Anatomy of Dactylopius longifilis Comst.

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The Anatomy of *Dactylopius longifilis* Comst.

by

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INTRODUCTION AND METHODS.

The purpose of this paper is to give a general account of the anatomy of *Dactylopius longifilis* Comst. It being impossible to write an exhaustive account at present, I have selected the more important anatomical peculiarities for special study.

This line of work was undertaken at the suggestion of Professor S. A. Forbes and carried on under his general direction, while much personal supervision and many helpful suggestions have been given by Dr. J. W. Folsom. To both of these gentlemen I take this opportunity of expressing my sincere gratitude for their aid and encouragement.

The specimens used were taken from *Cyperus alternifolius* Linn. growing in the University green house. Being unable to find any male *Dactylopius* I have confined my studies to the young and mature females. The results given in this paper are, with few exceptions, based upon serial sections which were studied by the method of reconstruction. The method of dissection was tried but abandoned, as being less serviceable for these particular insects. I employed either a saturated solution of corrosive sublimate with 1% acetic acid or absolute alcohol acidulated with a little acetic acid, with good results. In cutting sections I found twenty micra to be a favorable thickness for general work. Sections ten micra thick are better for histological purposes. I only tried two stains in this work, Ehrlich's haematoxylin and Grenacher's alcohol borax carmine. The former gave the more satisfactory results.
EXTERNAL ANATOMY.

*Dactylopius longifilis* Comst. is about three to five millimeters long and one and a half to two millimeters wide, oval in general outline and flattened dorso-ventrally. The separation into head, thorax and abdomen is not distinct, but is nevertheless present. The color is a light dull yellow, dusted sparingly on the back with a waxy substance which is secreted through numerous minute pores. There is found along the margin of the body extending from the back, a white fringe composed of a row of columns, seventeen on either side. The last two posterior on either side are elongated into filaments which are sometimes as long as the body.

The head is about one-fifth the length of the body and two-thirds as long as wide. At the anterior end, and well apart, are two eight-jointed antennae. The two small simple eyes are situated posterior and slightly dorsal to the antennae. The external mouth parts are ventral and far back, being near the anterior margin of the thorax. There is a jointed oral parilla from which protrude the three bristles which constitute the proboscis. Immediately anterior to the base of the papilla is a strongly convex surface to the inner wall of which the strong dilator muscles of the pharynx are attached. The sides and anterior margin of this convex surface form a horseshoe-shaped sinus. The ends of the horseshoe pass on either side of the base of the oral papilla and end opposite to the middle of the base.

The pro- meso- and metathorax are distinct. Of the three the mesothorax is the largest. The legs are well developed although much smaller in proportion to the size of the body than those of the larva.
The abdomen is composed of seven segments of which the first is the longest, the seventh the shortest, and the other five of about equal length. On the dorsal side of the sixth abdominal segment are a pair of papillae through which the honey glands open. The genital opening occurs at the suture between the sixth and seventh segments. It consists of two lips, one on either segment. On the last segment are two prominent lobes each bearing a long hair. The anus, surrounded by an anal ring bearing six tubular hairs, opens between these lobes.
DIGESTIVE SYSTEM.

The digestive system bears a general resemblance to that of other Hemiptera, in that the mouth parts are suetorial, the salivary glands are well developed and the oesophagus is very slender. Of the three primary divisions of the alimentary canal, as seen in figure 4, the stomodeum and mesenteron are of moderate length but the proctodeum is elongated to an extent unusual among insects.

The pharynx opens through a papilla, from the edge of which three bristles protrude to form a sucking proboscis. This papilla is composed of two heavily chitinized segments and contains well developed systems of longitudinal and oblique muscles, by means of which the papilla may be inclined forward and backward. On its surface are a number of long slender spines, probably tactile in function. The bristles of the proboscis extend upward through the oral papilla, as shown in figure 3, enclosing a slender canal which dilates to form a pharynx immediately above and anterior to the base of the papilla. The bristles diverge and gradually expand as they enter the pharynx and increase in thickness to about twice the diameter of the external portion. They originate from the dorsal wall of the pharynx. The pharynx is supplied with a highly developed series of dilator muscles which extend from the chitinous wall of the pharynx within to the skull. There is, in addition, a feebly developed set of circular, or constrictor, muscles, the function of which is to counteract the action of the dilators just mentioned. Finally, there are a few longitudinal muscles lying along the pharynx, their function being to bend the pharynx in various directions.
The slender oesophagus, into which the pharynx opens, extends upward through the opening between the commissures which connect the brain and the suboesophageal ganglion. It then turns sharply backward, passing closely above the suboesophageal ganglion and opening into the stomach in the mesothorax. There are two salivary glands situated above the oesophageal ganglion, extending upward and outward. Each gland consists of six principal lobes, as represented in figure 5. The evacuating ducts receive the secretion from the anterior side of the lower lobes, lead forward and downward on either side of the suboesophageal ganglion and empty into the sinus above the base of the oral papilla. The external openings of these ducts are shown in figure 4.

A large median unpaired gland occupies the floor of the mesothorax and part of the pro- and metathorax. Its form is largely determined by the pressure of the organs around it. This is especially true of the mature female, in which the form of the ventral gland is greatly modified by the pressure of the ovaries and other organs; the ventral gland when unconfined is smoothly elongate and elliptical. As seen in a frontal section, the diameter is about one-third the length. In sagittal section it tapers at either end. The ventral gland consists of cells so compressed as to leave only small intercellular spaces, and is surrounded by a limiting membrane. The cells are usually round or oval in cross section, with dense cytoplasm which takes a very deep stain. The diameter of one of these cells is from thirty to forty micra and the length, fifty micra. The nuclei are large, being about ten micra in diameter and twenty five micra in length with large chromatin granules. These cells are shown in figure 6. The single evacuating duct, I have been able to trace only as far backward as the anterior end of the
gland; it takes a median ventral course, passing beneath the nerve cord and emptying into the pharynx at the base of the oral papilla; it is very thickly chitinized and its lumen is about two-thirds wider than that of the oesophagus.

Of the three glands described, I infer that only this ventral gland is immediately concerned in the process of digestion; because it is the only one that opens directly into the alimentary canal. Since the paired glands open externally at the base of the oral papilla they probably bathe the external mouth parts with their secretions.

In order to understand the course of the alimentary canal farther, it will be necessary to refer to figure 4. The anterior part of the mesenteron and the part of the proctodeum shown in figure 7 have not only grown together but the proctodeum also in-closes about one-third of the mesenteron. The oesophagus also passes within this inclosure extending about five times its own width, where it opens into the mesenteron. The mesenteron soon turns upon itself toward the right and passes forward for a distance equal to about five times its own width. Then it turns at right angles to the left, passing over the oesophagus. Immediately it turns again at right angles and passes back beside the oesophagus. It follows the anterior part of the mesenteron, turning with it, first to the right, then forward, extending as far as the place where it passes over the oesophagus, then passes beneath the proctodeum and forward. In this part of its course the stomach varies in its position. In two specimens it turned to the right, in three it turned to the left and in one it occupied a median position. In the specimen from which figure 4 is drawn, the mesenteron, after passing forward, turns
at right angles to the left and for a distance equal to about one-fifth the width of the body. At this place the Malpighian tubules open into the canal. The intestine turns forward and downward but soon takes a turn to the left, for a short distance, and then turns on itself and crosses to the other side of the body, passing backward until it is about one-fourth the length of the body from the posterior end. It now turns again to the left, passing just over, but in close contact with, the median ventral gland described above. When about two-thirds the way across the body it turns and passes as far forward as the beginning of the mesenteron. It then turns at right angles to the right until just in front of the mouth of the above described invagination of the proctodeum. The proctodeum now turns backward leaving a short broad caecum at the turn as shown in figure 7 and enters the invagination. Here it passes beneath the oesophagus and the greater part of the mesenteron, but over that portion of the mesenteron leading out of the invagination. This invagination is formed by the alimentary canal being pushed back into itself telescopically, as shown in figure 8. In size and structure the mesenteron and all of the proctodeum except the posterior portion are similar. I could distinguish no essential difference between the two parts. In section as seen in figure 9, they show a layer of longitudinal muscles, a thin basement membrane, a very prominent glandular layer and a very delicate intima. The glandular cells are large and irregular in form and project into the lumen. In the proximal ends of the cells the cytoplasm is very dense, taking a deep stain. The clear transparent tips appear to be distended by the fluid secreted by the glands.
The proctodeum now takes a different character. Instead of being thick and glandular, the walls are clear and very thin. When distended it is about five times the diameter of the mesenteron at the anterior end and gradually tapers posteriorly for about one-third the length of the body where it is about equal in diameter to the mesenteron. It then dilates to five times the diameter of the mesenteron and gradually tapers for about one-sixth the length of the body until once more of the same diameter as the stomach. The presence of the constriction between the two dilations is due to the position of the Malpighian tubules, which press in at either side. The proctodeum forms a third small dilation or rectum. The anus is situated in an extreme posterior position on the last, or seventh, abdominal segment.
THE EXCRETORY SYSTEM.

The excretory system is represented by a pair of Malpighian tubules which unite into a common tube that empties into the alimentary canal. The position of the mouth of this tube has been described under the head of digestive system. This single tube curves forward and to the right until near the median plane. Here the two tubes lead out, one to either side of the body just above the proctodeum and extend back as far as the third abdominal segment. Such is their position in the young female. In the mature female the tubes are frequently rushed upward and curved about between the follicles of the ovaries. In size the Malpighian tubules are about one-tenth to one-twelfth as wide as long. This width of the Malpighian tubules is greater than is usually found among insects.

In structure the Malpighian tubules consist of a single thick layer of cells. The lumen is not straight but takes rather a tortuous course, owing to the difference in the turgidity of the varicous cells, some of which project far into the lumen. A portion of the Malpighian tube in section is shown in figure 10. The cells are large, clear and transparent, are usually three or four times as long as they are wide and have, as already mentioned, a marked tendency to bulge into the lumen; the outer walls, however, are flat as contrasted with the convex inner walls. The oval nuclei are very large in proportion to the size of the cells. A thick intima and a delicate basement membrane are evident.
RESPIRATORY SYSTEM.

There are two pairs of spiracles present in Dactylopius. One pair is found on the metasternum, the other pair is situated on the suture between the pro- and mesosternum. The posterior pair of stigmata appear only to supply air to the abdomen and metathorax. As shown in figure 12, they give off three small and one large pair of tracheae on either side. Two small tracheae on either side, a and b, turn back and supply the first few abdominal segments; a third small branch goes to the metathorax. The large trachea d passes toward the posterior part of the body, soon dividing into two tracheae which, in turn, branch repeatedly to form the fine network of tracheae in the posterior part of the abdomen. In addition to the smaller tracheae, there are three main branches given off from each anterior spiracle. These all pass forward connecting with the small branches in the prothorax and the head.

The spiracles are simple openings surrounded by chitinous rings; they appear to have no apparatus of closure. I did not distinguish taenidia in any of the tracheae.
NERVOUS SYSTEM.

The nervous system is highly centralized. The brain is well developed and the remaining ganglia are so strongly cephalized that they form a single compound ganglion which terminates behind in the prothorax.

The brain occupies an extreme ventral position and is in one plane with the suboesophageal ganglion; i.e., is not above the latter, but is in front of it. The brain plainly shows a division into two pairs of lobes, the optic and antennal. Leading from these lobes the nerves can be traced to the antennae and eyes as shown in figure 13. The eyes are rather small, are posterior and slightly dorsal to the antennae and have strongly convex and elongated corneae.

The circumoesophageal commissures necessarily take a horizontal position. They are stouter and longer than usually found among insects. Since the oesophagus passes directly back of the brain, the commissures diverge immediately after leaving the brain, and meet just back of the oesophagus. Thence they pass back side by side for about forty to forty-five micra before connecting with the compound ganglion.

The compound ganglion consists of six pairs of lobes as seen in figure 14. The three middle lobes on either side are thoracic, as they supply nerves to the legs. The posterior lobe must therefore be abdominal; it sends nerves far back into the abdomen. The two anterior pairs of lobes I infer, both from their position and isolation, to represent the suboesophageal ganglion. The suboesophageal lobes as shown above, are not close behind the oesophagus, as in most insects and are but five in number. In none of my
sections was I able to find any branches leading from these ganglia. This is doubtless due to my not using a special stain for the differentiation of nerves.

The thoracic ganglia, although united to the suboesophageal ganglia are still clearly distinguishable from them. The branches from these ganglia are evident. The anterior ganglion gives off a pair of branches to the first pair of legs, the second ganglion sends a pair of branches to the second pair and the posterior ganglion supplies the remaining pair.

The abdominal ganglion shows no division into lobes, or other evidence of being compound, and I therefore regard it as the ganglion of the first abdominal segment simply. Near its posterior end it gives off a pair of nerves. These pass back on either side through sheaths, in common with the branches from the last thoracic ganglion. The thoracic and abdominal branches soon separate, the latter passing back into the abdomen.

The ganglia consist of a clear nonstaining core of "Punktsubstanz" surrounded by a denser, deeply staining, cortical layer of ganglion cells. The nuclei of these cells are about 3 micra in diameter. Some of these cells near the cortex appear to have long cytoplasmic processes which are not traceable far from the cells from which they originate but are lost in the Punktsubstanz. From the Punktsubstanz originate fine fibrillae, which eventually enter into the composition of a nerve. The bases of the nerves are enveloped in a sheath or neurilemma, which is also continued over the ganglia.
REPRODUCTIVE SYSTEM.

The reproductive system of the female is extensive. In the young female the ovaries are conspicuous; in the sexually mature individual they occupy almost the entire abdomen at the expense of the other organs. The reproductive system consists of two oviducts, completely surrounded by clusters of follicles, and a vagina with its accessory glands.

In the young female the thickly clustered lobes of the ovaries are small and pyriform and open directly into the oviduct by means of short tubes as shown in figure 14. The lobes of the ovary clustered about the oviduct are represented in figure 15. The lobes of the ovaries, as seen in the mature female are made up of a layer of follicular cells. Their arrangement and structure are shown in figure 16. In all the specimens examined only one ovum was found in each follicle. In the mature female the ovaries are distended with ova and eggs: they crowd all the other organs, taking up all the available space in the dorsal part of the body and extending almost into the head region. The eggs and ova present all stages of development. There are to be seen, side by side, the small undeveloped ova and the well advanced egg. Previous to oviposition, the embryo is so far advanced in development as to show the segmentation of the body and the fundamentals of the paired appendages.

The two oviducts are simple unbranched tubes communicating with the ovaries along their entire length. They occupy a dorsal position, extending forward three-fifths the length of the body, in the young female. In the mature female they extend almost into the head region. Posteriorly they turn downward and inward, opening in-
to the extreme anterior end of the vagina. In structure they are very thin walled, have well defined nuclei but do not show cross partitions between the cells.

The vagina is a thick, muscular walled tube, median and ventral in position. It opens externally between the sixth and seventh abdominal segments. It has four evaginations. Three of these (of which two are lateral and one ventral) are similar in form being large pockets, reniform in cross section. These rockets, probably glandular in function, are shown sectioned transversely in figure 20, which is taken from a mature individual. They are ultimately so large as almost entirely to surround the vagina and to appear as one continuous mass. In the young female, however, they are clearly three distinct structures. The thick wall of each pocket surrounds a central cavity which opens into the vagina. In the young female the pockets are smaller and have thinner walls. The cells which compose the walls are large and turgid with a deeply staining basal or cytoplasmic portion, containing a large oval nucleus; and a clear vacuolar region adjacent to the lumen. These characteristics indicate the glandular nature of the walls; the clear unstainable arices of the cells doubtless contain a substance secreted in the basal portions. These glands I regard as shell glands. A ventral view of the vagina and its glands is shown in figure 17. The fourth or dorsal pocket is quite different in structure from the other three. It consists of a long slender tube extending as far forward as the anterior end of the vagina and opening as the other glands. At its anterior end there is a spherical enlargement. The walls of this enlargement, while dense enough in places to appear glandular, are still very thin as compared with the other glandular pockets. Because of its form, structure and posi-
tion, I infer that this must be the receptaculum seminis, and that the few small glandular cells secrete the fluid for the preservation of the spermatozoa. A lateral view of the vagina and receptaculum is shown in figure 19, while in figure 16, a dorsal view is given.

SILK GLANDS.

At the time of oviposition, the female spins a mass of threads which entangles the eggs as they are extruded. As oviposition advances, this tangle becomes more complex, especially at the posterior extremity of the insect, until the coccid is raised a millimeter or more above the substratum, usually with the abdomen higher than the thorax. In this mass of threads may be found, at the same time, both young larvae and eggs. This silk is produced by numbers of unicellular glands such as are shown in figure 21, which are confined to the ventral side of the last five segments of the abdomen and extend, on the one hand, as far as the fringe of wax at the sides; on the other hand, as far as the ventral edge of the anus.
Explanation of the Abbreviations used on the plates.

a. anus.
ab.g. abdominal ganglion.
b.m. basal membrane.
br. brain.
ca.e. caecum.
g. genital opening.
gl. glandular cell.
i. intima.
il.e. lateral evagination of vagina.
l.m. longitudinal muscles.
mes. mesenteron.
mt. Malpighian tubules.
mt.o. opening of Malpighian tubules.
c. follicles of ovary.
oe. oesophagus.
c.p. oral papilla.
c.s. oral sinus.
ovd. oviduct.
ph. pharynx.
proc. proctodeum.
r.s. receptaculum seminis.
s. sriacle.
s.g. salivary gland.
sub.g. suboesophageal ganglion.
th.g. thoracic ganglion.
v. vagina.
v.e. ventral evagination.
v.g. ventral gland.
PLATE I.

Fig. 1. Ventral view of abdomen of Dactylopius.

Fig. 2. Ventral view of last four segments of the abdomen showing genital and anal openings.

Fig. 3. Sagittal section to show position of salivary glands, ventral glands, and the ganglia.
PLATE II.

Fig. 4. Reconstruction from sections of a young female to show the digestive system, as seen from above.
PLATE III.

Fig. 5. Anterior view of one of the salivary glands. Reconstructed.

Fig. 6. Frontal section of a few of the cells that constitute the ventral gland.

Fig. 7. Dorsal aspect of the alimentary canal, showing the mesenteron enclosed within an invagination of the proctodeum.

Fig. 8. A diagram to show the form of the invagination just mentioned.

Fig. 9. Longitudinal section of the intestine showing its histological structure.
Fig. 10. Longitudinal section of a portion of a Malpighian tubule.

Fig. 11. Dorsal aspect of part of a Malpighian tubule.

Fig. 12. A diagram of the respiratory system.

Fig. 13. Reconstruction from frontal sections to show the central nervous system of a young female.

Fig. 14. Frontal section of the central nervous system more highly magnified than in figure 13.
PLATE V.

Fig. 14. b. Dorsal view of the reproductive system of a young female, as reconstructed.

Fig. 15. Frontal section of a portion of an oviduct showing the clustered follicles.

Fig. 16. Dorsal aspect of vagina and the accessory glands, as reconstructed.

Fig. 17. Ventral view of vagina and the accessory glands, as reconstructed.
PLATE VI.

Fig. 18. Section of the wall of a follicle showing follicular cells.

Fig. 19. Sagittal section of vagina and its accessory glands, as reconstructed.

Fig. 20. Cross section of vagina and accessory glands.

Fig. 21. Silk glands as seen in a sagittal section.