few at a time from hibernation in window crevices, from moldings, and from behind furniture.

Acknowledgements are due the following members of the Zoology-Entomology faculty of Iowa State College: Dr. W. H. Wellhouse, under whom this study was made for graduate credit, for his direction of the problem and for helpful critical suggestions; to Dr. C. J. Drake and Dr. E. R. Becker for technical facilities; and to Dr. H. H. Knight for facilities for checking the identification. The excellent library facilities of Iowa State College were also appreciated.

The drawing of the anatomy of the digestive tract (Fig. 1) is freehand from approximately twenty-five dissections under a binocular microscope. The scales given do not apply to this figure. The remainder of the figures are drawn to scale from camera lucida outlines from slides made by the paraffin method. All such dissections were made under binocular in a ten per cent formalin solution from which they were removed to the fixative. Fixatives used were Carnoy's fluid, ten per cent formalin, and Bouin's fluid. A cold mush modification of the standard technique was found necessary between clearing and the paraffin. This mush was made from the clearer (xylene or chloroform) and paraffin. Tissues in the clearer were gradually transferred to the mush by pouring small amounts of melted paraffin at intervals into the clearer until a stiff mush resulted. This was allowed to stand cold for three or four hours to infiltrate. The preparation was then warmed until it became liquid, after which the tissues were changed to barely melted paraffin for a half hour interval, during which they were changed to fresh, barely melted paraffin as many times as possible to eliminate the xylene before imbedding. The object of this mush modification is to avoid the distorting effect of heat in


thorax
head
Anatomy of the digestive tract of
Pollenia rudis
cardia
oesophagus
pharynx
fulcra
apodeme of the labrum
labial salivary glands
maxillary palpi
rostrum
labrum
mentum
haustellum
duct of the crop
anterior ventriculus
labella or oral sucker
pseudotracheae
aperture of the oral sucker
posterior ventriculus
Malpighian tubule
thorax
abdomen
crop
cs
anterior intestine
rectal glands
posterior intestine (rectum)
1.


2.
t
c
p
Cross section of anterior lobes of oral sucker near their junction with the haustellum
5.
3.
Sections through anterior ventriculus
4.
Labial salivary gland in section
l.m.
c.m.
m
s
6.
Posterior ventriculus in section
c.s.
c.s.
7.
Cross section through lobe of the crop, contracted
ch.
8.
Oesophagus
h
9.
Section through portion of cardia
l.m
12.
Detail
c.m
l.m.
l.m.
Tangential section of posterior ventriculus.
10.
Duct of the crop.
11.
Anterior intestine.
14.
ch.
13.
Normal
Detail through a mid-section of rectal gland.
Detail
Malpighian tubules.
conidiophores
conidia of fungus
Scales
0.1mm.
0.1mm. (enlarged detail)
Cross sections of posterior intestine.
15.

infiltration to as great a degree as possible. Sections were cut at eight micra, and mounted on the slide in incomplete short serials as for cytological work. The slides were then alternately stained with (1) Delafield's hematoxylin and eosin, and (2) Heidenhain's acid hematoxylin.

In an article of this length obviously descriptive detail must depend largely on the drawings. The following comments, therefore, are to be regarded as supplementary to the drawings, to which simultaneous reference should be made. In this study the proboscal portion of the digestive tract is considered in some detail, but the postrectal portion and its relation to the reproductive ducts is deferred as more properly belonging to a discussion of the reproductive system.

The first portion of the digestive tract is the proboscis, which is divided into a distal portion, the oral sucker; a middle portion, the haustellum; and a proximal portion, the rostrum. That curved portion of the oral sucker which is approximated to the food forms an oral disc, over the surface of which extend delicate sucking tubes, the pseudotracheae (Fig. 5, p.), the structure of which for the blow-fly has been studied in detail by Graham Smith (Graham Smith, 1911, also 1930). The interior of the oral sucker is supported by a few chitinous spicule-like sclerites, which appear dark in cleared preparations, but which can be sectioned. Internally the cavities of the oral sucker contain many striated muscle cells (Fig. 5, c.) which in cross section are with difficulty distinguished from small lingual salivary glands which moisten the surface of the oral disc. In *Musca domestica* these are most apt to lie in the basal region of the oral sucker, near the haustellum (Hewitt 1914, Fig. 31). In our material striated muscle cells predominated with occasional scant evidence of mucous glandular structure.

The haustellum externally is partially covered by two chitinous shields, (1) a moveable labrum, and (2) a mentum, situated on the side opposite the labrum. The latter bears long bristles as shown. Underneath the labrum is a hollow chitinous needle, the hypopharynx, which transmits the common duct of the labial salivary glands. When the labrum is closed a sub-labral cavity is formed which distally communicates with the aperture of the oral sucker and through which the food passes inward to the mouth. It is into this cavity that the secretion of the labial salivary glands is discharged through the hypopharynx. Chitinized rods or sclerites are found also in the walls and cavities of the haustellum. Some

of these rods are extensions of the labrum, e.g. the apodemes of the labrum which extend into the rostrum, the apices of which serve as attachment for certain muscles of the proboscis.

The true mouth of the fly, situated under the hinged base of the labrum, is but a small opening. In this species the digestive tract as it enters the rostrum does not expand into the usual oral cavity, but gradually enlarges into a thin pharyngeal sac, lining the inner surfaces of the two chitinized fulcra. This pharynx narrows into an oesophagus. Just before leaving the head, the oesophagus passes through the ganglionic mass known as the "brain." Posteriorly the rostrum consists of a soft (non-sclerotized) postmentum which contains the bulb of the common duct of the labial salivary glands. This duct is faintly annulated for a short distance above the bulb. As it proceeds toward the thorax, this common duct bifurcates in the "neck" region, which is very much constricted in the Muscidae. As both the oesophagus and the duct of the labial salivary glands are freely moveable in the neck region, the cardia and the coiled portion of the labial salivary glands can be pulled almost up to the anterior edge of the thorax in pulling off the head. In life their position is somewhat variable near the middle of the thorax. On the front sides of the rostrum are the maxillary palps, each attached to a small imbedded maxillary sclerite. While having no connection with the digestive tract they are a valuable "landmark" in dissections of the rostrum.

To recapitulate, this fly in "eating" probably can use only liquid food as its oral disc is comparatively dry and so far as known its lingual salivary glands are not so extensive as to secrete much fluid for dissolving solids. It is very fond of apple juice, as sucked from the broken surface of the apple core, but can use with fair success the viscous fondant from the center of chocolate candies. These liquids are sucked into small apertures in the pseudotracheae, which converge either directly into the aperture of the oral sucker or into collecting ducts that run thereto. This aperture leads into the sub-labral cavity, where the liquid food is further thinned by the juices from the labial salivary glands. The food is then sucked through the small mouth opening into the pharynz, then through the oesophagus and crop duct into the crop. From the crop it is regurgitated into the cardia, where it is enclosed in a thin chitinous peritrophic membrane, which for some distance at least keeps it from direct contact with the delicate cells of the ventriculus. Its course beyond the cardia is evident from the drawing (Fig. 1). The peritrophic membrane is more or

less continuous throughout the entire tract posterior to the cardia, usually less continuous in the region of the intestine. It might be emphasized here that neither cardia nor crop are homologous with the proventriculus of other insects. The former in part and the latter wholly are differentiations apparently of the posterior oesophagus.

The sucking action of the anterior digestive tract has been variously explained physiologically. The consensus of opinion at present explains it rather by movements of the proboscis and of proboscal and pharyngeal muscles than by any sucking action of cardia or of crop. The emptying of the crop is evidently accomplished by circular strands of muscle, quite evident macroscopically (Fig. 1, c. s.) when the crop has discolored for a week or so in formaldehyde solution. These muscle cells are also evident in section (Fig. 7, c. s.). No valve has yet been found which would close the oesophagus during regurgitation of food from crop to cardia. There is, however, the possibility that a movement of the head might constrict the oesophagus in the "neck" region so as to close it.

Both the oesophagus and the nearby duct of the crop (Figs. 8 and 10) have a smooth (non-spiny) chitinous lining which is characteristic of stomodeal derivatives. The crop should have such a lining, but if it is present, it is so thin as to be imperceptible. The contracted crop wall consists of much folded epithelial cells. We have no slides showing its expanded condition. The oesophagus (Fig. 1) is invaginated into the cardia, forming an intussuscepted plate of oesophageal epithelium which is separated (Fig. 9) from the outer wall of the cardia (o) by the homogeneous membrane (h). From the surface of this epithelial plate or "Drüsenpolster" the peritrophic membrane (m) is secreted.

The labial salivary glands are delicate structures (Fig. 1) of variable length. In this species the coiled portion is quite localized and opposite the cardia, while the remainder is comparatively straight. The straight portion may arise far back in the abdomen. In the thorax it proceeds ventral to most of the viscera, among which it is packed tightly. It is in this congested region that it turns dorsally to continue into the coiled portion. In dissections it often breaks at that point. However, careful dissections of a number of flies indicate that in some flies the tube arises in this region. Whether this condition represents individual variation or the healing of a former break, with subsequent degeneration and disappearance of the broken stub, is doubtful. The coiled portion

in this species lies opposite the cardia, relatively further forward than in other species. There are from four to six loops, rather irregularly coiled. The further course of the two tubules in uniting to form a common duct has been described above. Sections of the coils (Fig. 4) show the wall of each tubule to be composed of a single layer of cuboidal cells. Nuclei are small, as are also the chromosomes. In *Sciara* and certain other small Diptera these chromosomes are of giant size. From them studies in the structure of chromosomes have been made. The labial salivary glands are well supplied by tracheoles (t).

The ventriculus presents varied aspects. The anterior ventriculus in this fly usually has areas of constrictions as shown (Fig. 1), which suggest peristaltically contracted regions. In sections (Figs. 2 and 3) this region shows considerable variation. The muscularis of one or two striated muscle cells, circularly or obliquely placed, is a fairly constant feature. There is scarcely any submucosa or connective tissue. The mucous membrane is of columnar or cuboidal epithelium, in places appearing stratified, though more probably these are only oblique cuts. Portions of the anterior ventriculus approach the appearance of sections of the posterior ventriculus, particularly as to epithelium (Fig. 6). There is no line of sharp demarcation between anterior and posterior ventriculus. In this species the thoraco-abdominal boundary was arbitrarily so used.

The posterior ventriculus is thinner walled, is more variable in diameter (because of greater distensibility), and is more richly supplied with tracheoles than is the anterior ventriculus. The tracheoles as shown (Fig. 1) frequently hold this portion of the digestive tract in permanent folds. In *Stomoxys calcitrans,* a blood-sucking fly, parts of the posterior ventriculus may be greatly distended with blood. In *Pollenia rudis* only moderate distensions as shown (Fig. 1) have been noted. In cross section (Fig. 6) the structures that superficially appear to be serosal cells are actually large muscular strands (l.m.), circularly arranged. Beneath these, apparently in, but more likely under, the epithelial cells, are oblique or circular muscular strands (c.m.). A study of tangential sections (Fig. 12) clearly reveals this relationship. The epithelium of the posterior ventriculus is often found in a state of physiological activity with pseudopodial projections (Fig. 6). Within the pseudopodia are found in some cases a secretory apparatus (s) and vacuoles (v). Nuclei and cytoplasms often stain differentially dark or very light. It is probable that much of the

absorption occurs in this portion of the digestive tract. The peritrophic membrane (m) is here yet quite intact.

The Malpighian tubules are yellowish in color, some parts having a distinctly beaded appearance. Their morphology is adequately shown in Fig. 1, their histology in Fig. 13. A cross section near the tip will generally cut only one cell, while if taken near the junction with the alimentary tract, five or six cells will usually be involved. Of all parts of the body of this fly, the Malpighian tubules alone are susceptible to attack by a fungus (Fig. 13, detail). Lintner (1892) states that in *Pollenia rudis* this is not *Empusa muscae* but *Empusa americana* R. Thaxter. At an extreme stage the wall becomes exceedingly thin, and the nucleus more flattened and compressed against the wall than our figure shows. Flies which gyrate in their flight through meaningless spirals and finally end up bumbling on their backs, are found to have Malpighian tubules in this extreme condition. Uremic poisoning is suggested. The Malpighian tubules in this species enter the digestive tract as two tubules, marking not only the junction of the posterior ventriculus and anterior intestine but also the junction of the embryonic proctodeal inpouching with the mid-gut.

The anterior intestine is of approximately the same structure as the posterior ventriculus, though the cells often become more regularly cuboidal (Fig. 11). This same condition is also evident in the posterior intestine beyond the region of the rectal glands. As a proctodeal derivative the anterior intestine might be expected to show a chitinous lining, other than the peritrophic membrane which is loose in its lumen. However in this species no such lining is evident, except in the posterior intestine, where it becomes thick enough to be discernable over the surface of the rectal glands (Fig. 14).

The posterior intestine or rectum is of considerably greater diameter, especially in the region of the four rectal glands (Fig. 1). A rectal gland consists of an outer hemispherical protrusion of spongy cells (Fig. 15) and an inner papilla (Fig. 1, dotted; also Fig. 14). In longitudinal section, each papilla is shown to to have a core of tracheloes which are packed in among other tissue which on comparison with nerves in the same animal appears identical. The chitinous lining over the surface of the papilla shows occasional breaks and chitinous spines. Hewitt (1914, p. 41) mentions these breaks or perforations in *Musca domestica*. The function of the rectal glands is yet problematical. If secre-

tory, these perforations may prove similar to the pores in the external cuticle of the earthworm over each goblet cell. The wall of the rectum has a thicker muscularis than has that of other portions of the digestive tract. Its epithelium shows very evident interstitial or replacement cells near the basal membrane. Similar simple replacement cells were observed throughout the tract, but none were found in nidi or crypts.

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