SOME OBSERVATIONS ON THE ANATOMY AND FUNCTION OF THE ORAL SUCKER OF THE BLOW-FLY (*CALLIPHORA ERYTHROCEPHALA*).

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(With Plates IV—VIII.)

In the course of a long series of experiments on the distribution of bacteria by non-biting flies (*Musca domestica* and *C. erythrocephala*)[1] it became evident that such flies are able to filter off and reject the larger particles contained in the fluids on which they feed. This fact seems to have escaped the notice of most observers, and although the proboscis of the blow-fly has been a favourite subject of study for many years no observations appear to have been recorded which throw any light on the means by which the filtration is effected. In order to ascertain the mechanism by which the filtration is accomplished a large number of dissections of the proboscis of the blow-fly have been made, and experiments have been carried out on the living fly to test the degree of its efficiency.

The present paper deals with (A) the anatomy of the distal end of the proboscis, which is the part alone concerned in filtration, and (B) feeding experiments affording experimental evidence of the efficacy of the filter.

(A) *The anatomy of the distal end of the proboscis of the blow-fly.*

The proboscis of the blow-fly has been carefully described by Lowne (1895) and others, and consequently there is no necessity to describe in detail the principal parts of the structure[2].

[1] Graham-Smith (1910–1911).

[2] Wherever possible the names applied by Lowne (1892–5) have been used.

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Briefly the proboscis of the blow-fly consists of two parts, a proximal conical portion, the rostrum, and a distal half, the proboscis proper, or haustellum, which bears the oral sucker. The relationship of the structures, which compose the main portions of this organ, may be seen by reference to Pl. IV, fig. 1, which represents a schematic longitudinal section through the proboscis, constructed from drawings made from numerous dissections and serial sections which were studied in order to ascertain whether any valvular structures exist in the proboscis. These observations failed to reveal any valve-like structures.

The filtering mechanism is situated in the oral sucker or suctorial disc which is described by Lowne (1895, p. 136) as "a fleshy oval disc, deeply cleft at its anterior margin. The edges of the cleft are continuous with the margins of the groove in the theca, and are united as far as the edge of the disc by a remarkable bead and channel joint. The thick edge of one lobe, or labellum, of the disc fits into a corresponding cylindrical channel in the other. The distal or oral surface of the disc is channelled by the well-known pseudo-tracheae. In the centre is a deep longitudinal fissure, which extends into the tubular mouth situated between the labrum and the theca. The proximal or aboral surface of the sucker is convex and covered by setae; those near its margin are very long and form a fringe."

Lowne (p. 390) describes the mouth as "a cylindrical tube extending from the thecal (or discal) sclerites to the prepharyngeal tube, which may be regarded as its posterior limit or isthmus faucium." The deep cleft between the two lateral halves of the oral disc into which the mouth opens he terms the prestomum (p. 143).

The dissections and feeding experiments described in this paper show that the liquid food is sucked into the pseudo-tracheae and drawn through the collecting channels and along the gutters of the prestomum into the mouth, and it seems probable that crop contents and saliva may be forced at will in the reverse direction for distribution over solid food which has to be moistened and dissolved. In order to explain the process of sucking food into the mouth the structures involved, namely the oral surface of the suctorial disc, the pseudo-tracheae, and the prestomal cleft, must be described in detail.

The pseudo-tracheae, varying in number between 28 and 32, run transversely across the labellum or lobe of the oral sucker. They form three sets. The seven anterior pseudo-tracheae run into a common longitudinal collecting channel which opens into the prestomum between the first and second prestomal teeth, and the posterior eight to twelve in the same way run into a common posterior collecting channel, which opens into the prestomum at its shallow posterior extremity. The central pseudo-tracheae terminate in short channels which run directly into the prestomum without the intervention of common collecting channels. By this arrangement all the pseudo-tracheae are made to converge to the prestomum. The arrangement of the pseudo-tracheae is clearly shown in Pl. VII, fig. 9, which is a photograph of the oral surface of the expanded suctorial disc of a blow-fly with 30 pairs of pseudo-tracheae. On each side the anterior eight run into a common anterior collecting channel, and the posterior twelve into a common posterior collecting channel, while the ten central pseudo-tracheae are continued separately into the prestomum. Fig. 5 shows ten pseudo-tracheae running into the posterior common collecting channel.

From the points at which they cease to be tubular in structure the collecting channels are continued along the prestomal cavity to the mouth as grooves or gutters, whose lateral walls are formed by the prestomal teeth.

The pseudo-tracheae.

The pseudo-tracheae are deep furrows or incomplete membranous tubes embedded, more or less deeply according to the degree of its inflation, in the substance of the oral surface of the labellum, but under any conditions projecting sufficiently to produce distinct ridges. Along the apex of the ridge the wall of the pseudo-trachea is lacking so that the interior of the tube is in communication with the oral surface of the disc through a very narrow zigzag fissure. The lumen of the tube is kept open by means of incomplete chitinous rings running transversely round the tube, each of which has one fork-like bifid extremity, enclosing a rounded space between the prongs, and one extremity slightly expanded and flattened so as to resemble the tail of a fish. The rings are arranged in such a manner that along each side of the central fissure the bifid extremity of one ring alternates with the expanded extremity of the next ring. In consequence of this arrangement, which is very clearly seen in preparations treated with potash for the purpose of demonstrating the chitinous structures, the margin of the pseudo-trachea at each side of the central fissure has a deeply indented or scalloped appearance. The really effective entrances into the pseudo-tracheae are through the spaces between the bifid extremities of the rings and not through the narrow continuous zigzag

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fissure, which is at any time extremely narrow and is probably closed during the act of feeding, as will be explained later.

The pseudo-tracheae gradually diminish in diameter as they approach the margins of the disc, and the size of the forked extremities of the rings and consequently of the spaces between them also diminishes though not to a corresponding degree.

The term "interbifid space" is used to indicate the area enclosed between the forks of the bifid extremity of a ring.

Fig. 7 illustrates two consecutive rings with their bifid and flattened extremities, and Fig. 6 illustrates a side view of one of these rings. Fig. 13 is a photograph of several consecutive pseudo-tracheal rings which have been treated with potash and compressed. The terminations of the consecutive rings are well shown. Fig. 11 is a photograph of the oral surface of the disc of a blow-fly after treatment with potash showing portions of four pseudo-tracheae. The longitudinal fissures of the pseudo-tracheae and the forked extremities of the rings and interbifid spaces can be clearly seen. Fig. 12 is a photograph of a section of the disc showing four pseudo-tracheae cut transversely. The chitinous rings, the openings of the longitudinal fissures and the ridges caused by the projection of the tubes above the surface are clearly shown.

The pseudo-tracheae of several of the common non-biting flies closely resemble each other, though they exhibit slight and apparently unimportant differences in their structure. The average measurements of the various parts in six common species are as follows.

	Pseudo-tracheae		Interbifid spaces	
	Diameter at proximal end	Diameter at distal end	Diameter near the proximal ends of the pseudo-tracheae	Diameter near the distal ends of the pseudo-tracheae
Calliphora erythrocephala ...	·02	·01	·006	·004 mm.
Sarcophaga carnaria	·02	·01	·005	·004 mm.
Lucilius caesar	·02	·01	·006	·004 mm.
Fannia (*Homalomyia*) *canicularis*	·016	·008	·006	·004 mm.
Ophyra anthrax	·016	·008	·006	·004 mm.
Musca domestica	·016	·008	·004	·003 mm.

The cuticle lining the oral surface of the labellum dips down into the pseudo-tracheae through the longitudinal fissure and also forms the lining of these tubes, as may be seen by reference to Fig. 12. In passing downwards into a pseudo-trachea the cuticle accurately follows its chitinous margins, being closely adherent not only to the chitinous sides of the interbifid spaces but also to the intervening elevations

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between them produced by the projection of the expanded ends of the alternate rings, and the application to them of the adjacent forks of the neighbouring rings on either side.

Owing to this arrangement a remarkable series of folds is produced in the cuticle forming channels or grooves leading into the interbifid spaces. If the cuticle is traced along the edge of the longitudinal fissure from the bottom of one interbifid space to the bottom of the next it can be observed to be very closely attached to the chitin along the base of an interbifid space and up the side of a fork to its pointed extremity. It then passes over the expanded portion of the alternate ring and down the adjacent fork of the next ring, binding the two forks mentioned and the expanded portion of the intermediate ring into an elevated mass which lies between the deep depressions of the interbifid spaces. The arrangement described can be most easily understood by reference to Fig. 15, a longitudinal section through a pseudo-trachea just to one side of the central fissure. The depressions caused by the cuticle adhering to the bases of the interbifid spaces are continued outwards as folds or grooves in the cuticle for a considerable distance which are gradually lost on the surface of the labellum. Each "interbifid groove" thus forms a well defined channel leading into the pseudo-trachea through the interbifid space with its long axis at right angles to the line of the pseudo-trachea. The deepest part of the groove is at its entrance into the pseudo-trachea, and at this point it loses its groove-like character and becomes a tunnel, though still communicating with the surface by a very narrow slit. When the proboscis is erected by slight pressure on the head and the oral sucker viewed with a microscope these grooves can be easily seen as regularly placed channels running at right angles to each pseudo-trachea.

Though difficult to describe the arrangement can be easily understood by reference to Fig. 4, representing a dissection of a portion of a pseudo-trachea. On the right-hand side the integument of the oral surface of the labellum has been removed so as to show a portion of the pseudo-trachea with the alternate bifid and flattened extremities of the chitinous rings and the membrane lining the interior of the tube stretching between them. On the left-hand lower portion the appearance of the surface integument is represented. Two interbifid grooves leading to their interbifid spaces are shown. Between the interbifid spaces are elevated masses, each of which is produced by a fold of the integument enclosing the flattened end of a ring and the extremities of the adjacent forks on each side. In the left-hand upper portion of the diagram is

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shown the appearance of these structures as seen by transmitted light so as to indicate the relationship of the integument to the rings.

Fig. 19 is a photograph of a wax model of short segments of two pseudo-tracheae. The cuticle and internal lining membrane have been stripped off the outer side of the pseudo-trachea on the left exposing the chitinous rings. On the inner side of this pseudo-trachea and over the whole of the pseudo-trachea on the right the cuticle is represented *in situ*. The interbifid grooves leading into the interbifid spaces can be easily seen. In Fig. 12 illustrating transverse sections of four pseudo-tracheae the interbifid groove is indicated on the left side of each pseudo-trachea, but is perhaps best seen in the central ones. In each case the point of bifurcation of the chitinous ring is indicated by a dark spot above which the forks are curved inwards. From the point of bifurcation a distinct line, which represents the reflection of the cuticle at the base of the interbifid groove, passes obliquely upwards and outwards to the surface of the integument. Fig. 6 illustrates diagrammatically the condition seen in transverse sections. Fig. 16 is a photograph of the oral surface of part of a disc including portions of two pseudo-tracheae. The interbifid grooves can be seen as somewhat oval-shaped regularly arranged areas on each side of the pseudo-tracheae. The zigzag line in the centre is the median longitudinal pseudo-tracheal fissure.

Anthony (1874), Wright (1884) and Lowne (1895, p. 395) all regarded the interbifid grooves as suckers. The latter figured them as blind sacs attached to the forks of the rings with openings into the pseudo-tracheae only. None of these authors seemed to regard them as channels leading into the pseudo-tracheae.

The fact that these interbifid grooves are really channels leading into the pseudo-tracheae can be demonstrated however by a very simple experiment. If the proboscis of a blow-fly is placed in alcohol, formalin or other preserving agent, and the suctorial disc is later mounted in water under a cover-glass and examined with the aid of a microscope the grooves can be clearly seen. As the specimen begins to dry air bubbles often form in the slight depressions on the oral surface of the disc between the pseudo-tracheae. As the drying continues the bubbles run into the interbifid grooves and through them into the pseudo-tracheae, clearly showing that the grooves lead into the pseudo-tracheae.

The collecting channels.

It has already been stated that the anterior and posterior sets of pseudo-tracheae run into common collecting channels, and that the central pseudo-tracheae also run into separate closed channels. These channels, which are kept open by incomplete chitinous rings without bifid extremities, communicate with the exterior by narrow fissures which are continuations of the longitudinal fissures of the pseudo-tracheae. Since there are no interbifid spaces there are no interbifid grooves or other openings into these channels. Each channel opens into its corresponding gutter between the prestomal teeth in a remarkable manner, the more deeply situated portions of the proximal rings being expanded and prolonged towards the prestomum, so as to form a spout-like opening to the channel.

Fig. 5 illustrates the posterior common collecting channel of one labellum with ten pseudo-tracheae opening into it. It will be noticed that throughout the greater part of its length the extremities of the rings are either quite plane, or slightly expanded, or possess only the rudiments of forks. Consequently the channel opens to the exterior by a longitudinal fissure only. At its proximal end the chitinous bars representing the rings are elongated and form a shallow groove leading towards the discal sclerite which forms the side of the entrance of the mouth. Two pseudo-tracheae opening through their own collecting channels into gutters between the prestomal teeth are shown at the right-hand side. In Fig. 2 the proximal portions of three of the central pseudo-tracheae with their collecting channels terminating in spout-like openings are illustrated, and Fig. 18 is a photograph showing several of these channels and gutters.

When at rest the oral surfaces of the labellae or oral lobes are in apposition, but during feeding they are spread out over the surface of the food so as to form an oval disc. In order to attain this position that part of the oral surface of the labellum adjoining the prestomum, which is situated just external to the teeth, in fact all that area bordering the longitudinal sulcus, is capable of being bent through a right angle. It is over these highly flexible regions of the suctorial disc, which are invariably bent during the act of feeding, that the pseudo-tracheae are converted into closed collecting channels.

The prestomal teeth.

On each side of the prestomum is arranged a series of rows of chitinous teeth, usually ten in number (Fig. 18). The central rows each consist of three teeth. The innermost teeth are the strongest and are articulated at their proximal extremities on to the chitinous side of the lateral plate of the discal sclerite, while their distal free extremities are bifid. Except at their bases they are free from investment with integument. The intermediate teeth are longer than the inner and their distal extremities are placed directly external to those of the inner set. Their distal extremities are bifid. Immediately behind the free extremities of the inner set these teeth branch, and the two branches pass behind and to the sides of the inner set to be inserted into the discal sclerite. The upper thirds only of these teeth are free from integument. The outer teeth resemble the intermediate set in their general shape and disposition, but are longer. Their distal extremities are bifid, but their proximal branched extremities are not inserted into the discal sclerite, but seem to articulate with it indirectly through the intervention of plates of chitin. Only the distal ends of the outer set are free from integument.

The arrangement of these teeth will be best understood by reference to Fig. 2 which represents the teeth as seen from the oral aspect, and Fig. 3 which represents them as seen from the aboral aspect after the removal of the overlying structures, and indicates the extent to which they are free from integument.

The spaces between the rows of teeth form the gutters, leading into the prestomum, which have already been mentioned. The gutter is bordered by the teeth of the inner set, whilst its floor is formed by the branches of the intermediate and outer sets of teeth, and the integument investing these structures.

The arrangement described is only found near the centre of the prestomum. On either side of the two or three central pseudo-tracheae each tooth of the outer set is represented by two bars of chitin, which are not united at their distal extremities (see Fig. 2). Still further from the centre the outer set is lacking, while at either end of the series both the outer and intermediate sets are lacking.

The arrangement of the teeth varies greatly in different species. *C. erythrocephala* has as described three teeth in each row, *S. carnaria* has four, and *L. caesar* has three. In *M. domestica, F. canicularis* and

O. anthrax there seems to be only one definite series corresponding to the inner set of *C. erythrocephala*. In these species the sets which are lacking seem to be represented by modified plates of chitin.

When fluid food is being taken the teeth merely aid the conveyance of the fluid into the mouth by assisting in the formation of the gutters. They may be used however under suitable conditions in scraping the surfaces of hard substances to render their solution more easy. In order to bring the teeth into action as scrapers the lobes of the suctorial disc have to be more widely separated than they usually are when liquid food is being taken. When the teeth are in action as scrapers the prestomal cavity is open to the surface, and if sucking efforts are made probably large particles can pass into the mouth.

(B) *Feeding Experiments.*

If hungry flies are fed on drops of syrup or other fluids they rapidly suck up large quantities. The general behaviour of flies during the act of feeding and subsequently has been previously described (Graham-Smith, 1910, pp. 5–11; 1911, p. 41) and need not be repeated in detail. In all cases the suctorial disc is inflated and the lobes spread out so that the oral surfaces of the labellae are nearly in one plane. If viewed from its oral surface the disc presents the appearance seen in Fig. 9, the adjacent sides of the lobes being pressed together so that the prestomal cavity is almost completely closed.

If the flies are fed on shallow drying drops of somewhat concentrated syrup containing finely ground Indian ink deposited on glass, proboscis marks, recognizable as white areas where the ink deposit has been removed, can frequently be observed (Fig. 20). These areas correspond with the shape of the inflated proboscis showing that the margins, and probably the greater part, of the suctorial disc are closely applied. The firmer the application of the disc to the surface supporting the food the more completely are the walls of the prestomal cavity pressed against one another. Hence under these circumstances no material can enter directly into the mouth but has to be conveyed into it through the agency of the pseudo-tracheae and collecting channels.

If the head of a blow-fly is removed and the proboscis erected by slight pressure on the head and fixed in that condition with plasticine it is possible to obtain an excellent view of the expanded disc. In this position each lobe of the disc is convex in its transverse diameter and the entrance to the prestomal cavity is recognizable as a longitudinal sulcus slightly expanded near its centre. By applying a cover-glass to the oral surface of the disc it can be readily shown how pressure exerted on the disc closes the prestomal cavity in proportion to the degree of the pressure.

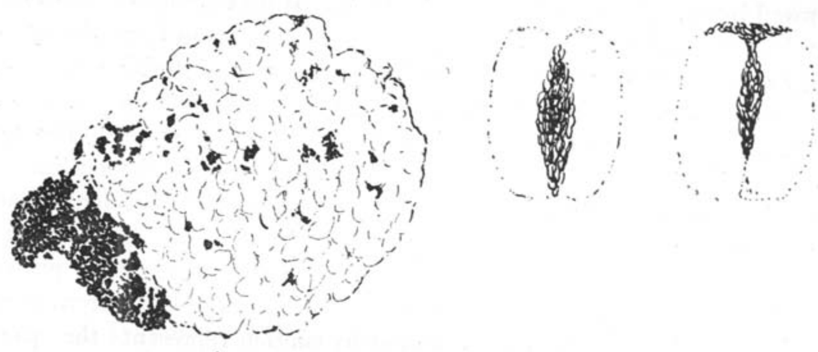
Under natural conditions flies probably seldom have the opportunity of feeding on large drops but suck up thin films of moisture and consequently feed with their proboscides so closely applied that the longitudinal prestomal sulcus as well as the longitudinal fissures of the pseudo-tracheae are to a great extent obliterated. Under these conditions it seems impossible that food should enter the mouth except through the interbifid grooves, and that this is actually the case can be proved by experiments with suitable fluids. If flies are allowed to suck at films of partially dried Indian ink they often remove from the glass only those portions which lie immediately under the interbifid grooves. In such cases beautiful patterns like gratings are left on the glass. Fig. 21 is a photograph of a portion of one of these patterns. The fly has applied the proboscis firmly to the surface so that the outline of the disc is clearly visible. It may also be seen that the longitudinal prestomal sulcus was almost completely closed. The lines of the pseudo-tracheae are marked by double parallel rows of regularly placed clear oral areas separated by thin black lines. Each of these areas from which the pigment has been removed by suction represents the space covered by an interbifid groove. Fig. 22 is a photograph of a portion of a similar pattern more highly magnified. It will be noticed that no traces of the zigzag fissures running longitudinally along the pseudo-tracheae can be seen. These fissures are entirely obliterated by the pressure of the proboscis on the surface causing the free ends of the rings to meet, as can be readily understood by reference to Fig. 12.

The longitudinal axis of each pseudo-trachea is marked by a zigzag black line. On each side of this line are clear areas caused by the removal of pigment through the interbifid grooves. The way in which this pattern is produced is best understood by reference to Fig. 4 (left-hand side).

The broader black lines represent the inter-pseudo-tracheal plain areas of the disc.

If fed on a drop of moderate depth the proboscis does not seem to be so closely applied to the surface on which the drop is placed, though the disc is in an erected condition.

If a fly is allowed to feed on a large drop containing particles of various sizes it often sucks up all the fluid and leaves the larger particles in an irregular mass at one edge of the drop. When the area originally covered by the drop is examined with the aid of a lens it is found to be covered with numerous clear oval proboscis marks, indicated by fine lines of pigment at their peripheries. It is evident therefore that the fly at each application of its proboscis has sucked up and swallowed the fluid and smaller particles which are capable of passing through the interbifid spaces, and that the suction has caused the larger particles to adhere to the disc. After all the fluid has been swallowed the larger particles adhering to the proboscis are deposited either through the cessation of the suction, or by a small quantity of fluid being forced in a reverse direction to wash off the deposit.



A. The appearance of a drop of syrup, containing in suspension particles of Indian ink of various sizes, after being sucked by a blow-fly. All the larger particles have been left in an irregular mass at the edge where the fly stopped feeding. Numerous oval proboscis marks cover the rest of the surface, and here and there a few of the larger particles are left stranded. (Drawn from a photograph.)

B. Lens-shaped mass of pollen grains, a cast of the longitudinal sulcus, deposited by a fly while sucking a drop of fluid containing very large numbers of pollen grains in suspension.

C. T-shaped mass deposited under the same conditions.

Occasionally when large particles such as pollen grains are present in great numbers in shallow drops of fluid the fly deposits the larger particles at frequent intervals. Such deposits may be irregularly rounded masses or may sometimes be lens- or T-shaped. The latter condition probably indicates that the disc has not been applied very closely, for under such conditions the longitudinal prestomal sulcus is slightly open and may be recognized in inflated specimens as a groove slightly expanded near its centre. The stem of the T which is often slightly expanded near its centre is produced by particles which

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have been drawn into the longitudinal sulcus and the cross piece by particles which have been drawn against the walls of the anterior fissure of the disc. Often the cross piece of the T is lacking, when the majority of the larger particles have been drawn into the longitudinal sulcus, and a lens-shaped deposit results.

The mode of formation of these deposits can be followed when flies are fed on drops of fluid containing very large particles, for the currents set up can be easily examined. Since suction is created in all the pseudo-tracheae crossing the oral surface of the disc the particles are drawn towards the disc from all points, and if too large to enter the interbifid grooves form a ring round the circumference of the disc. Those which are drawn towards the anterior extremity are sucked into the anterior fissure. If the proboscis is very closely applied they remain at its outer margin, but if it is less closely applied they may be drawn into the partly closed longitudinal prestomal sulcus and form a cast of that cavity. Consequently either the outline of the proboscis is marked by stranded particles or the longitudinal sulcus is also indicated. In these cases the fly has probably ceased sucking when it lifts its proboscis. On the other hand the irregular masses of deposit, which have been described, are formed by the particles running together as the fly lifts its proboscis while still sucking.

The fly is apparently capable of slightly lifting the outer edge of the disc while feeding by means of the epifurca. Occasionally in this way particles may pass under the centre of the outer margin of the disc.

A large number of experiments were carried out in order to ascertain the size of the largest bodies which could be swallowed. For this purpose flies were made to feed on drops of various fluids containing in suspension bodies of definite size and shape such as spores of moulds, pollen, etc. Immediately after feeding they were killed and dissected and the crop and intestinal contents examined for the presence of the suspended particles. It was found that the spores of *Nosema apis* and of various moulds measuring up to ·006 mm., in fact all bodies measuring in their smallest axis less than the diameter of the interfibid space, could be readily swallowed.

The case is however different with larger bodies such as pollen grains. Many feeding experiments were carried out with emulsions of the contents of bees' colons, containing many easily recognizable bodies of various sizes, including pollen grains in various stages of digestion. In most cases pollen grains, except of very small size, could not be detected in the crop or intestinal contents of the flies. On rare occasions however numerous pollen grains were found, both in the crop and in the intestine. On closer examination many of these were found to be empty flattened shells, readily distorted to a slight degree, but afterwards regaining their shape. Such bodies could be easily sucked through the interbifid spaces. Still more rarely one or two apparently undigested pollen grains were found. Also in some experiments with recently gathered pollen from the pollen baskets of the healthy bees the grains (·02 × ·04 mm.) could be detected in the crop or intestinal contents of a small proportion of the experimental flies. No object measuring more than ·02 mm. in its smallest diameter was ever swallowed.

It was found that objects of comparatively large size were more frequently ingested when suspended in viscid fluids, such as honey, or when flies were endeavouring to extract the fluid from semi-solid masses composed of large particles.

In experiments on the part played by flies (*M. domestica*) in the dispersal of parasitic eggs Nicoll (1911, p. 18) found that the flies were "apparently unable to ingest particles of larger size than ·045 mm." His tables show that the ova of *Hymenolepis diminuta* (·07×·065 mm.—33 experiments), *Toxascaris limbata* (·08×·07—12 experiments) and *Ankylostoma caninum* (·06×·04 mm.—8 experiments) were never swallowed. Occasionally the ova of *Trichuris trichiurus* (·05×·025—1 out of 12 experiments) and of *Taenia marginata* (·035×·035—4 out of 19 experiments) were ingested. The ova of *Taenia serrata* (·035×·035) however were sometimes ingested in considerable numbers (13 out of 31 experiments). Judging from the writer's experiments it is undoubtedly rare for particles whose smallest measurements exceed the diameter of the larger interbifid spaces to be ingested even in small numbers. Occasionally however such particles may be swallowed in considerable numbers. Two explanations are possible, either that the particles are forcibly drawn into the pseudo-tracheae or that they pass directly into the mouth. By reference to Figs. 4, 11, 16 and 19 it will be noticed that the interbifid spaces and grooves are not placed symmetrically on opposite sides of the pseudo-tracheae, but a narrow diagonal fissure, a branch from the main longitudinal fissure of the pseudo-trachea, connects the openings of each pair placed nearly opposite to one another. Though under normal conditions the food passes through the interbifid spaces and bodies larger than these spaces are filtered out, yet by strong suction and a slight degree of distortion the fissures connecting two nearly opposite interbifid grooves may be forced open and allow of a body equal in diameter to the length of a line connecting the two most distant points of the interbifid spaces to be drawn through. The length of this line is nearly equal to the transverse diameter (·02 mm.) of the pseudo-trachea. Consequently it is possible that in this way bodies which just fill the lumen of a pseudo-trachea may be drawn through the pseudo-trachea into the mouth. Further, if the pseudo-tracheal rings are capable of considerable distortion slightly larger bodies just capable of engaging two opposite interbifid grooves may be sucked in and along the pseudo-trachea, if it is distorted in such a manner that the longitudinal fissure is opened to allow of its passage.

According to the writer's experiments however bodies too large to pass along the pseudo-tracheae are very rarely ingested.

The presence of ova of tape-worms in the intestinal canal of *M. domestica* cannot be explained in this way. These objects are extremely attractive to flies, which may suck at segments of tape-worms for several hours in order to extract their contents (Nicoll, 1911, p. 20). The flies appear to make great efforts to swallow the ova and probably the prestomal cavity is at times open so that the ova pass directly into the mouth without passing through the pseudo-tracheae. This view is supported by the curiously uneven results obtained by Nicoll, who for example in one series of experiments fed seven flies on ruptured segments of *T. serrata* and found 400 ova in the intestines of two flies, two ova in one fly, and none in the other four flies. The most likely explanation seems to be that in the latter five flies the filter acted efficiently, whereas in the two former ova were allowed to pass into the mouth while the prestomal cavity was open. Possibly in their endeavours to swallow these ova the flies attempt to use their teeth to reduce their size. In order to do so the labellae have to be so widely separated that the prestomal cavity is open, consequently if suction is made during the process of scraping large particles may pass into the mouth.

All the observations hitherto made indicate that under most conditions the filter acts very efficiently and prevents the entrance of particles larger than ·006 mm. in their smallest diameter into the mouth of the blow-fly. Exceptionally a few larger particles may be drawn forcibly through it, or pass directly through the prestomal cavity into the mouth.

Summary.

All the non-biting flies examined, *C. erythrocephala*, *M. domestica*, *S. carnaria*, *F. canicularis*, *L. caesar* and *O. anthrax*, possess a filtering apparatus situated in the pseudo-tracheae of the suctorial disc. The anatomy and action of this filter have been most thoroughly studied in *C. erythrocephala*. The suctorial disc is grooved by pseudo-tracheae which end near its centre in closed collecting channels. The latter open into furrows or gutters formed by the peculiar disposition of the prestomal teeth on the walls of the prestomal cavity. The opening of the mouth is situated at the base of the cavity. During natural feeding the lobes of the suctorial disc are pressed together so that the lumen of the prestomal cavity is obliterated, and no food can enter the mouth except through the collecting tubes. The pseudo-tracheae are channels kept open by chitinous rings situated in their walls. Each ring has one bifid extremity, enclosing between the horns the "interbifid space," which forms an opening of definite size into the pseudo-trachea. A fold in the cuticle, the "interbifid groove," leads to each interbifid space.

The fluid food is sucked first along the interbifid grooves through the chitin-lined interbifid spaces into the pseudo-tracheae. Particles of larger diameter than the interbifid spaces (·006 mm.) are usually prevented from entering the mouth and are rejected. The fluid and smaller particles are drawn along the pseudo-tracheae, through the collecting channels and gutters between the prestomal teeth into the mouth. By means of strong suction two opposite interbifid grooves may be made to communicate with each other owing to the lateral fissures connecting with the longitudinal pseudo-tracheal fissure being forced open, and consequently a few larger particles, up to ·02 mm. in diameter, may be drawn into the pseudo-tracheae.

Certain relatively large and very attractive objects, such as the ova of tape-worms, too large to pass through the filter, may occasionally be swallowed. Such objects probably pass directly into the mouth, when the prestomal cavity is open, during the prolonged sucking efforts made by the flies.

The large number of experiments which have been made leave little room for doubt that under natural conditions, especially when the fly is feeding on a thin film of moisture, the filtering apparatus works with a high degree of efficiency.

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DESCRIPTION OF PLATES IV—VIII.

Fig. 1. The right lateral half of the proboscis of the blow-fly divided in the middle line, and seen from the cut surface. The diagram has been reconstructed from dissections and serial sections. The mouth, prepharyngeal tube and pharynx are shaded.

1. Oesophagus. 2. Pharyngeal tube. 3. Salivary duct. 4. Fulcrum (with pharyngeal muscles). 5. Salivary valve. 6. Apodéme of the labrum. 7. Hyoid sclerite. 8. Flange at proximal end of ligula. 9. Cavity of prelabrum (passing up to prepharyngeal tube). 10. Thyroid sclerite and contained muscles. 11. Paraphysis. 12. Ligula. 13. Hypoglossal sclerite. 14. Cavity of prelabrum. 15. Salivary gland of oral disc. 16. Prestomal teeth and prestomal cavity. 17. Labellum showing pseudo-tracheae, the anterior and posterior sets opening into common collecting channels. The epifurca can be seen running downwards behind the pseudo-tracheae. 18. Lateral plate of discal sclerite with nodulus (black). 19. Anterior portion of prelabrum with contained muscles.

The smaller figures are transverse sections at *A—A* and *B—B*, and are numbered as in the larger figure.

Fig. 2 represents four rows of prestomal teeth and the corresponding portion of the labellum seen from the oral surface. In the upper part of the figure three of the central pseudo-tracheae, showing the alternate bifid and flattened ends of their rings and the longitudinal fissures, are represented. Each passes into a collecting tube with non-bifid rings which terminates by a spout-like opening between the distal extremities of two rows of prestomal teeth. The inner, shortest set of teeth are lightly shaded. They are unbranched and articulate with the lateral plate of the discal sclerite by their strong proximal extremities. The teeth of the intermediate set, which are more darkly shaded, branch behind the distal extremities of the inner set. The branches diverge to each side of the corresponding inner teeth to articulate with the lateral wall of the discal sclerite. The teeth of the outer set are most darkly shaded. The two central teeth of this set branch behind the distal extremities of the intermediate set. The branches diverge widely behind those of the intermediate set, but do not articulate directly with the discal sclerite. At each side of the figure this set is represented by separate chitinous bars which do not unite to form definite teeth.

The teeth of the inner set form the side walls of gutters whose floors are formed by the branches of the intermediate and outer sets of teeth and the integument covering them. Fluids drawn through the collecting tubes pass along the gutters into the mouth.

The tendinous chords described by Lowne (p. 395) are indicated between the pseudo-tracheae.

Fig. 3 represents a view of a single collecting tube and its corresponding teeth from behind, after the removal of the integument of the aboral surface of the disc, to show the relationship of the teeth to the cuticle. The distal halves of the inner set of teeth and the distal thirds of the intermediate set of teeth are free from integument.

Fig. 4 represents a dissection of a portion of a pseudo-trachea. On the right-hand side the integument of the oral surface of the labellum has been removed so as to show a portion of the pseudo-trachea with the alternate bifid and flattened extremities of the chitinous rings and the membrane lining the interior of the tube stretching between them. On the left-hand lower portion the appearance of the surface integument is represented. Two interbifid grooves leading to their interbifid spaces are shown. Between the spaces are elevated masses, each of which is produced by a fold of the integument enclosing the flattened end of a ring and the extremities of the adjacent forks on each side. In the left-hand upper portion of the diagram is shown the appearance of these structures as seen by transmitted light so as to indicate more clearly the relationship of the integument to the rings.

Fig. 5 illustrates the arrangement of the chitinous structures of the posterior common collecting channel of one labellum with 10 pseudo-tracheae opening into it. Throughout the greater part of the length of the common collecting channel the extremities of the rings are either quite plane or slightly expanded or possess only the rudiments of forks. At its proximal (right-hand) end the chitinous bars representing the rings are elongated and form a shallow groove leading towards the discal sclerite which forms the side wall of the entrance to the mouth. Two pseudo-tracheae opening through their own collecting channels into gutters between prestomal teeth are shown on the right-hand side.

Fig. 6 is a side view of a pseudo-tracheal ring. At its right-hand end the ring has a flattened expanded extremity; at its left-hand end a bifid extremity. The opening of the longitudinal fissure is seen between the flattened end of the ring and the tips of the forks. The arrangement of the fold of integument forming the interbifid groove is indicated by means of shading.

Fig. 7 represents two consecutive pseudo-tracheal rings, showing the relationship of their bifid and flattened extremities, as seen from the oral surface of the disc.

Fig. 8 is a schematic representation of a transverse section through the oral surface of part of labellum and prestomal cavity. The free extremities of the teeth are shown projecting above the integument (dotted line).

Fig. 9 is a photograph (× 66) of the oral surface of the erected suctorial disc of a blow-fly. The pseudo-tracheae and anterior and posterior common collecting channels are well seen.

Fig. 10 is a photograph of the oral lobe of the blow-fly treated with potash and flattened out. The pseudo-tracheae can be clearly seen as well as some of the prestomal teeth and the gutters between them.

Fig. 11 is a photograph (× 340) of part of the oral surface of the labellum treated with potash showing portions of four pseudo-tracheae. The flattened and bifid extremities of alternate pseudo-tracheal rings are well seen.

Fig. 12 is a photograph (× 600) of a transverse section of part of the oral surface of a labellum. Four complete pseudo-tracheae are included in the section. In each case the chitinous ring and the opening of the longitudinal fissure is very distinct. It happens that in each case the bifid extremity is situated on the left side of the pseudo-trachea. The point of bifurcation is indicated by a dark spot above which the forks are curved inwards. From the point of bifurcation a distinct line, which represents the reflection of the cuticle at the base of the interbifid groove, passes obliquely upwards and outwards to the surface of the integument (see Fig. 6).

Fig. 13 is a photograph (× 700) of ten consecutive chitinous pseudo-tracheal rings treated with potash and compressed, showing their alternate flattened and bifid extremities.

Fig. 14 is a photograph (× 700) of two separated and partially distorted pseudo-tracheal rings.

Fig. 15 is a photograph (× 600) of a longitudinal section through a pseudo-trachea slightly to one side of the median line. The interbifid spaces and the manner in which the integument passes over and binds together the flattened extremities of the rings and the contiguous forks of the adjacent rings on each side can be clearly seen.

Fig. 16 is a photograph (× 1300) of the oral surface of a part of a labellum including portions of two pseudo-tracheae. The interbifid grooves are seen as regularly placed oval markings on each side of the pseudo-trachea. The zigzag longitudinal fissure is also indicated (see Fig. 4).

Fig. 17 is a photograph (× 770) showing a side view of three pseudo-tracheae (with bifid rings) passing into their collecting channels (with non-bifid rings) which run down between the teeth.

Fig. 18 is a photograph (× 226) of part of the side of the prestomal cavity, showing rows of teeth and the gutters between them. The spout-like openings of the collecting tubes can be very distinctly seen.

Fig. 19 is a photograph of a wax model of short segments of two pseudo-tracheae. The cuticle and internal lining membrane have been stripped off the outer side of the pseudo-trachea on the left exposing the chitinous rings. On the inner side of this pseudo-trachea and over the whole of the pseudo-trachea on the right the cuticle is represented *in situ*. The interbifid grooves leading into the interbifid spaces can be easily seen.

Fig. 20 is a photograph of proboscis marks produced by a fly feeding on a thin layer of Indian ink spread on glass. The position of the anterior cleft is indicated in every proboscis mark. The marks show that in each case the proboscis has been firmly and evenly applied.

Fig. 21 is a photograph (× 77) of a portion of a proboscis mark left by a fly attempting to suck up a layer of partially dried Indian ink deposited on glass. The outline of the suctorial disc is clearly shown. The marks indicating the position of the longitudinal sulcus are very narrow, showing that the prestomal cavity was almost completely closed. The lines of the pseudo-tracheae are marked by double rows of regularly placed clear oval areas, separated by thin black lines. Each of these areas, from which the pigment has been removed by suction, represents the space covered by an interbifid groove.

Fig. 22 is a photograph of part of a proboscis mark similar to that shown in Fig. 21, more highly magnified (× 770). The longitudinal axis of each pseudo-trachea is marked by a zigzag black line, showing that the longitudinal fissure was closed. On each side of the zigzag black line are clear areas produced by the removal of the pigment through the interbifid grooves. Their shapes are very clearly defined. The way in which this pattern is produced can be readily comprehended by reference to Fig. 4 (left-hand side). The broad black lines, separating the clear areas, represent the inter-pseudo-tracheal plane areas of the disc.

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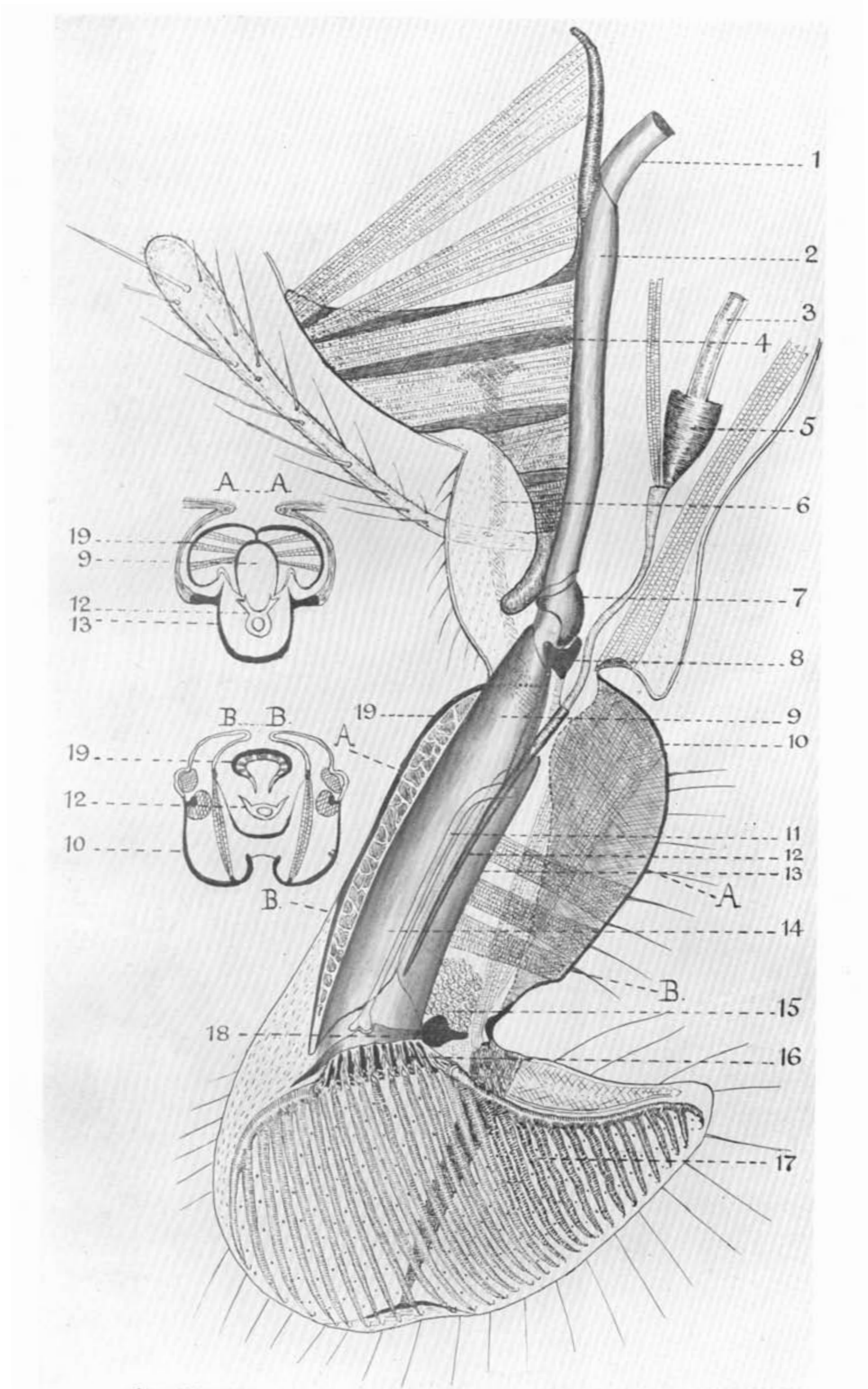

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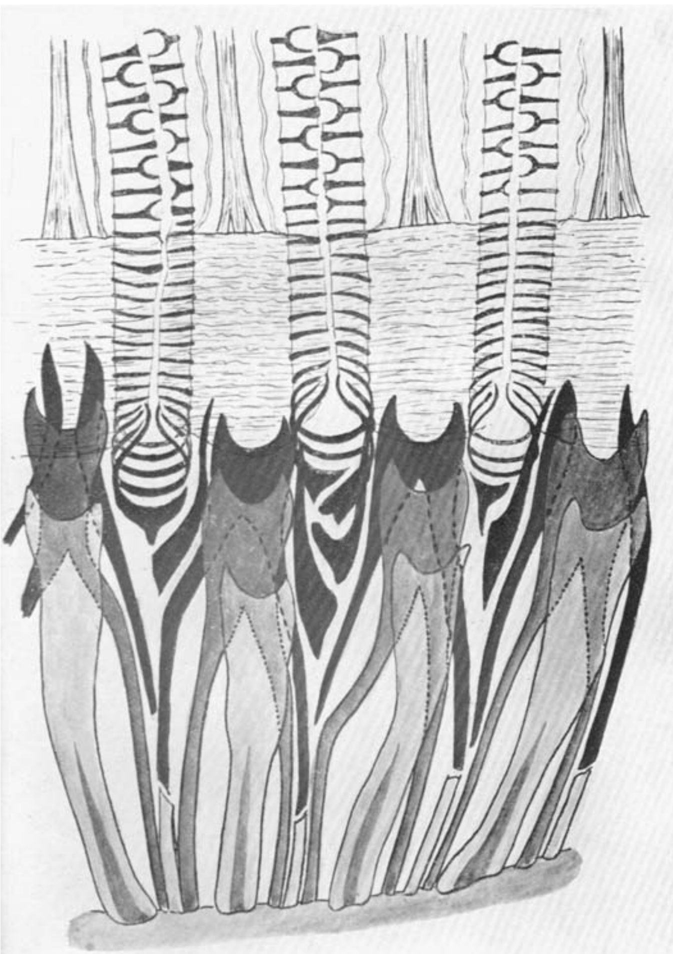

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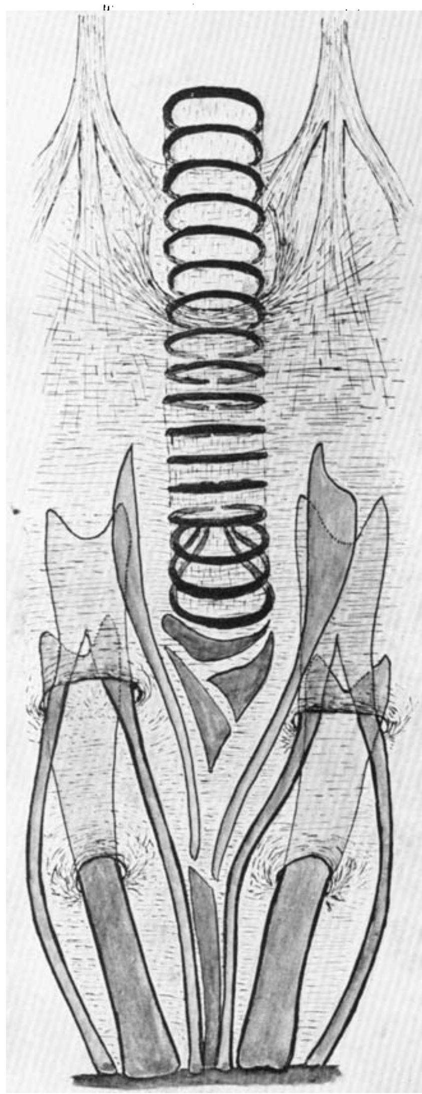

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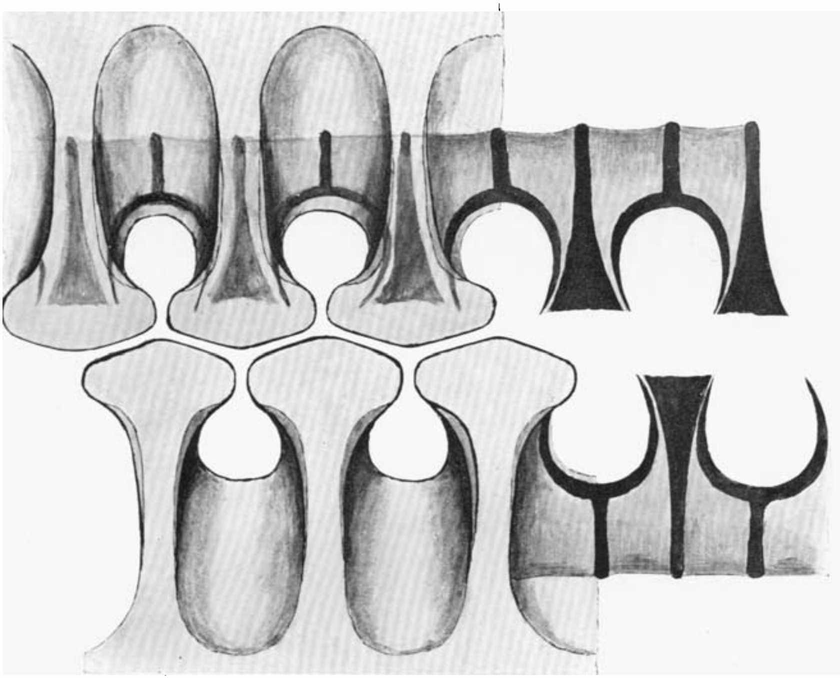

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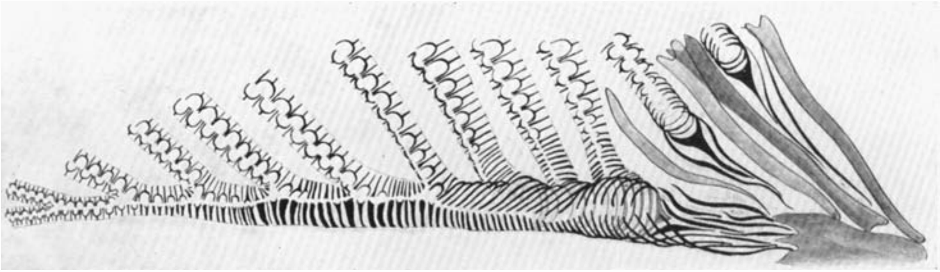

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Fig. 6.

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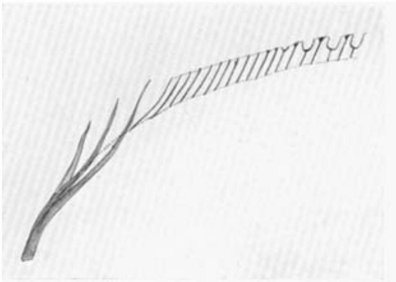

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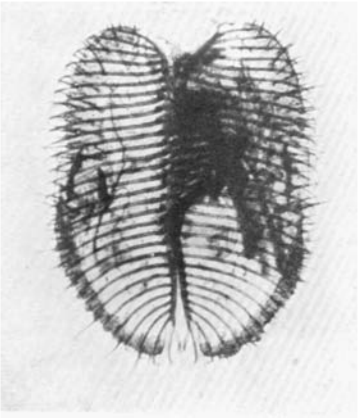

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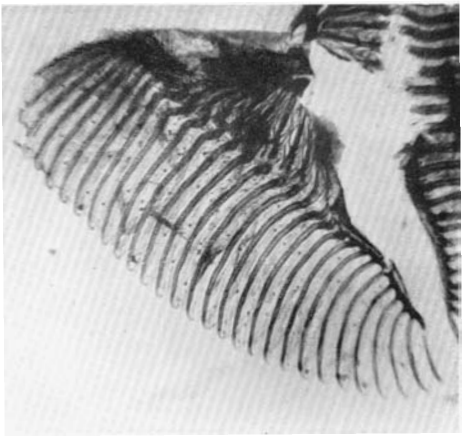

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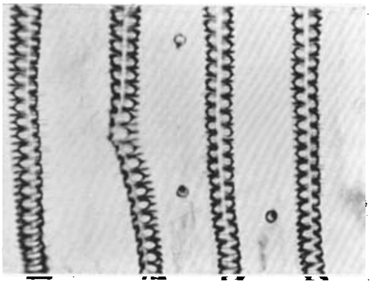

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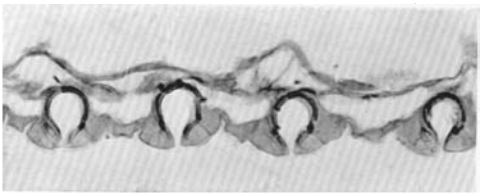
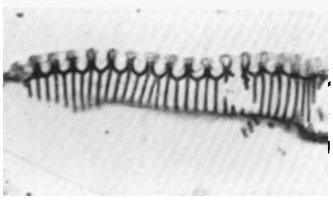


Fig. 12.

Fig. 14.

Fig. 13.



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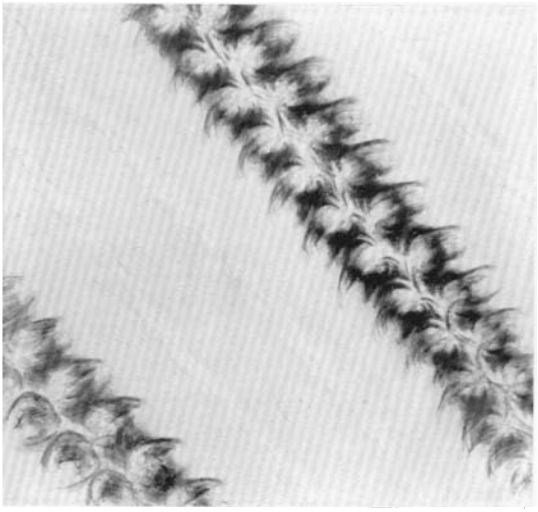

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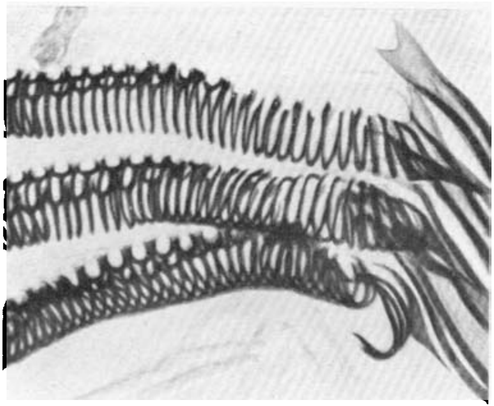

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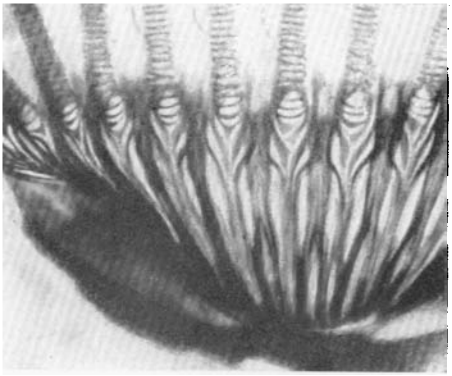

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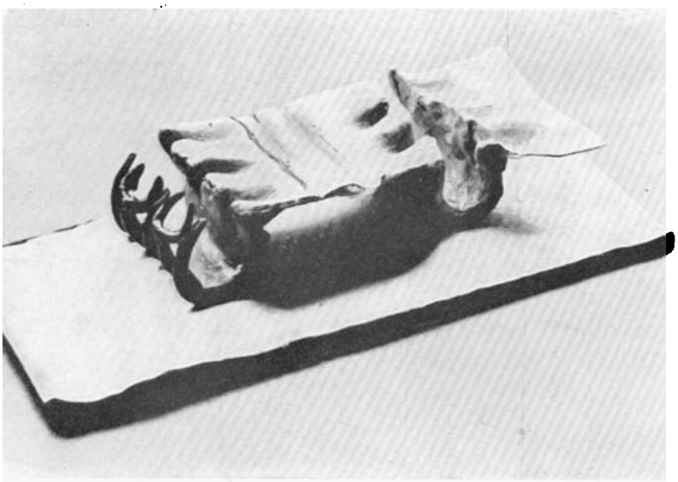
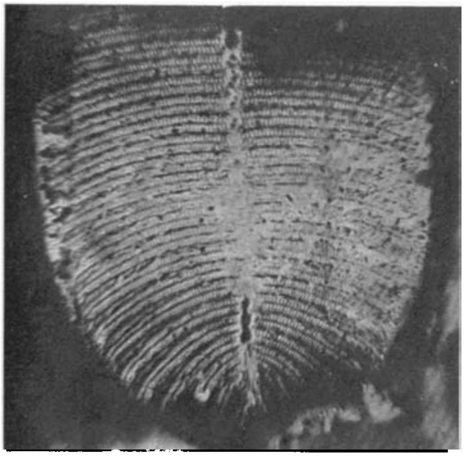


Fig. 19.

Fig. 20.



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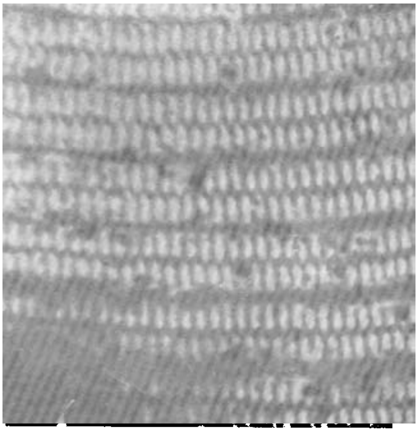

Fig. 22.

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