

The Development and Homologies of the Mouth-parts of the Head-Louse.

By

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With 10 Text-figures.

INTRODUCTION.

IN 1903 Cholodkovsky published his work on the development of the mouth-parts of *Pediculus*. He asserted that the mandibles and the maxillae appeared in the germ-band at an early stage, but subsequently disappeared, the stylets and the stylet sheath of the adult animal being only a modified labium. This view was criticized by Enderlein (1904) who studied, by dissection, the mouth-parts of several members of the Siphunculata. According to him the mouth-parts of the adult louse are homologous with the maxillae, hypopharynx, and labium of other insects. He further stated that the mandibles were rudimentary in *Pediculus*, but persisted in *Haematopinus*. Thus the views of Cholodkovsky, based on embryological evidence, were diametrically opposed to those of Enderlein, based on comparative anatomy, but no attempt had been made to reinvestigate the development of the mouth-parts of the louse.

The present investigation is an attempt to settle by confirmation or otherwise of Cholodkovsky's work on *Pediculus* the problem presented by the conflict of views outlined above. In it no attempt is made to deal with a detailed study of the structure of the mouth-parts of the adult, as their structure has been thoroughly investigated already, only their development and homologies are considered. The work was done only on the head-louse (*Pediculus humanus*, var. *capitis*).

My thanks are due to Mr. D. R. R. Burt, Lecturer in Zoology,

Ceylon University College, for the interest he has taken in my work. I am indebted to my brothers, Dr. S. E. Fernando and Dr. S. F. Fernando for the material which they obtained from the Hospitals in Colombo and Kandy.

TECHNIQUE.

The eggs were fixed in picro-nitric acid and Henning's fluid. The embryos were then dissected out of the egg capsules and were doubly embedded, first in celloidin and then in paraffin, and sections were stained in Delafield's haematoxylin. At the suggestion of Prof. J. W. Munro, of the Imperial College of Science and Technology, London, sections were stained in order to verify the presence of chitinous structures in the mouth-parts. For this purpose Brilmayer's modification of Delafield's haematoxylin and Mallory's connective tissue stain were employed.

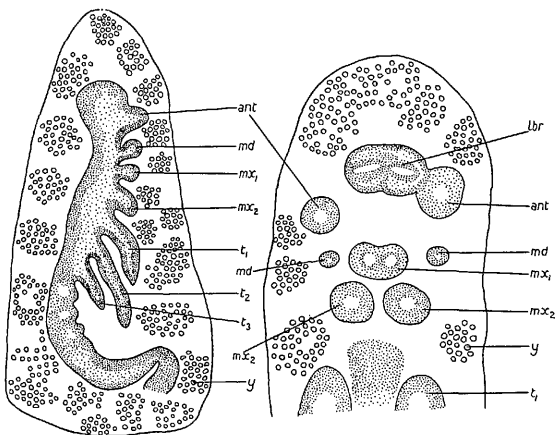
DESCRIPTION.

The limb-buds appear in the germ-band as paired outgrowths. The rudiments of the three pairs of thoracic limbs make their appearance first, followed by the labium and the other head appendages. This results in an embryo in which all the appendages of a typical insect are present, though rudimentary (Text-fig. 1). The antennae (*ant*) are the most anterior appendages in the head region; then follow the rudiments of the mandibles (*md*) which are smaller than the antennae; the rudiments of the first maxillae (*mx₁*) are almost of the same size as those of the mandibles. The labium, representing the second maxillae (*mx₂*), consists of a pair of rudiments, but these are slightly larger than those of the mandibles and the maxillae. The rudiments of the three pairs of thoracic legs then follow and the abdominal region also shows signs of segmentation, but no appendages are present on the abdomen.

As development proceeds the head region elongates gradually and the antennae become longer. The mandibles and the first maxillae, however, show no signs of elongation, but the labial rudiments grow as rapidly as do the antennae. The differentiation of the thoracic limbs takes place very rapidly, but as we

are concerned only with the mouth-parts, we shall confine our attention solely to them.

The stomodaeum arises as an invagination in the region



TEXT-FIG. 1.

TEXT-FIG. 2.

FIG. 1. Sagittal section of an early embryo (combined from two sections).
 FIG. 2. Frontal section showing union of the first maxillae.

ABBREVIATIONS.

ant., antenna; *bf.*, buccal funnel; *bt.*, buccal teeth; *dls.*, dorsal lip of embryonic stylet sheath; *d.st.*, dorsal stylet; *hyp.*, hypopharynx; *lbr.*, labrum; *m.*, mouth; *md.*, mandible; *mx.*, first maxilla; *mx.*, labium; *nc.*, nerve cord; *oes.*, oesophagus; *Pg.*, Pavlovsky's gland; *ph.*, pumping pharynx; *sal.d.*, salivary duct; *st.s.*, stylet sheath; *sub.g.*, suboesophageal ganglion; *sup.g.*, supraoesophageal ganglion; *t.*, *t.*, *t.*, thoracic legs; *vs.*, ventral lip of embryonic stylet sheath; *v.st.*, ventral stylet; *y.*, yolk.

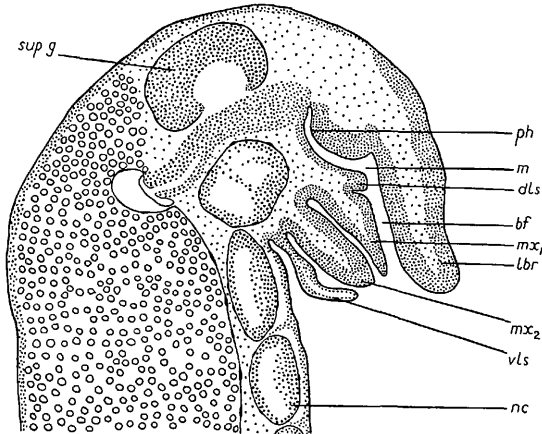
between the antennae and the mandibles. The antennae, meanwhile, become displaced so as to assume a more lateral position. Almost on a level with the bases of the antennae, there appear two projections immediately above the mouth. These are the rudiments of the labrum.

With the appearance of the labral rudiments differentiation of the other mouth-parts begins. The mandibles do not appear to grow and remain in their original position (Text-fig. 2, *md*). The first maxillae, however, shift their position more towards the median line, where the two rudiments come so close together that they ultimately fuse into a single projection (Text-fig. 2, *mx*₁). The double origin of this is always evident in sections from two haemocoelic spaces which it encloses. The fused first maxillae then increase gradually in size. The rudiments of the labium (*mx*₂) also move towards the median line, but they do not fuse with one another as early as do the first maxillae.

At a later stage the rudiments of the labrum unite with one another, as do the rudiments of the labium. The embryo now presents the following appearance. The labrum is represented by a single structure lying above the mouth, which leads into the stomodaeum. Situated along the middle line posterior to the mouth are the fused first maxillae and the fused labium, each represented by a single projection. During development the former is transformed into the dorsal stylet of the adult, and the latter into the ventral stylet. This transformation takes place during the later embryonic stages. The mandibles, however, retain their original lateral position.

The rudiments of the fused maxillae and of the labium elongate, and at the same time they become withdrawn or sunk into a depression formed immediately posterior to the mouth (Text-fig. 3). The lips of this depression, which surround the first maxillae and the labium, become raised as these rudiments elongate, growth being greater in the ventral lip. The cavity of the depression, now tubular, in which the maxillary and labial rudiments lie, becomes the stylet sac, while the inner surface of the raised lip becomes the stylet sheath of the imago. The result of this development is that the labium appears longer than the first maxillae and the ventral lip of the stylet sheath appears in sagittal section as an appendage formed by the splitting up of the labium. In other words, the ventral lip of the stylet sheath (*vl*s) appears like a distinct 'lower lip'. Meanwhile, the labrum has elongated considerably, forming a flap over the other mouth-parts. The original

stomodaeal invagination now lies at the base of a canal-like depression which is bounded by the elongated labrum in front and the raised lip and apices of the maxillae and the labium behind. This canal represents the 'buccal funnel' of the adult.



TEXT-FIG. 3.

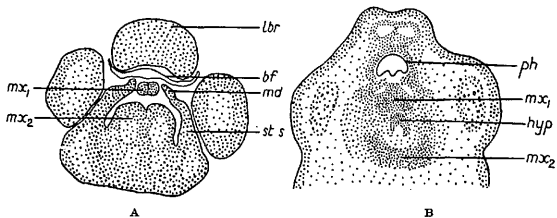
Sagittal section showing the formation of the stylet sheath.

The portion of the alimentary canal behind the original mouth develops a thick muscular wall becoming the 'pumping pharynx' (*ph*) of the adult.

We have shown that the stylet sheath is formed from the integument surrounding the first maxillae and labium. The mandibles lie on the dorsal lip of the stylet sheath and appear as two small projections directed inwards (Text-fig. 4 A, *md*). Thus the mandibles lie in close proximity to the original mouth opening, but on the smaller anterior (dorsal) lip of the stylet sheath guarding the opening from the buccal funnel into the stylet sac.

In the posterior region of the head, on a level with the bases

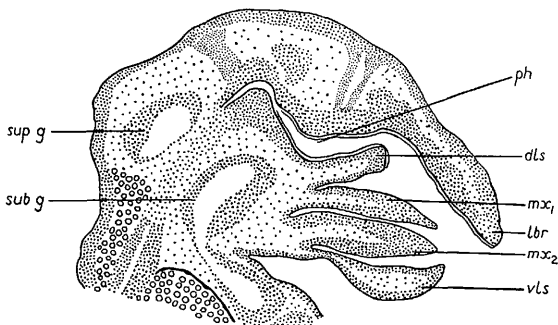
of the first maxillae and the labium, there is a small projection lying below the first maxillae (Text-fig. 4 B, *hyp*). It corresponds



TEXT-FIG. 4.

Transverse sections of the head of an embryo.

- A. Section passing through the lip of the stylet sheath.
 B. Section passing through the base of the stylet sheath showing the developing hypopharynx.



TEXT-FIG. 5.

Sagittal section showing further development of the stylet sheath.

in position with the hypopharynx. Groups of cells being differentiated into the salivary glands lie deeper in the head in the region of the hypopharynx.

The stylet sheath gradually becomes tubular, while the invagination deepens dorsally. Thus the bases of the first maxillae

and the labium are gradually carried backwards, and these structures, which at first pointed backwards, now lie horizontally. The ventral lip of the stylet sheath becomes much thicker (Text-fig. 5) and grows out beyond the developing stylets later becoming the ventral and lateral walls of the buccal funnel.

We shall now consider the fate of the various embryonic head appendages. The hypopharynx was shown above to have arisen as a slight projection at the base of the first maxillae. This projection now elongates and assumes the nature of a rod-like structure lying between the first maxillae and labium (Text-fig. 6, *hyp*). The hypopharynx gradually elongates and lies closely applied to the ventral surface of the fused first maxillae. It becomes tubular (Text-fig. 7, *sal.d*) and later on it loses its cellular structure by becoming chitinized as in the imago. We have thus the salivary duct of the adult formed from a modified hypopharynx. At its base lie the salivary glands.

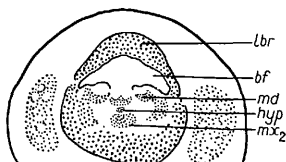
Pavlovsky's glands develop on the sides of the stylet sheath, into which they open at a later stage.

The first maxillae and the labium, as we have seen, were originally paired, their double origin being evident at early stages by the appearance of double haemocoelic spaces (Text-fig. 7). Union of the two rudiments in each case results in the production of a rod-like structure, the first maxillae lying in front of the labium. With the development of the stylet sheath these elongate and become pointed at the tips. An examination of serial transverse sections of old embryos shows a difference in structure in the maxillae and labium. Distally each is single with a single haemocoelic space. Proximally the maxillae remain the same, but the labium divides into an anterior and posterior element (Text-fig. 8 B, *v.st*), and basally the labium is represented by four elements (Text-fig. 8 C, *v.st*).

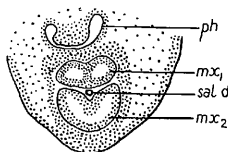
The mouth-parts of the embryo have now almost assumed the characters of those of the adult. The pumping pharynx and the buccal funnel are lined by chitin. This chitinization also spreads to the maxillae and the labium and, as stated above, to the salivary duct. With the growth of the embryo the epidermal (hypodermal) portions of the maxillae and labium gradually become reduced and withdrawn from the anterior

region so that the epidermal elements of the maxillae and labium are only found towards the base of the stylet sheath, while the chitinous covering becomes the definitive stylets of the adult.

The first maxillae become chitinized on the dorsal surface,



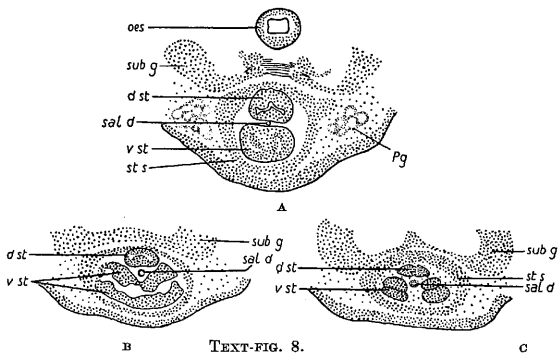
TEXT-FIG. 6.



TEXT-FIG. 7.

FIG. 6. Transverse section of the head of an embryo in the region where the stylet sac communicates with the buccal funnel.

FIG. 7. Transverse section showing the salivary duct.

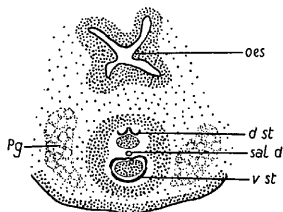


TEXT-FIG. 8.

Transverse sections at different levels of the head of a late embryo.

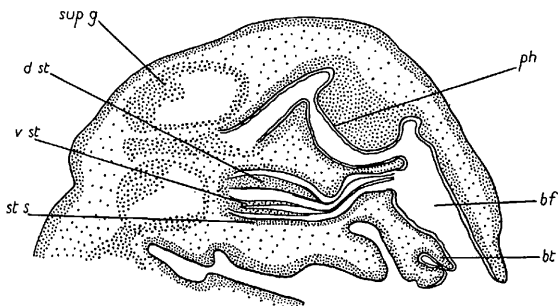
the chitinized areas taking the form of two grooves which diverge at the base of the sheath. In this they reflect the origin of the dorsal stylet from two maxillae. Below the dorsal stylet and almost continuous along its lower surface is the long, slender, chitinous salivary duct (Text-fig. 9, *sal.d*), which is the

transformed hypopharynx. Below this lies the ventral stylet (Text-fig. 9, *v.st*) on which chitin is laid down distally on the



TEXT-FIG. 9.

Transverse section of the head of an embryo before hatching.



TEXT-FIG. 10.

Sagittal section of the head of an embryo before hatching.

dorsal and ventral surfaces and proximally the four elements described above are chitinized.

The stylet sac lies below the foregut, its base lying close to the suboesophageal ganglion. It opens in front of the pumping pharynx, so that the stylets can be thrust out through the buccal funnel. The buccal funnel was shown to be a canal enclosed dorsally by the elongated labrum and ventrally and

laterally by the ventral lip of the stylet sheath. The buccal funnel is lined by chitin. The distal portion of the buccal funnel becomes the rostrum, and we find on it small outgrowths which become the buccal teeth (Text-fig. 10, *bt*).

As regards the mandibles, we were not able to find any traces of them in very old embryos. At no stage were they chitinized, and they disappear completely from the anterior end of the stylet sac.

DISCUSSION.

The present work shows that Cholodkovsky's interpretations of the homologies in the mouth-parts of *Pediculus* are incorrect, and it is in general agreement with the views of Enderlein. A comparison of Cholodkovsky's and Enderlein's views with that arrived at in this paper shows that the stylet sheath, which Cholodkovsky identified as a portion of the labium, is formed by the integument surrounding the stylets. Enderlein also stated that the ventral portion of the sheath was formed from a part of the labium, but made no reference to the dorsal portion of the sheath.

The labrum was stated by Cholodkovsky to disappear altogether, while Enderlein said that it was represented by a chitinous plate at the tip of the mouth opening. The present work shows that the labrum elongates and forms the dorsal portion of the buccal funnel.

The mandibles, which disappeared according to Cholodkovsky and which were rudimentary in *Pediculus* according to Enderlein, are here shown to disappear entirely before the insect emerges from the egg. At no stage were the mandibles chitinized.

According to Cholodkovsky the maxillae also disappeared at an early stage, but Enderlein stated that they formed the dorsal stylet. This work confirms Enderlein's conclusion that the maxillae of the embryo become the dorsal stylet of the imago. With regard to the labium, which formed both the stylets and the stylet sheath according to Cholodkovsky, the present paper shows that they are represented by the ventral stylet, as was also asserted by Enderlein.

Cholodkovsky made no mention of the hypopharynx, but Enderlein stated that it was situated between the maxillae and the labium, and we have shown the identity of it with the salivary duct.

SUMMARY.

1. Mandibles, first maxillae, and labium appear in the germ-band at an early stage.
2. The rudiments of the first maxillae unite to form the dorsal stylet, while those of the labium unite to form the ventral stylet.
3. The hypopharynx arises below the first maxillae or dorsal stylet; it becomes tubular and is transformed into the salivary duct.
4. The stylet sheath arises from the integument as a raised lip; it surrounds the dorsal and ventral stylets.
5. The labrum persists as the upper half of the buccal funnel.
6. The mandibles are throughout in a rudimentary condition; they disappear in the adult without becoming chitinized.

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