III. THE PHYSIOLOGICAL ANATOMY OF THE MOUTH-PARTS AND ALIMENTARY CANAL OF THE INDIAN RAT FLEA, *PULEX CHEOPIS*, ROTHSCHILD.

(Plate IX.)

The key to the anatomy of the mouthparts of the flea and to the understanding of the mechanism of blood sucking is the recognition of the pricking epipharynx and of the hypopharynx with its salivary pumping apparatus. In general it may be stated that the epipharynx makes a way through the skin for the mandibles, that the mandibles enlarge and lacerate the hole thus bored and convey into it the salivary secretion which is pumped, by means of the salivary pump, down the salivary canal contained in them, and that the aspiratory pharynx aspirates blood from the now congested wound along the blood channel formed by the approximation of the epipharynx and the two mandibles. The whole complex of parts is adapted to form two channels, an effluent along which saliva is pumped down and an affluent along which blood is pumped up.

Anatomy. Epipharynx. (Fig. **1** 3, Fig. **2** B 3, Fig. **3** 4, Fig. **4**, Fig. **6** 5.) A pointed pricking organ, a prolongation of the dorsal wall of the pharynx. The organ is hollow and shows a double contour by transmitted light; this hollow ends blindly at the distal extremity and proximally is in communication with the hoemocoel; it has no connection with the aspiratory canal. Ventrally it is grooved and laterally is provided with extremely delicate expansions which interlock with similar membranes on the mandibles forming with them the aspiratory canal (Fig. **5** 12).

In section the organ itself is seen to be composed of a dorsal and a ventral half similarly joined by the interlocking of lateral membranous expansions. This is shown in Fig. **5**, where 11 and 11′ are the two halves of the epipharynx, 10 the mandibles with their salivary ducts and 12 the aspiratory canal. Proximally the dorsal of the two halves terminates in a blunt end which is seen just within the head in Fig. **1** 25. The ventral half is continuous with the dorsal wall of the pharynx.

Immediately behind this junction is situated the *mouth* (Fig. **1** 26, Fig. **2** B 4, Fig. **6** 3). In front of the mouth the ventral half is swollen into a solid bulb of chitin (Fig. **2** B, Fig. **4** A 1).

In Fig. **4** the epipharynx is seen in two characteristic sections; in Fig. **4** B, taken along the line *c—d* in Fig. **2** B, the two halves are seen D (dorsal) and V (ventral); in Fig. **4** A, taken along the line *a—b*, further back, the dorsal half has terminated and the ventral (**1**) is swollen into the solid bulb just mentioned. Transverse sections present different appearances along its length; distally the section is that of a closed omega with lateral wings (Fig. **3** 4)[1].

Hypopharynx. (Fig. **1** 10, Fig. **2** B 6, Fig. **3** 5, Fig. **4** A 2, Fig. **4** B 2, Fig. **6** 6.) A chitinous plate concave downwards situated under the aspiratory pharynx, and extending backwards from the mandibulo-basal articulation to the suboesophageal ganglion. It supports the salivary pump, the muscles for operating which occupy its concavity. Fig. **3** shows a ventral view; Fig. **2** B a lateral, and Fig. **1** its general relations.

The dorsal convex surface is in relation with the under side of the aspiratory pharynx from which it is separated by a space. This space

[1] Considerable difference of opinion has prevailed as to the true morphology of the appendage described as epipharynx. Landois in his classical memoir (*Nova Acta Akad. Leop. Carol.* 1867) employs the term "unpaariges Stechorgan"; Karsten uses the term epipharynx; Gerstfeld and Grube (*Arch. f. Naturgesch.* 1854) on the contrary call it hypopharynx; Kraepelin (*Ueber die system. Stellung der Puliciden*, Hamburg, 1884) and more recently Heymons (*Zool. Anzeiger*, 1899) regard this organ as a true labium, "Oberlippe." Jourdain (*Bull. Soc. Entomol. de France*, 1899, p. 294) has proposed the name syringostome, stating that it "est le prolongement même, en forme de bec tubule, de l'orifice buccal, et la lumière de ce prolongement est en continuité directe et interrompue avec la première part du tube digestif." That this view is not correct will be seen on referring to the description above, the only lumen the "syringostome" possesses being in direct continuity with the hoemocoel.

Wagner (*Horae Soc. Entom. Rossicae*, 1889–1903) states that it is a constant feature among the Aphaniptera for the walls of the "pricker" (epipharynx) to be prolonged laterally in the form of delicate chitinous lamellae which, interlocking with the mandibles, form with them a canal which he considers as the true sucking tube ("Saugrohr"); the cavity of the pricker he considers as the salivary excretory canal. It will be seen that Wagner is right in his designation of "Saugrohr," but that his interpretation of the function of the pricker canal as a salivary canal is erroneous, the latter being situated in the mandibles.

Tiraboschi (*Archives de Parasitologie*, VIII. 1904, p. 214) will not accept the term "pricker" (piquant impair) and adopts that of tongue (langue). He states that the blunt form of the end and the presence on it of numerous small spinules directed forward would effectually prevent it being used as a pricking organ and considers it functions as a sucking tube. Here again the absence of any lumen within the organ communicating with the aspiratory pharynx effectually negatives this view.

is bridged by a ligament (Fig. **1** 27), which divides it into two parts, an anterior and a posterior. The posterior space is hoemocoel. The anterior space is aspiratory canal, immediately under the mouth opening. In Fig. **2** B 4′ is the separating ligament, 4 the mouth, 6 the hypopharynx.

The ventral surface is concave and incurved at the margins and is entirely occupied with the muscles operating the salivary pump.

The anterior margin at its centre is prolonged into a pointed process which contains the exit duct of the salivary pump (Fig. **3** 7, Fig. **4** A 2) and which lies between the two mandibulo-basal joints (*vide* mandibles). Antero-laterally are two horns which form on each side with the anterior process a fossa, in which lies the joint formed by the proximal end of the mandible and its basal element (point of intersection of lines *AB* and *CD* in Fig. **1**).

The *salivary pump* is situated medially at the anterior end of the under surface of the hypopharynx. It receives the saliva from the glands by means of the salivary ducts and propels it through the exit duct of the pump into the salivary grooves in the mandibles. It is a hollow chitinous organ, horse-shoe shaped in section (Fig. **3** 6). Normally its cavity is obliterated by the spring-like action of the chitinous walls, but the muscles attached to the posterior wall (Fig. **3**, under 5) when contracted cause a lumen to appear which then becomes full of salivary secretion. On the muscles relaxing the elastic reaction of the walls closes the lumen and the secretion is expelled through the exit duct (Fig. **3** 7). The opening of the salivary duct is in apposition with the salivary canals in the mandibles (Fig. **4** B 2 and 3), which canals extend down the mandibles (Fig. **5** 10).

Mandibles. Paired sawing organs (Fig. **1** 4, Fig. **2** C 9, Fig. **3** 2, 2′, Fig. **4** 3, Fig. **6** 10) articulated proximally to two basal elements (Fig. **1** 8, Fig. **2** C 10, Fig. **3** 3, Fig. **4** A 4, Fig. **5** 6, Fig. **6** 9). These basal elements are articulated latero-ventrally to the perioral ring. The perioral ring is the chitinous margin of the end of the head case, and forms an aperture which looks downwards and forwards and through which all the mouthparts project. Each basal element is provided with operating muscles (Fig. **5** 7).

In section the mandibles are shaped as shown in Fig. **5** 10. Each contains on its mesial surface a salivary groove which proximally widens out into a trough and distally is nearly closed by the approximation of its lips forming a practically closed canal. The mandibles are amply provided with serrations along their distal two-thirds.

Maxillae. Not to be confounded with antennae, which lie in the antennal pits and are usually concealed. They are sufficiently described by Fig. **1** 1, 2, Fig. **2** A, Fig. **3** 1, Fig. **5** 8. They are provided with palps.

Labium. A bifid organ acting as a sheath to the other mouthparts. It is sufficiently indicated in Fig. **1** 5, 6, 7, Fig. **2** D, and Fig. **6** 11, 12. It is provided with a basal element (Fig. **2** D 14, Fig. **5** 13, and Fig. **6** 12) which is articulated to the perioral ring at its medio-ventral point.

The Mouth (Fig. **1** 26, Fig. **2** B 4, Fig. **6** 3) is situated at the base of the bulb of the ventral portion of the epipharynx, and forms the definitive opening into the alimentary canal[1].

The Aspiratory pharynx (Fig. **1** 12, Fig. **2** B 5, Fig. **5** 2) extends from the mouth to the oesophageal commissure. In section (Fig. **5** 2) it is seen to be provided with an aspiratory arrangement. Under the action of the muscles attached to its dorsal chitinous plate a lumen appears, which on the relaxation of the muscles vanishes owing to the elastic reaction of the walls. The operating muscles are shown in Fig. **1** 13 and Fig. **5** 1.

The Salivary glands. (Fig. **1** 16.) Four in number, two on each side; situated on each side of the anterior end of the stomach, embedded in the fat body. Each is a simple acinous gland lined with secretory cells resting on a basement membrane. The ducts from each pair unite and the two ducts thus formed (Fig. **5** 5) run forward under the suboesophageal ganglion and under the mesial plate formed by the opposed walls of the antennary pits, to open into the salivary pump. They are lined with a spirally arranged chitinous membrane and may be mistaken for tracheal tubes, but the absence of air therein and the presence of an external protoplasmic sheath surrounding the chitinous lining makes recognition easy[2].

Method of sucking. The epipharynx and mandibles are inserted together into the skin, the labium doubling back and the V-groove of this organ serving as a guide. The entire epipharynx-mandibles combination is inserted by a pushing action of the whole body of the flea, but once

[1] *Mouth.* Tiraboschi describes the mouth as being situated at the antero-inferior margin of the head and as being bounded above by the maxillae and below by the labium; he is here describing what is designated in the text as the perioral ring.

[2] Wagner describes the ducts as uniting just before entering the head, the single duct thus formed passing in the walls of the pharynx to become continuous with the cavity of the pricker. Kraepelin correctly describes and figures the salivary canals as situated in the mandibles.

inserted the mandibles, owing to their basal element, are capable of independent action, sliding up and down but maintaining their relative positions and preserving the lumen of the aspiratory channel. Simultaneously the salivary pump probably acts and sends a supply of secretion into the salivary groove of the mandibles, the long overhanging lip of the hypopharynx serving to conduct saliva to the grooves even in the extended position. Or we may imagine that the salivary secretion is only injected into the mandibular groove in the retracted position, in which case each mandible would receive a supply once in each stroke. It is impossible to say which method is the actual one. In any case a supply of saliva is introduced into the wound. A minute drop of blood now collects at the aperture through which the pricking organs were inserted into the skin and this is drawn up into the pharynx by the action of its aspiratory muscles already described.

The "gizzard" (Fig. **1** 17) is a remarkable organ, the function of which it is impossible to state. It is a bulbous expansion situated at the junction of the pharynx and the stomach. It consists of a basement membrane implanted on which are a multitude of chitinous finger-like processes. Each process is hexagonal at its base, thus mapping out the basement membrane into a series of hexagonal areas; and is tapered towards its extremity, its length being about two-thirds that of the diameter of the whole organ. Each process is closely applied to its neighbour throughout its whole length. The general direction of the processes is axial, and their free extremities point backwards.

The processes are chitinous on the surface and each encloses a readily staining "nucleus." No movement can be detected in these processes during life.

From their general arrangement the complete collection of processes would act as an effective valve preventing regurgitation of the fluids in the stomach. And as during life the stomach is constantly churning its contents this is very likely its function. Some valvular arrangement between the pharynx and stomach is *à priori* necessary from the fact that the pharynx is normally collapsed, being provided with a lumen only during the time of action of the muscles attached to its dorsal chitinous plate. On the pharynx becoming filled with blood, the muscles relax and the blood is forced into the stomach by the elastic reaction of its chitinous walls. As the stomach is already tensely full of blood in many cases, some valve is therefore necessary to prevent regurgitation into the pharynx at the time of contraction of the pharyngeal muscles.

In this connection it is obvious that if the contraction of the pharynx (by elastic reaction) is sufficient to force the blood into an already tensely filled stomach, it will be sufficient to force it out of the mouth whereby it entered and which is unprovided with a valve. The difficulty is overcome by the pharyngeal muscles contracting and relaxing in regular sequence, thus causing a peristaltic action of the pharynx and forcing the blood in a steady stream stomachwards. In a lightly coloured flea this action may be seen during life; it is well seen in the case of the louse, the musculature and structure of the pharynx of which are strikingly similar to those of the flea. The gizzard marks the downward limit of the chitinous lining of the alimentary tube.

The stomach (Fig. 1 18) consists of a basement membrane, two oblique layers of muscle fibres and a lining layer of cubical cells. The muscles are simple fibres disposed in all directions. The lining layer of cells has some peculiarities. In section the cells have the character of excreting cells, their surfaces towards the lumen of the stomach being often ragged, suggesting that part of the cell itself formed part of its excretion.

The blood remains in the stomach in a partially haemolysed condition and gradually diminishes in volume, showing that absorption takes place. At what is probably the end of the stomach-digestive process, the contents are reduced to a thick slimy dark red mass; this is passed on to the rectum in which it accumulates, probably being submitted to further action under the influence of the so-called rectal glands; it is finally passed from the rectum as minute round dark red or black tarry droplets.

Many observers (Simond, *Ann. l'Inst. Pasteur*, XII. 625 (1898), Zirolia, *Centralbl. f. Bacteriol.* XXXI. 687, and Tiraboschi, *loc. cit.*) have remarked on the habit the flea possesses of squirting bright red blood from the anus during the operation of sucking. This phenomenon has been frequently observed and appears to be a common practice amongst blood-sucking insects. It has been observed also in the louse commonly found on *Mus decumanus* when feeding on that rat, as well as in the case of the human head louse when feeding on the same animal, which it does with avidity.

Practical methods.

Dissection. The stereoscopic microscope of Braus and Drüner so greatly facilitates the dissection of the minute portions of the flea's

anatomy that its employment soon became necessary; dissections that could only just be performed by its aid are impossible under a simple lens.

Dissection is best carried out in salt solution using fine needles mounted in penholders. The point of even the finest commercial needle is not sufficiently sharp for fine dissections, and it becomes necessary to sharpen it. This is best done by arranging to revolve the needle rapidly about its long axis, the point the while pressing on a rapidly revolving emery wheel (revolving in the *same* direction). The inclination of the axis of the needle to the plane of the surface of the emery wheel should be capable of being varied so as to get points of different angles.

In the left hand should be held a needle with a blunt cone point, in the right a needle with an oblique cone point. The flea is placed in a drop of salt solution on a slide placed on the stage of the dissecting microscope and the antennary pit transfixed and held by the left hand needle. The point of the right hand needle is then inserted under the edge of the third or fourth abdominal segment and the abdominal segments peeled off much as a shrimp is skinned. The internal organs float out in the salt solution and may be further separated, using two fine oblique pointed needles. In some cases a hooked end to one of the needles will be found useful, in others the needle may be fashioned into a minute knife, the finest emery wheel or better still an oil stone wheel being used for this purpose.

The salivary glands will be found at the side of the stomach, embedded in the fat body. Their extraction is not difficult. The needle with the hook may be employed to hook the duct.

The tracing of the ducts forward is not so easy, and many fleas will probably be wasted before a successful dissection is made. Particularly difficult is the dissection of the hypopharynx. It is best to remove the head and transfix it with the left hand needle, then to "scalp" the head by removing the dorsal half of the chitinous carapace by a bold plunge of the right hand needle. In most cases the pharynx and hypopharynx will be left and a successful pull on the epipharynx will generally bring out the pharynx with the hypopharynx attached.

It must be confessed that successful dissections are often obtained more by luck than good management.

The use of dilute potash facilitates the investigation of chitinous parts by "jellifying" the muscles.

Sections are made with difficulty. Paraffin is not rigid enough and

celloidin alone is too flexible. Double embedding (Jordan, *Zeitschr. f. wiss. Mikrosk.* XVIII. p. 191, 1900) gives good results, but it is difficult to get a series even with this method. The sections drawn in the plate have been obtained by this means. Prolonged soaking in celloidin is necessary to obtain penetration and very slow thickening of the celloidin is essential. A minimum exposure in the paraffin bath is advisable to prevent the chitin becoming brittle.

Of many softening agents for chitin tried, the only successful ones have been dilute alkali or natural decomposition, but even here the effect on the chitin is small, the soft parts being mostly altered.

DESCRIPTION OF PLATE IX.

Fig. 1. Diagrammatic mesial sectional view of *Pulex cheopis*.

1. Maxillary palp.
2. Maxilla.
3. Epipharynx.
4. Mandibles.
5. Labium.
6. Undivided portion of labium.
7. Basal portion of labium.
8. Basal portion of mandibles.
9. Salivary pump.
10. Hypopharynx.
11. Salivary duct.
12. Aspiratory pharynx.
13. Muscles operating the aspiratory pharynx.
14. Supra-oesophageal ganglion.
15. Sub-oesophageal ganglion.
16. Salivary glands.
17. Gizzard.
18. Stomach.
19. Malpighian tubules.
20. Rectum.
21. Rectal glands.
22. Claspers.
23. Pygidium.
24. Ante-pygidial bristle.
25. Termination of dorsal contour of epipharynx.
26. Mouth.
27. Ligament.

Fig. 2. A. Maxilla with its palp.
B. Epi- and hypopharynx.
3. Pricker (epipharynx).
4. Mouth.
4′. Ligament.
5. Aspiratory pharynx.
6. Hypopharynx.
7. Salivary pump.
8. Salivary duct.
C. Mandible.
9. Salivary groove.
10. Basal element.
11. Mandibulo-basal joint.
D. Labium.
12. Paired terminal portion.
13. Unpaired portion.
14. Basal element.

Fig. 3. Horizontal section of head in plane *AB* of Fig. 1 showing the hypopharynx and salivary pump viewed from below. The epipharynx is shown in section at 4, but the mandibles and their basal elements are shown fore-shortened and pointing forwards instead of downwards and backwards which is the position in which they are normally carried:

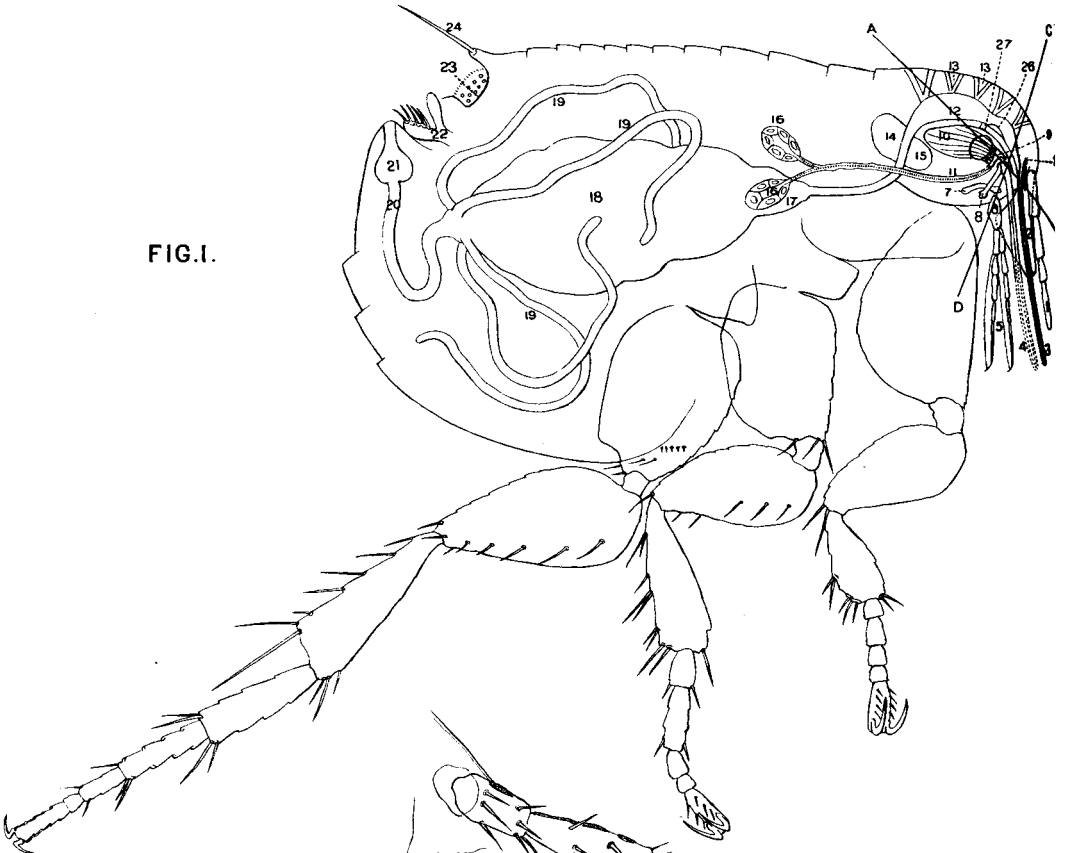
1. Maxillary palp.
2. Mandible. 2′. Mandible with salivary groove.
3. Basal element of mandible. The line *XY* passes through the two mandibulo-basal joints. The salivary groove in 2′ is shown as occupying the ventral surface of the mandible. Actually it occupied the internal surface—and so its upper end is in close proximity to the exit duct of the salivary pump.
4. Epipharynx shown in section.
5. Placed on the hypopharynx. The muscles operating the salivary pump 6 are diagrammatically indicated.
6. Placed in the lumen of the salivary pump.
7. The anterior process of the hypopharynx containing the exit duct of the salivary pump.
8. The antennary pits.

Fig. 4. Two successive sections.
A in plane of *C—D* Fig. 1, or *a—b*, Fig. 2 B:
B in plane of *c—d* Fig. 2 B:
showing how the exit duct of the salivary pump communicates with the salivary grooves in the mandibles.

Section A passes through the exit duct in a plane posterior to that through which B passes. In A the duct is still a closed tube, in B it has opened out to a channel. In A the salivary grooves in the mandibles (3) have not yet commenced, in B they are seen with their margins applied to the margins of the exit duct, permitting the passage of fluid from exit duct to salivary groove.

1. Epipharynx: D. Dorsal portion.
V. Ventral portion.
2. Anterior prolongation of hypopharynx containing salivary pump duct: No. 7 of Fig. 3.
3. Mandible with salivary grooves.
4. Basal element of mandible, omitted in B.

FIG. 1.



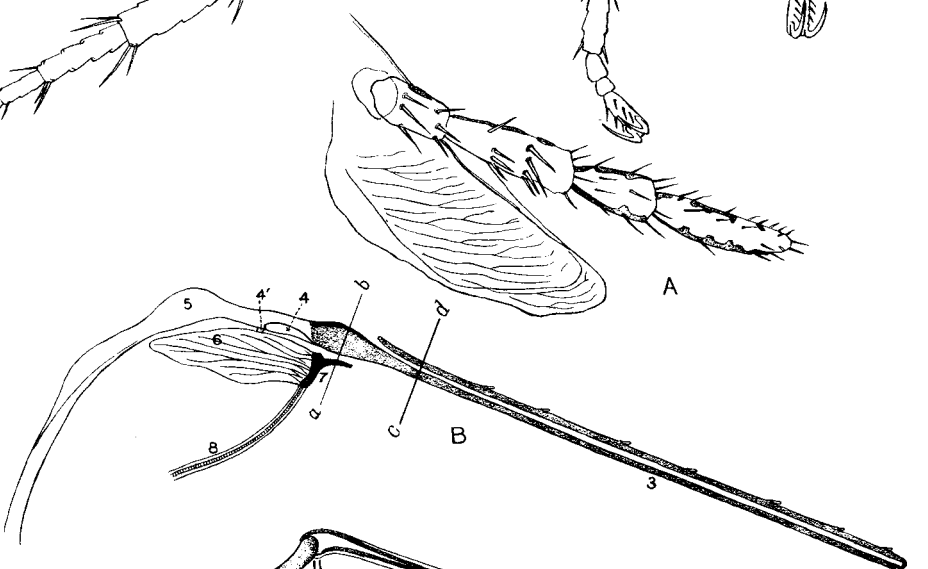
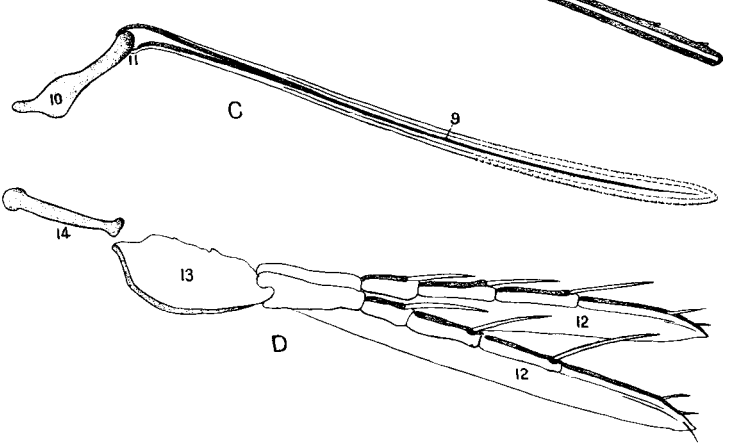


FIG. 2.



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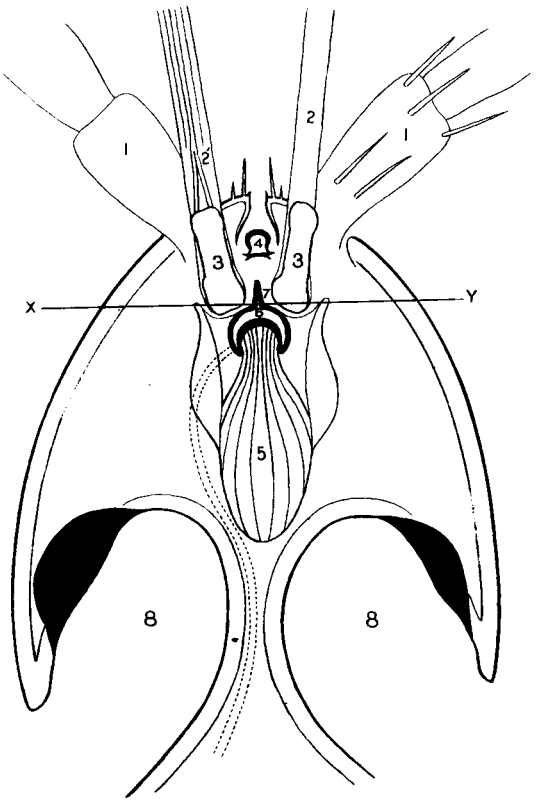


FIG.3.

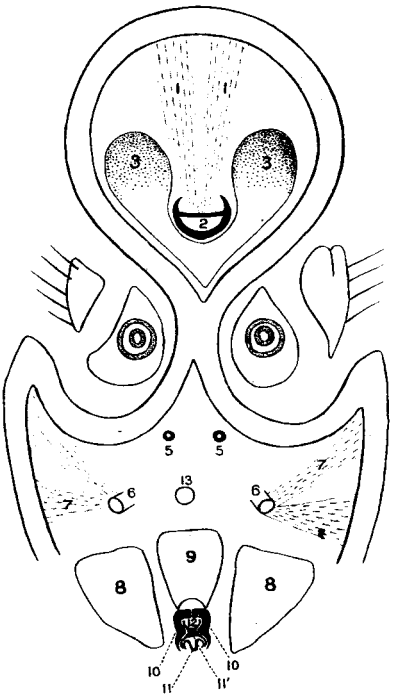
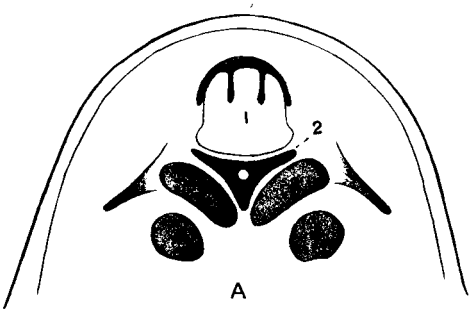


FIG.5.



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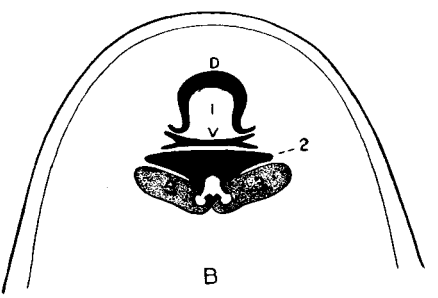

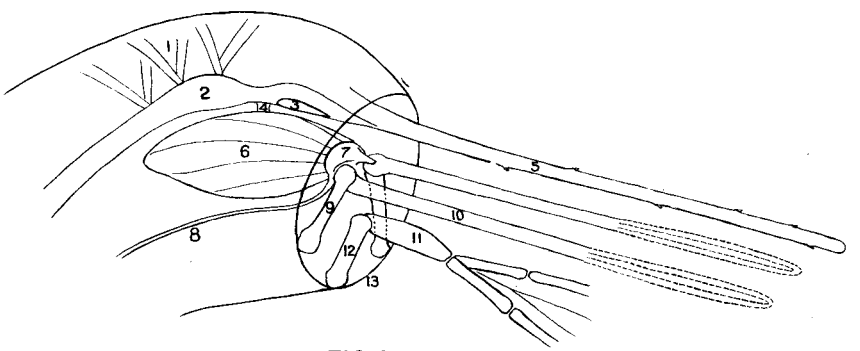

FIG.6.

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Fig. 5. Oblique transverse section through the head in a plane passing through the antennary pits and immediately behind the posterior end of the hypopharynx. The section cuts the alimentary canal twice, once passing through the aspiratory pharynx at 2 and again passing through the aspiratory canal at 12. Normally the mouthparts at rest are carried folded back and pointing backwards and downwards.

The conjunction of the mesial walls of the antennary pits is seen, dividing the head cavity into two parts, an upper containing the aspiratory pharynx and a lower containing the salivary ducts.

1. Muscles operating the aspiratory pharynx.
2. Aspiratory pharynx.
3. "Brain" oesophageal commissure and part of sub-oesophageal ganglion.
5. Salivary ducts.
6. Basal elements of mandibles.
7. Muscles operating 6.
8. Maxilla.
9. Undivided portion of labium.
10. Mandibles.
11, 11′. Epipharynx.
12. Aspiratory canal.
13. Basal element of labium.

Fig. 6. Diagram of the mouthparts of the flea.

1. Muscles operating aspiratory pharynx.
2. Aspiratory pharynx.
3. Mouth.
4. Ligament.
5. Epipharynx.
6. Hypopharynx and muscles operating salivary pump.
7. Salivary pump.
8. Salivary duct.
9. Basal element of mandible.
10. Mandible.
11. Labium.
12. Basal element of labium.
13. Perioral ring.