Studies on the Mouth Parts and Sucking Apparatus in the Blood-Sucking Diptera.

No. 1.

PHILAEMATOMYIA INSIGNIS, AUSTEN.

BY

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Philæmatomyia insignis is a small greyish-brown fly, found throughout the Oriental region, and recorded also from Tropical Africa. The genus is closely allied to *Musca*, and in general appearance, breeding habits, venation, etc., there is little to distinguish it. The characteristic feature, on account of which the genus was founded, is the presence of a ring of stout chitinous teeth at the tip of the proboscis. It is, in fact, in spite of its innocent appearance, a voracious blood-sucker. It preys exclusively, so far as is known, on cattle, and in the neighbourhood of this Institute it is much the commonest blood-sucking fly found on them. It is especially fond of feeding on the abdomen of calves which have been shaved for vaccination. Both male and female suck blood, and possibly also feed on the dung in which their eggs are laid.

The proboscis is completely retractile, like that of *Musca*, and it is only exceptionally the case that the teeth can be seen in dried specimens ; even if the proboscis happens to be extended the teeth are not visible unless the labellar walls are retracted so as to disclose them. It is therefore probable that it will be found to be much commoner and more widely distributed than the present records state, when it is more systematically looked for.

Methods.

For the study of the chitinous parts the material was cleared in 2 per cent. potash solution for varying periods. The best results are obtained by allowing the potash to act for a prolonged period in the cold, rather than by boiling, as this is apt to distort the parts on account of the sudden expansion of the contained air. The biting parts are extremely densely pigmented, and it was necessary to decolorize them, to a degree varying in different preparations, with chlorine gas. The soft parts were studied chiefly by dissection of freshly killed flies. Sections of newly hatched flies were prepared by the combined paraffin and celloidin method and stained with Iron-hæmatoxylin and Eosin. Sections are, however, rather

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difficult to interpret, since one cannot be certain of the exact degree of extension of the proboscis and eversion of the teeth once the material is placed in the fixative. The best results were obtained by dropping whole heads of etherized flies into absolute alcohol, and immediately pressing on the head with a needle above the lunule. This manœuvre causes the proboscis to shoot out and distends the oral lobes, and one can sometimes get the parts definitely fixed in this position.

I am greatly indebted to Captain Patton, I.M.S., Acting Director of this Institute, for many valuable hints on the habits of the fly, and for a batch of pupæ.*

General Account.

As indicated above, the proboscis bears a close resemblance to that of *Musca*, and in the following description the terms generally used for the mouth parts of *Musca* will be adhered to as far as possible, leaving the question of the relation of the parts to the corresponding ones in other blood-sucking muscids to be discussed later. The proboscis consists of three parts, *viz.*, the *rostrum, haustellum*, and the *labella.* The *rostrum* is shaped like a truncated cone, the broad base of which fits into an orifice on the under surface of the head. It is composed of a chitinous framework, the *fulcrum,* and a loose investing membrane, which serves to attach the fulcrum to the head, and also encloses the soft structures of the rostrum. The *haustellum* is about the same length as the rostrum. It is somewhat cylindrical in shape, with the middle portion expanded. Its posterior and lateral walls, which are rounded so as to form about two-thirds of a circle in cross sections, are formed by a chitinous plate, the *theca.* The anterior side, which is flattened, is membraneous, and has running down the whole length in the middle line a thick pigmented chitinous rod, which is deeply grooved on its anterior surface. This groove contains the labrum-epipharynx and the hypopharynx, and the rod may be called the *labial gutter*, since it corresponds to the structure described in *Stomoxys* by Stephens and Newstead under that name. The *labella* are attached to the end of the haustellum. When fully expanded they form a gently rounded globular extremity to the proboscis. The two labella are fused together, and their walls are continuous except on the anterior surface, where there is a narrow and deep groove, which contains the teeth, and is continuous with that of the labial gutter. They closely resemble those of *Musca.* The oral surface bears a well developed pseudo-tracheal membrane, while the aboral surface consists of a flexible membrane strengthened by the development of thin plates of chitin, the whole being supported by a strong horse-shoe shaped arch, the *furca.*

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* An account of the breeding habits of Philæmatomyia and the closely allied form Pristirhynchomyia Brunetti will be published shortly.

When fully extended the proboscis hangs down at a right angle to the long axis of the fly, the rostrum having a slight forward inclination. The whole organ can be completely retracted under the head, the rostrum being folded backwards on to the under surface of the head, the haustellum forwards on the rostrum and the labella backwards on the haustellum. In the subsequent detailed description, the organ will be considered as extended for use, so that the terms anterior and posterior will apply to those surfaces which are, in the extended position, continuous with the dorsal and ventral surfaces of the fly.

It is unfortunate that the term "proboscis" has no accepted meaning. It is used by some authors, as for instance Stephens and Newstead in their accounts of *Glossina* and *Stomoxys*, to indicate the haustellum and labella only, the rostrum being disregarded, while other writers use it for the labium only. In this paper the word is used to signify all the protruding mouth parts. The constituent parts of the proboscis have each commonly accepted names, and it would certainly conduce to clearness of description if the term were only used in a general sense, so as to be equally applicable to all insects.

The Rostrum.

The *Fulcrum* (Plate I, Fig. 1) consists of a posterior plate, two lateral plates, and a thick arch which connects the two lateral plates in front. Kræpelin described the corresponding structure in *Musca domestica* as resembling a Spanish stirrup iron; the posterior plate would then represent the foot plate, and the anterior arch the bar to which the stirrup leather is attached. The posterior plate is oblong, its greatest breadth, which is a little above the middle, being about one-third its length. It is slightly concave forwards, and the lateral edges are raised up into strong ridges, which project beyond the upper and lower borders as diverging cornua. The lateral plates, which are shaped roughly like isosceles triangles, pass directly forwards from these lateral ridges. The anterior border of each plate is deeply incurved in its lower third, and has on it, just above the recess so formed, a sharp spine projecting downwards and forwards. The upper border is also deeply incurved and is almost semi-circular in outline. The anterior arch is a thick and strongly ridged band of chitin which passes between the projecting anterior angles of the lateral plates. The ridges on this piece are continued into the upper and anterior margins of the fulcrum. The upper orifice of the fulcrum, bounded by the posterior and lateral plates, is quadrilateral in outline, and lies immediately below the epistomium.

The *Membrane* of the rostrum encloses the fulcrum. It is attached to the border of the epistomium, and to the clypeus, genæ, and gulomental plate, and to the anterior borders of the sides of the fulcrum, converting it into a closed cavity, which is occupied by the pharyngeal muscles. Posteriorly it runs downwards to the lower end of the rostrum, enclosing the muscles, tracheæ and salivary duct, which lie posterior to the fulcrum. The membrane is thrown into numerous folds when the proboscis is withdrawn.

The *Palps* are attached to the membrane on the anterior surface of the rostrum, in its lower third. Each arises from a small raised and partially chitinized area, on the outer projecting angle of which there are two large macrochetæ. The palps are clavate, moderately long, and clothed with numerous very fine recumbent hairs and many large pigmented chetæ. The palps are folded back against the anterior surface of the rostrum when it is withdrawn, and are erected when it is extended.

The *Pharynx* (Plate V, Fig. 22) is composed of two chitinous plates, normally superimposed and in contact with one another. The posterior of these is the posterior plate of the fulcrum. The anterior plate is of the same size and shape, but is somewhat thinner. It has a stout median ridge running down its anterior surface. The sucking action is produced, as in other diptera, by the separation of these two plates.

The sucking portion of the pharynx does not extend quite to the lower end of the rostrum. At the extreme end the food canal consists (Plate IV, Fig. 20) of a concave posterior plate, only partially chitinized, and a membraneous anterior wall. A little higher up (Plate V, Fig. 20) two lateral plates are developed, and the attenuated end of the anterior plate is seen appearing in the anterior wall. This arrangement permits of flexion at the junction of the rostrum and haustellum when the proboscis is withdrawn.

The *Salivary Duct* in the upper portion of the rostrum is a simple tube of thin chitin, lying in the middle line on the posterior surface of the pharynx. At the lower end the walls are membraneous, and the duct lies embedded in a dense mass of cellular tissue. A short distance above the point at which the duct emerges from the haustellum there is a small valve resembling that of Musca.

The *Muscles of the Rostrum* (Plate V, Fig. 22)) resemble those in *Musca,* though some of those described by Kraepelin have not been traced. Their function is to retract the proboscis and to assist in extending it.

The *Dilators of the Pharynx* (D. ph) arise from the sides of the fulcrum throughout its upper two-thirds, and from the adjacent membrane covering in the anterior surface. They run inwards and backwards to be inserted into the anterior plate of the pharynx, most of the fibres being attached to the median ridge on that plate.

The *Flexors of the Haustellum* (F. H.) arise from the sides of the occipital foramen, and are inserted into the distal ends of the labral apodemes; they lie external to the tracheal sacs in the rostrum.

The *Retractors of the Haustellum* (R. H.) are long round bundles, situated behind the pharynx and on either side of the salivary duct. They arise from the inner surface of the posterior wall of the head cavity, and, passing downwards behind the brain and external to the occipital foramen, are inserted into the thickened mass of chitin at the base of the theca, by a membraneous expansion.

The *Extensors of the Haustellum* (Ex. H.) arise from the cornua at the distal end of the fulcrum, and run obliquely upwards and outwards to the proximal end of the labral apodemes.

The *Retractors of the Fulcrum* (R. F.) arise on each side from the internal edges of the genæ, and are inserted into posterior cornua at the proximal end of the fulcrum. They lie in a fold of membrane at the anterior lateral angle of the rostrum.

The *Tracheæ* resemble those of *Musca*. There are two large tracheal sacs, lying on either side of the salivary duct. In dissection these sacs can frequently be separated out while still distended with air, appearing as large sausage-shaped white bodies. In sections they are usually constricted, and so come to have a corrugated outline and a relatively thick wall.

The Haustellum.

This comprises the true mouth parts, *viz.*, the labrum, epipharynx, hypopharynx and the labium. Of these only the labium can be distinguished without dissection, the other parts being concealed in the labial gutter. The labium consists of two pieces of chitin, the *theca* and the *labial gutter*, and a connecting membrane.

The *Theca*, which forms the main part of the labium, is a hollow scaphoid trough, much deeper in its upper part than below, and having its open side directed forwards. The margins of the space so formed are thickened into strong ridges, which run parallel to one another throughout the length of the labium. The upper end of the theca is somewhat truncated and narrowed, and contains at the extreme end a Y shaped median ridge for muscle attachment. The upper end of the labial gutter is fused with the converging margins at this end of the theca. At the lower end there is another Y shaped median ridge, the lateral arms of which are reinforced by fibrous bands from the lateral ridges of the theca, and which pass outwards, downwards and slightly forwards, to articulate, as will be seen later, with the furca of the labella. Near the tip of each of these rods there is a small barb-like projection. In preparations treated with potash for a prolonged time, it is seen that these projecting rods are not of equal thickness throughout, but that there is, about the middle of their length, a weaker portion which probably functions as a joint.

The *Labial Gutter* (L. G.) is a thick deeply pigmented rod, grooved on its anterior surface in such a way that it appears U shaped in transverse section. It lies in front of the theca, and is connected with it by a rather tough membrane, which stretches between the lateral ridges of the theca and the borders of the groove. At its upper end it is intimately fused with the theca so that no movement is possible between them. On the upper half of its posterior surface there is a thin chitinous expansion, projecting backwards into the cavity of the theca, and reaching almost to the posterior wall, which gives origin to an important pair of muscles. This expansion, when seen in profile, has the shape of the keel of a racing yacht, and corresponds exactly to the similar structure in *Stomoxys*. At the lower end of the labial gutter the sides are produced downwards a little beyond the bottom of the trough and terminate in gently rounded knobs which converge slightly towards one another. In this way a simple socket is formed, into which, as will appear later, a pair of labellar rods is articulated. (Plate II, Fig. 7.)

The *Hypopharynx* (Plate II, Fig. 2) is a slender slip of chitin arising from the base of the labial gutter and terminating in a fine attenuated point. It lies at the bottom of the gutter throughout and terminates just above its lower end, being slightly shorter than the labrum-epipharynx. It is pierced throughout by the salivary duct. When seen in cross section it is found to consist of two distinct laminæ, separated by a small amount of cellular tissue. The inner lamina is circular, and constitutes the duct, being directly continuous with the salivary duct in the rostrum and head. The outer lamina is flattened at the tip, but becomes rounded as it passes upwards in such a way as to accommodate itself to the bottom of the trough in which it lies. The base of the hypopharynx is enlarged into a thick knob of densely pigmented chitin, which projects upwards a little above the upper end of the theca, to which and to the superimposed labrum-epipharynx it is closely attached.

The *Labrum-Epipharynx* (Plate II, Fig. 3) is a lanceolate slip of chitin, flattened at its apex, but expanding gradually in an antero-posterior direction towards its upper end, so that at its base its depth is almost as great as its width. It is attached, so loosely that it is easily bent forward in dissection, to the thick mass of chitin at the upper end of the hypopharynx and labial gutter. As it passes downwards it closes in the open side of the labial gutter, its bluntly rounded tip lying in the hollow formed by the two projecting lateral tubercles. On its under surface there is a deep groove, the overlapping sides of which gradually converge backwards and inwards towards one another from the apex to the upper fourth, where they meet and so form a closed canal. On cross section the labrum-epipharynx, like the hypopharynx, is seen to consist of two distinct laminæ. The outer of these composes the anterior surface and the posterior surface as far as the edges of the groove, and in the upper fourth, where the groove has become a canal, presents a continuous contour, convex in front and behind. The internal lamina forms the wall of the groove and canal. At its tip it is semi-circular and concave backwards, but as the edges of the groove close in it becomes more circular, until, about the upper fourth, it forms a complete canal, the lumen of which is continuous with that of the pharynx in the rostrum. The inner and outer laminæ are united with one another at the edges of the groove throughout, and are also firmly attached to one another by a strong band of fibres lying in the middle line behind the groove. In this way two lateral spaces are formed, one on each side of the central canal; these are roughly triangular in shape, and contain a series of muscles and some cellular tissue. The upper end of the inner tube projects a little above the outer lamina and terminates in a thickened flange.

On each side of the groove of the labrum-epipharynx there is a row of minute oval flattened tubercles, projecting into the lumen; three similar ones are situated on the posterior surface of the flattened tip of the organ. These tubercles recall the similar structures found in *Stomoxys*, but they do not bear spines, and no suggestion as to their function can be offered.

The interval between the inner and outer laminæ of the labrum-epipharynx is occupied by a series of muscle bundles passing, in a somewhat fan-shaped manner, from the outer to the inner wall. They probably function as an accessory pump, by dilating the lumen of the groove and canal.

The labral apodemes pass from the two upper angles of the labrum-epipharynx upwards, and slightly forwards, into the rostrum. Each is a deeply pigmented slightly sinuous rod, about two-thirds the length of the labrum-epipharynx. The lower end is shaped like an arrow-head with a single barb, and is fitted into a small round socket on the lateral edge of the labrum-epipharynx, where it contracts sharply at the base. The upper end is flattened and expanded for muscle attachment.

The relations of the labial gutter, hypopharynx and the labrum-epipharynx to one another are best studied in serial transverse sections. At its lower end (Plate IV, Fig. 14) the labial gutter encloses a horseshoe-shaped space, at the bottom of which the hypopharynx, which here is very small and circular in outline, is seen. The front of the space is closed in by the flat tip of the labrum-epipharynx. A little higher up (Plate IV, Fig. 15) both the labrum-epipharynx and the hypopharynx are much enlarged, and the groove on the posterior surface of the former has become well marked, so that its lateral edges curve inwards, fitting inside the labial gutter, which has now become more V shaped. About the middle of the labial gutter (Plate IV, Fig. 16) the edges of the groove are seen to have approached still nearer to one another, so as to almost touch the hypopharynx, which is now triangular in section, the rounded posterior angle fitting into the bottom of the groove, the slightly concave base being opposite to the groove in the labrum-epipharynx. At this level the inner and outer laminæ of the labrum-epipharynx are firmly attached to one another by the median strand of fibres. At the level of the "keel" of the labial gutter (Plate II, Fig. 7) the labrum-epipharynx is considerably broader from side to side, and edges of the groove are almost in contact with one another. The gutter is now much contracted in its posterior half, forming a recess into which the hypopharynx, now also enlarged and more distinctly concave on its anterior surface, is fitted. The anterior half of each lateral wall of the gutter is bent outwards as well as forwards, so as to form with the anterior surface of the hypopharynx, an even surface on which the labrum-epipharynx, now broader than the labial gutter, rests.

Near the base of the labial gutter (Plate III, Fig. 8), where the keel is becoming narrower, the labrum-epipharynx appears as a closed canal with a double wall, the inner circular tube being continuous with the groove. The hypopharynx has become an oval tube of thick chitin with a circular lumen, and lies between the now contracted sides of the gutter. The theca is much reduced in its antero-posterior diameter, so that the upper end of the keel approaches close to the median limb of the Y shaped ridge on its anterior surface. At the extreme upper end of the haustellum (Plate V, Fig. 19) the labial gutter and the hypopharynx are completely fused to form a dense mass of chitin, which extends from the theca to the labrum-epipharynx, and to which the posterior surface of the food canal is fused. The salivary duct runs through this expansion, towards its posterior border, as a simple round tube.

It will be seen from the foregoing description that the food channel is formed in the lower part by the labial gutter and the flattened tip of the labrum-epipharynx; in the middle portion, by the apposition of the edges of the groove in the posterior surface of the labrum-epipharynx and the concave anterior surface of the hypopharynx; in the upper portion, by the closed canal in the labrum-epipharynx. There is no system of interlocking teeth such as that found in *Stomoxys*, the continuity of the channel depending on simple apposition of the parts. It will be noticed that the extreme tip of the hypopharynx projects into the lumen of the canal; the tip is extremely attenuated and ill-defined, and, as suggested by Stephens and Newstead, it may function as a valve to prevent the blood being drawn up the salivary duct.

The Labella.

The *Labella* are joined to form a single organ, the distinction between the two being indicated by a deep median groove on the anterior surface. The external wall, forming the aboral surface, consists of membrane, strengthened in certain areas by thin plates of chitin. It is supported by a horse-shoe shaped rod, the *furca,* which also functions as a joint between the labium and labella. The internal or oral surface, which when the labella are in use is expanded to form a globular end to the proboscis, is formed by a simple pseudo-tracheal membrane. The sides of the groove on the anterior surface are specially modified to form the cutting organ of the fly.

The *Furca* (Plate II, Fig. 6) lies immediately below the Y fork at the lower end of the theca, and encircles the posterior and lateral walls of the organ. Its distal ends are thickened into small tubercles, just behind which there is on each side a small spur projecting upwards and backwards, so as to form a small notch. The projecting arms of the fork at the end of the theca rest in this notch, which form the joint on which the labella are swung backwards and forwards.

The *External wall* of the labella is attached to the furca ; in addition there are three special plates, one posterior and two lateral, developed to give the furca, in its movements, more control over the loose membrane. The posterior plate is heart-shaped, and arises from the posterior part of the arch, running downwards almost to the edge of the pseudo-tracheal membrane and ending in a blunt point. The lateral plates are triangular in shape, the base arising indefinitely from the membrane near its edge about the middle of the external surface on each side. The apex terminates in a fine hook, which is attached to the tubercle at the extremity of the lateral arm of the furca.

Besides these plates, which are definitely chitinized and do not bear hairs, the external wall is stiffened in other less definitely outlined areas. There are two heart-shaped ones as the extreme anterior end of the labella, the apices of which are attached to the ends of the labellar rods, and two on the posterior surface, on either side of and below the posterior plate of the furca. The lateral area between these plates is thickened along the extreme edge, where it joins the pseudo-tracheal membrane. Except on the posterior and lateral plates, the external surface of the labella is loosely covered with large and small pigmented hairs, arranged in an irregular manner, some forming a loose fringe on the lower border. At the extreme edge of the external surface the ordinary epidermal membrane is replaced by a narrow band of scales. (Plate II, Fig. 8.) These are of three kinds. Immediately below the fringe of hairs there are rows of small irregularly rounded scales, loosely and irregularly set on the membrane, and about seven deep. These are succeeded by a definite row of larger semi-circular scales, the straight edge of which projects downwards. Below these there is another row of larger scales, resembling in shape axe-heads with the basal part somewhat expanded. The broad ends of these scales overlap the pseudo-tracheal membrane; from the narrower upper end of each there arises a small hair, which projects downwards towards the pseudo-tracheæ.

The *Pseudo-tracheal membrane* constitutes the oral surface of the labella. When the organ is extended for use the membrane presents a globular convex surface, traversed by the pseudo-tracheal channels, which converge from the periphery to the region of the teeth in the anterior median fissure. When at rest the oral surfaces of the two sides are in contact with one another, the lower margin of the organ being formed by the narrow scaly membrane of the external surface. The membrane resembles that of the non-blood-sucking muscids. It is homogeneous, transparent, and apparently structureless. The channels are minute folds, horse-shoe shaped in cross section, the edges being contracted so as to enclose about three-quarters of a circle. The lumen is maintained by a series of fine chitinous rings, closely set side by side, the extremities of each ring being turned outwards and backwards, so that when seen flat the edges of the channel have a beaded appearance. There are twelve channels on each side arranged as follows. Each channel arises from the edge of the pseudo-tracheal membrane, being overlapped at its origin by one of the hair-bearing scales of the external surface. The anterior set of four converge towards the middle line to form one large trunk, which dips inwards anterior to the teeth, at the lower end of the groove on the anterior surface of the labella. The next five channels remain separate and run to the middle of the oral pit. The posterior set of three unite to form a single larger channel, which dips inwards posterior to the teeth. Finally all those from one side unite to form a single channel, which, as it passes upwards, gradually looses its chitinous rings and becomes replaced by a short duct with cellular walls.

The Biting Apparatus.

The remarkable biting apparatus of this fly lies in the groove on the anterior surface of the labella, and is developed from their internal walls. It consists of two sets of strong teeth, four on each side, certain serrated scales, two lateral rods, which, for convenience in description, will be termed the *labellar* rods, and a median piece of chitin which connects the rods and also functions as a tooth. These structures are most conveniently described from above downwards.

The *Labellar rods* are of strong and deeply pigmented chitin. Each rod is about one-third the length of the labial gutter, somewhat flattened from side to side, and has its upper end turned slightly outwards and forwards. At the junction of the upper and middle thirds there is on the posterior surface a small tubercle, posterior to which the rod is considerably reduced in diameter and tapers to a blunt point. The lower end of each rod is expanded and hollowed out so as to form a shallow cup for the reception of the bases of the teeth. These rods lie on either side of the bottom of the groove on the anterior surface of the labella, and are attached throughout to the membrane forming the labellar wall. The tubercles on their posterior surfaces fit into the end of the labial gutter, and, when the labella are erected, press against the projecting tubercles of the lateral walls of the gutter, the arrangement forming, in fact, a simple ball and socket joint. The posterior thirds of the rods project upwards above the lower end of the gutter.

The *Axial apophysis* (Plate II, Fig. 4) is situated behind the lower ends of the labellar rods, and binds them firmly together. It is shaped like a shield, the lower end being produced to a sharp point, which lies a little below the bases of the teeth. It thus forms the floor of the labellar groove at the lower end; above it, the labellar rods are united by a tough membrane.

The *Teeth* (Plate III, Figs. 9 and 10) resemble rose thorns in shape except that the apex is blunt, and the borders serrated near the apex. They are arranged side by side in the antero-posterior axis of the labellum, arising from the internal wall by expanded bases which lie immediately below the lower end of the labellar rod. Their pointed ends project downwards in the lower end of the anterior groove. The two middle teeth are larger than the other two, and are inserted a little higher up, so that the upper limit of the bases of the four teeth shows a curved contour, corresponding to the cup-shaped end of the labellar rod. The short interval between the bases of the teeth and the labellar rod is occupied by a band of strong fibrous tissue, which serves to retain them in position.

The *Serrated blades* (Plate III, Fig. 9) are minute leaf-like organs with deeply serrated margins, which lie below the teeth. Each blade is a narrow lanceolate slip of chitin, about 20 μ long by 5 broad, and with about seven serrations on each margin, each incision going nearly to the middle line. They are arranged as follows. There are ten tufts consisting of five or six blades each, the blades arising at different levels and being superimposed. Each two tufts are carried on a common bifurcated stalk, which arises between the teeth at the level of the upper limit of their bases, and bifurcates at the lower limit. The tufts arising from each common stalk diverge from one another below the teeth, and turn upwards superficial to the pseudo-tracheæ. The whole of the blades are thus collected into twenty bunches, ten on each side, all of which turn outwards at the orifice of the labella, forming a sort of brush at the tip of the proboscis.

Other Structures.—In addition to the teeth and serrated blades there are certain minor structures to be noted. On the stalk of each of the serrated blades there are three pairs of short broad spines (Plate III, Fig. 11) which project downwards and slightly forwards. At the point of bifurcation each stalk bears a pair of leaf-like scales, resembling the serrated scales, but having an entire margin and a granular surface.

The *Muscles of the Haustellum* (Figs. 17, 18 and 19) are well developed, and fill up the cavity of the labium. Their main function is to bring the biting apparatus into action.

The *Extensors of the Labellar Rods* (*M′*) arise from the sides of the keel of the labial gutter, and run directly downwards, occupying the middle area of the theca. They are inserted into the posterior third of the labellar rods.

The *Retractors of the* Furca (*M″*) arise from the sides of the theca throughout its extent, and from the thickened chitin at its upper end. The upper fibres run downwards, the lower ones obliquely downwards and inwards to the furca, and are inserted along its upper border and into the tuberosities at the end of its lateral arms.

In addition to these muscles there is a small bundle of fibres arising in the upper part of the theca which pass downwards on either side of the labial gutter, in contact with the membraneous anterior surface of the haustellum. These are inserted in the membrane, some distance above the theca, and probably act as accessory retractors.

Cellular Structures.—The membraneous and chitinous walls of the proboscis are lined throughout by an indefinite layer of the small round cells, the hypodermis. In certain regions, chiefly on the posterior surface of the labial gutter and at the bases of the teeth, this layer is replaced by a definite row of cubical chitinogenous cells, usually separated from the pigmented chitin by a layer of fibrous non-chitinized tissue. This fibrous layer is very distinct at the lower end of the labial gutter.

In sections of the labella there is, if the organ was in the extended position, a considerable interval between the cellular walls on each side. This space represents the hæmatocœl. It has no definite boundaries, being, strictly speaking, an intercellular space. It is in this space that the blood collects when the labella are distended.

The *Labial Salivary Gland* resembles that of *Musca.* It lies behind the lower end of the labial gutter, and is enclosed in a thin membraneous capsule. It consists of large granular uninucleated cells, round or oval in shape, each containing a large vacuole with a chitinous lining. The ducts leading out of these cells have not been traced.

The *Tracheæ* in the haustellum are continuations of the air sacs in the rostrum. There are two small lateral tracheæ of the ordinary type, lying among the muscles and sending small branches to them and to the labial salivary gland. In the labella there are only a few very small trachea in the external walls.

The Mechanism of the Proboscis.

As has already been stated, *Philæmatomyia* possibly feeds both on dung and on blood, and the structure and mechanism of its proboscis are adapted to both these methods of feeding. So far as the first is concerned, there are no notable differences between this fly and the house fly. The proboscis is extended chiefly by the distension of the large air sacs in the rostrum, and by the contraction of the extensor muscles of the haustellum. The oral lobes are distended by blood, and the fluid sucked up the pseudo-tracheal channels. The mechanism of extension can be readily demonstrated in a freshly-killed insect, in which the proboscis is withdrawn, by laying it on a slide and compressing the front of the head, above the lunule, with a pair of needles. The rostrum at once distends and shoots out from the under surface of the head, and the haustellum straightens itself on the rostrum. The labella are then erected, and can be seen to fill up with a yellowish fluid, which pushes out the pseudo-tracheal membrane of the oral surface, and renders the pseudo-trachea visible. That it is fluid and not air which distends the oral lobes is readily shewn by continuing the pressure: the tracheæ can then be ruptured, and small bubbles of air collect in the fluid in the labella, floating to whichever surface happens to be uppermost. By further pressure on the rostrum from above downwards one can sometimes rupture the pseudo-tracheal membrane; the labella then collapse and a small drop of fluid escapes.

The labella when extended for use are converted into a bag filled with fluid. The upper portion of the bag, formed by the external walls, is stiffened by the chitinous plates to give a certain amount of rigidity to the organ; the lower part, limited by the flexible pseudo-tracheal membrane, is readily adapted to the surface on which the fly is feeding, the pseudo-tracheal channels being kept intact by the chitinous rings, and opened out as the membrane is stretched.

The proboscis is withdrawn by the contraction of the retractor muscles in the haustellum, and by the relaxation of the tension in the air sacs. The folding of the labella on the haustellum appears to be brought about by the elasticity of the membraneous walls, which, when the air sacs are no longer distended, and the muscles in the labium relaxed, drives out the blood.

Before discussing the mechanism by which the insect obtains blood it is necessary to consider the position of the labella, relative to the labium, in the open and closed positions. When the labella are not in use, the oral surfaces are contracted and in contact with one another, the lower limit of the organ being formed by the scaly border of the external surface. The labella are rotated backwards, the heart-shaped sclerite in the posterior surface coming to lie in contact with the posterior surface of the theca. The labellar rods rotate backwards on the fixed point provided by the attachment of their tubercles to the end of the labial gutter, carrying the teeth and the serrated blades with them. The rods continue to lie in the long axis of the labella as they are turned backwards, so that, when the labella are closed, the upper ends of the rods project forwards and slightly downwards.

The method by which the wound is made is best studied by the dissection of freshly killed flies, the actions of the muscles being tested by pulling on them with a needle. The anterior or mesial sets are found to erect the labellar rods and to bring them into line with the labial gutter. The posterior muscles pull the furca upwards, and so exercise a tension on the labellar walls to which the furca is so intimately attached, pulling the pseudo-tracheal membrane away from the teeth, and by traction on the membrane to which they are attached rotating them into a horizontal plane. When this occurs their cutting edges are turned upwards. What appears to occur when the fly commences to feed is this. The labellar rods are erected and the tip of the proboscis pressed against the skin of the host with the teeth in the closed position ; the labellar rods being fixed in this position by their muscles, the furca and the walls of the labella are pulled upwards so that the pseudo-tracheal membrane is drawn away from the teeth, which by a continuation of the traction are rotated through a right angle into a horizontal plane, their cutting edges being pressed against the skin of the host. This is repeated with very great rapidity, and imparts to the head of the fly a vibratory motion which can often be observed at the commencement of feeding. At each successive contraction the teeth are thrust a little further into the skin, until eventually blood is reached. The action is rather a scarification than "biting." Whether the blood once it begins to flow is sucked up through the medium of the pseudo-tracheal membrane or whether it goes directly into the mouth it is difficult to say, but I am inclined to think that the membrane is drawn entirely out of the way, and that its function as a filter is performed by the remarkable serrated blades. These structures, like the teeth, are attached to the membrane, and must be drawn upwards in the same way, but in advance of them, and will therefore sweep away the cellular debris produced by the teeth, each time they are drawn through the wound, and will prevent the ingress of large particles into the mouth. When the teeth are drawn up the axial apophysis becomes the lowest part of the proboscis, and projects beyond the teeth ; it probably materially assists in the cutting operations by fixing the distal ends of the labellar rods.

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Explanation of Reference Letters.

ap.	Labral apodeme.
a. p. h.	Anterior plate of pharynx.
a. pm.	Anterior membraneous wall of pharynx.
ax. p.	Axial apophysis.
c.	Chitin of head capsule.
d. ph.	Dilator muscle pharynx.
ds, ds′, ds″.	The sclerites of the external wall.
ex. h.	Extensor muscle of haustellum.
f. h.	Flexor do. do.
fr.	Furca.
fu.	Fulcrum.
hy.	Hypopharynx.
j.	Joint on the fork of the theca.
l. d. m.	Dilator muscle of labrum-epipharynx.
l. ep.	Labrum-epipharynx.
l. g.	Labial gutter.
l. gl.	Labial salivary gland.
l. k.	Keel of the labial gutter.
l. r.	Labellar rod.
l. s. d.	Lateral sclerite of pharynx.
l. t.	Fibres from the lateral margins of the theca.
m.	Membraneous portion of the wall of the proboscis.
m′.	Extensor muscle of the labellar rods.
m″.	Retractors of the furca.
m″′.	Accessory retractors.

p.	Palp.
pt.	Pseudo-trachea.
ptm.	Pseudo-tracheal membrane.
r.	Spines of the stalk of the serrated blades.
r′.	Rod like hairs.
r. h.	Retractor muscles of the haustellum.
s.	Stalk of the serrated blades.
s′.	Leaf-like scales.
s″.	Serrated blades.
s. d.	Salivary duct.
t.	Teeth.
t. f.	Fork of the theca.
th.	Theca.
tp.	Expanded end of labellar rod forming a socket for the teeth.
tr.	Trachea.

Plate I.

Fig. 1.—The proboscis in profile, drawn from a potash preparation. The labella are in a semi-erected position; when fully erected the labellar rods come into line with the labial gutter. × 33.

Plate II.

Fig. 2.—The hypopharynx, torn from the base of the labial gutter. × 44.

Fig. 3.—The labrum-epipharynx, posterior surface. × 44.

Fig. 4.—The labellar rods and axial apophysis as seen from the front. The distal end is expanded and ill-defined, forming a cup for the reception of the teeth. × 80 about.

Fig. 5.—The fork at the lower end of the theca. × 44.

Fig. 6.—The furca; the ends of the thecal fork ride in the notches at the end of the furca. × 44.

Fig. 7.—The distal end of the labial gutter. × 250.

Fig. 8.—The edge of the external wall of the labella. × 250.

Plate III.

Fig. 9.—The teeth and connected structures of one side, as seen from the inner side of the labellum. Note how the bases of the teeth fit against the expanded end of the labellar rod. × 250.

Fig. 10.—One of the lateral teeth seen in profile, detached. × 250.

Fig. 11.—The spines on the stalk of the blades (r. in figure 10). Very highly magnified.

Fig. 12.—One of the small rod-like hairs. r′ in figure 10. Very highly magnified.

Fig. 17.—Section through the haustellum in the region of the keel. Note the concave surface formed by the labial gutter and the hypopharynx, on which the labrum-epipharynx rests. × 250.

Fig. 18.—Section at the upper end of the haustellum. The labrum-epipharynx has here become a closed canal; the keel of the labial gutter is approaching the theca. × 250. The tracheæ are large and shew an irregular contour, indicating that they are capable of distension.

Plate IV.

Fig. 13.—Oblique section through the labella and lower end of the labium. The labella were in a semi-erected position in this preparation, so that the end of the labial gutter and the teeth appear in the same section. The pseudo-tracheal channels are seen turned inwards on the internal surfaces of the labellæ, beneath the serrated blades. The appearance of a space below the pseudo-trachæ is due to the presence of an indentation on the posterior surface of the labella. Note also the fibrous tissue separating the labial gutter from the subjacent chitinogenous cells. × 250.

Fig. 14.—Oblique section through the lower end of the labium and the labella; from the same series as Fig. 13, but a little higher up. The pseudo-tracheæ, now only one on each side, are seen terminating in a duct with a cellular lining, cut here almost in longitudinal section. The labrum-epipharynx and hypopharynx are cut in section at their tip. × 250.

Fig. 15.—Transverse section through the lower end of the labial gutter. × 250.

Fig. 16.—Transverse section through the lower end of the labial gutter, in the region of labial salivary gland. Note the thickness of the walls of the labrum-epipharynx, and the incurvation of the edges of its groove. × 250.

Fig. 20.—Transverse section of the lower end of the pharynx in the rostrum. Note the membraneous anterior wall, and the salivary duct, lying in a mass of cells and inter-cellular fibres. The wall of the duct is not chitinized. × 250.

Plate V.

Fig. 19.—Transverse section through the labium at its extreme upper end. The labial gutter and hypopharynx are fused in a dense mass of pigmented chitin, which is pierced by the salivary duct. The labrum-epipharynx is adherent to the central chitinous mass. × 250.

Fig. 21.—Transverse section through the lower end of the pharynx in the rostrum, showing the lateral sclerites and the mass of cells in which the salivary duct is embedded. × 250.

Fig. 22.—Oblique section through the rostrum when partially withdrawn beneath the head. Note the infolding of the lax membrane, and the wrinkled contour of the contracted air sacs (tr.). The salivary duct is here definitely chitinized. × 250.

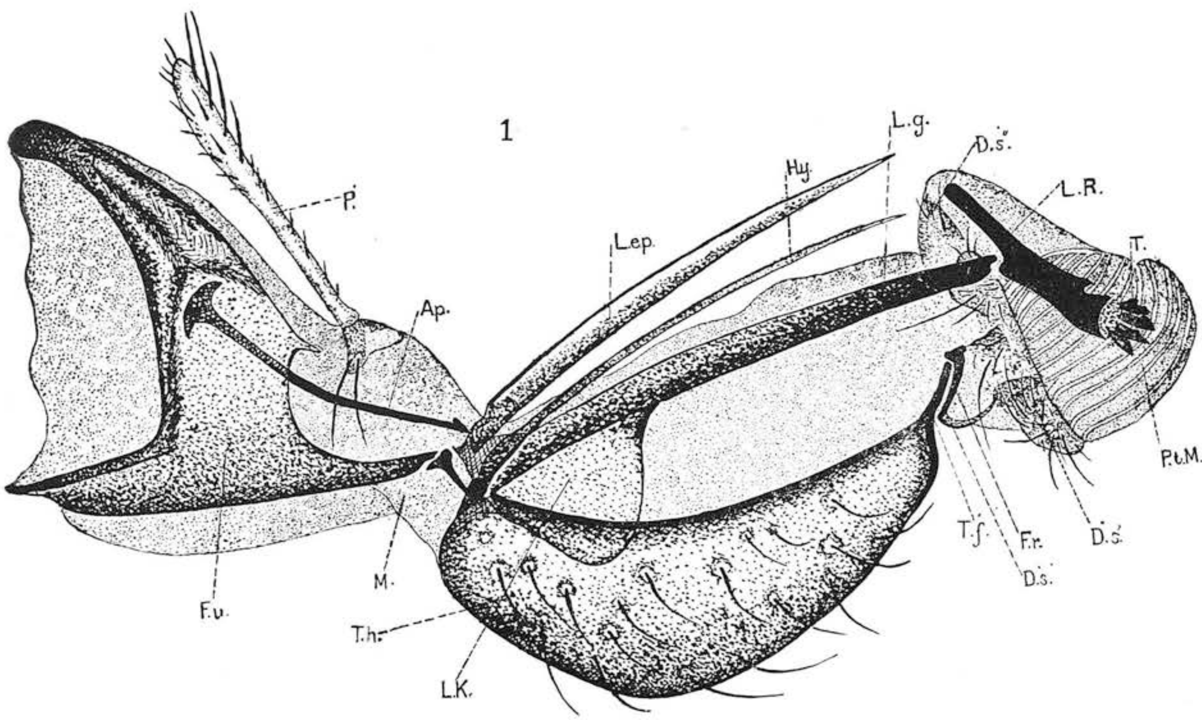

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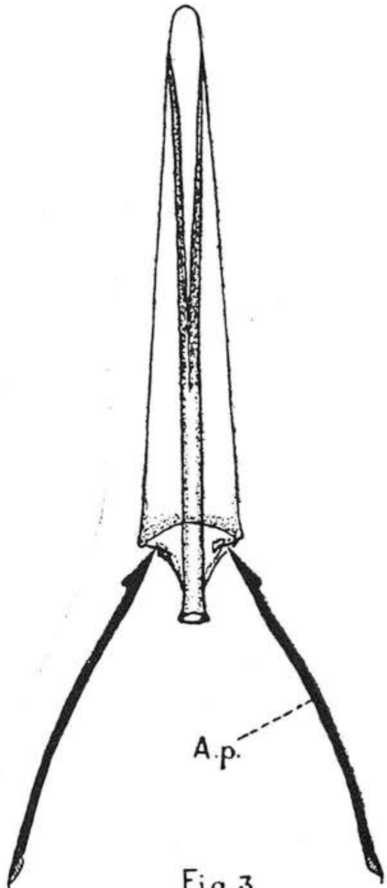
Fig. 2.



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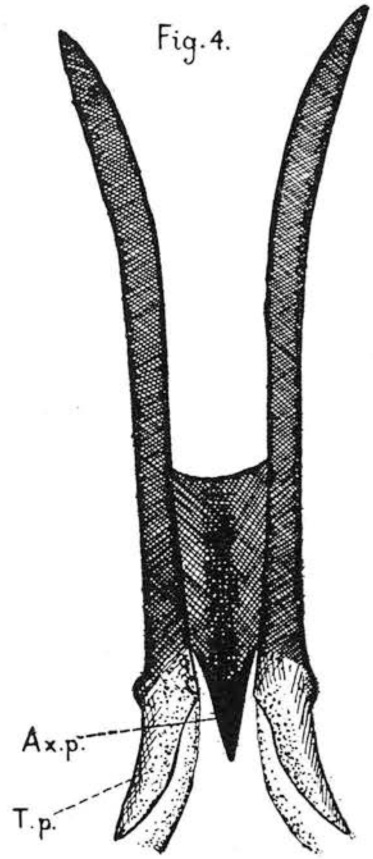

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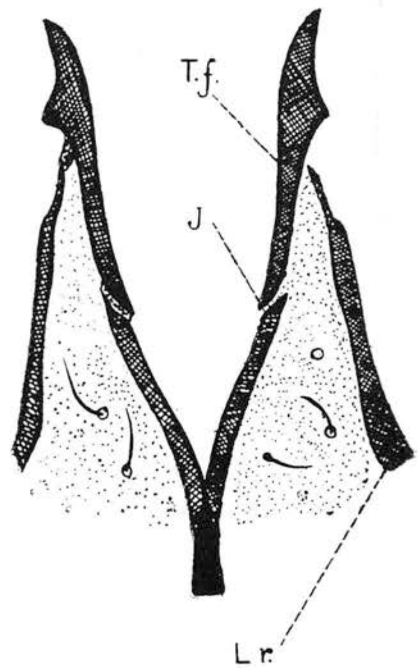

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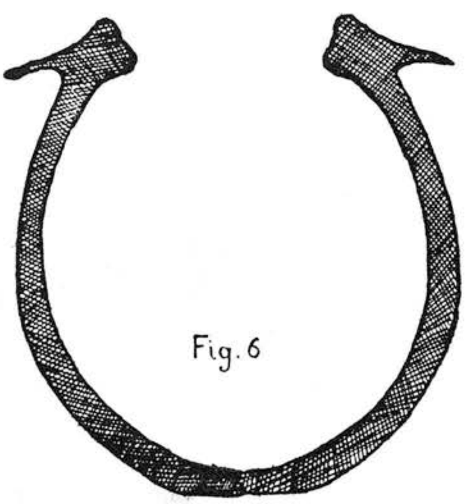

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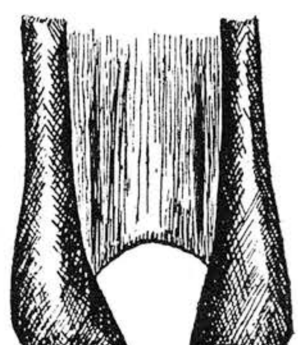

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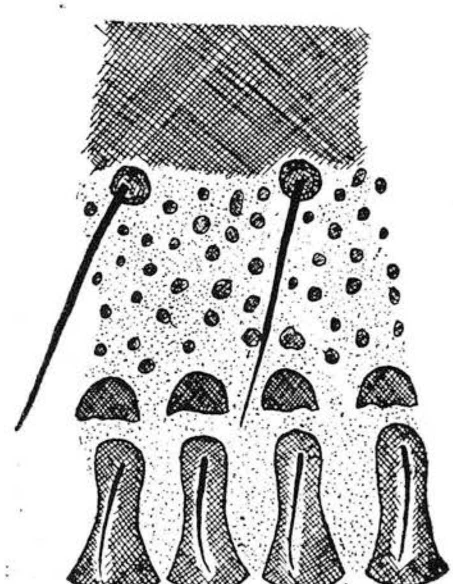

Fig. 8.

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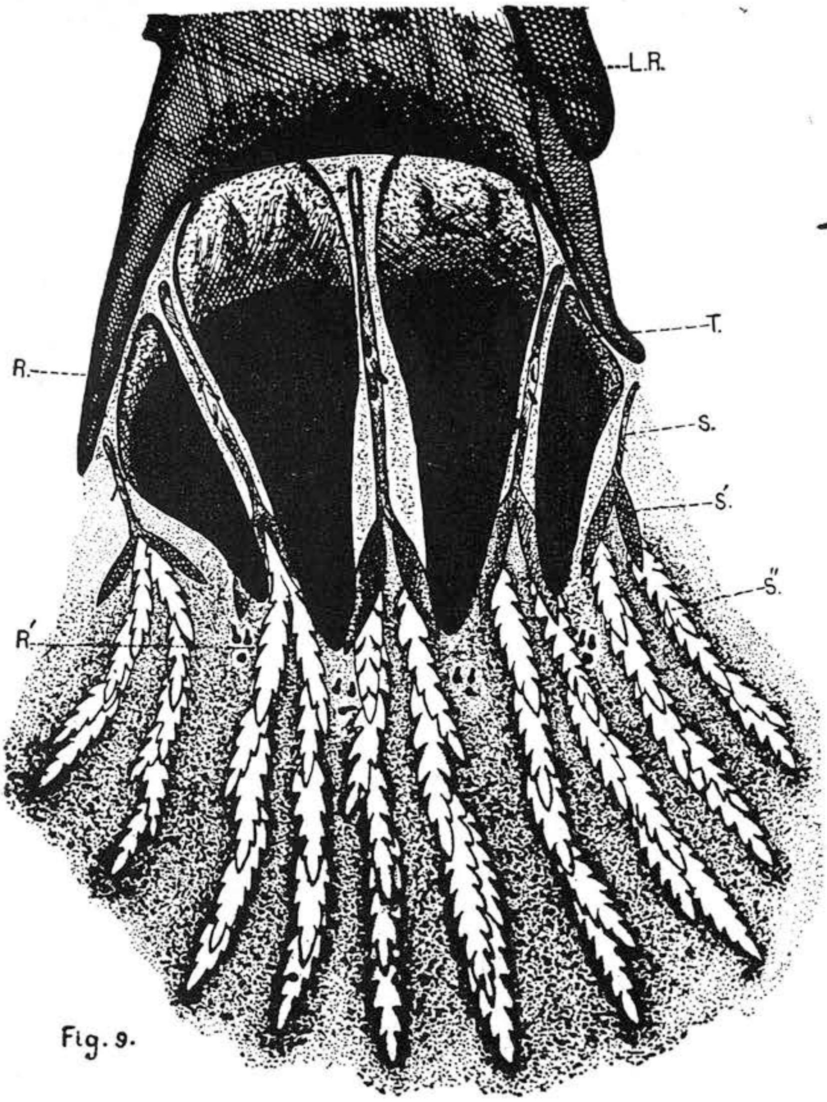
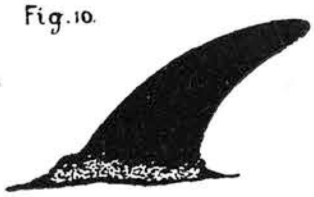


Fig. 9.

Fig. 10.



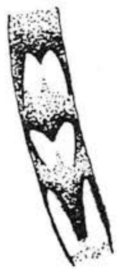


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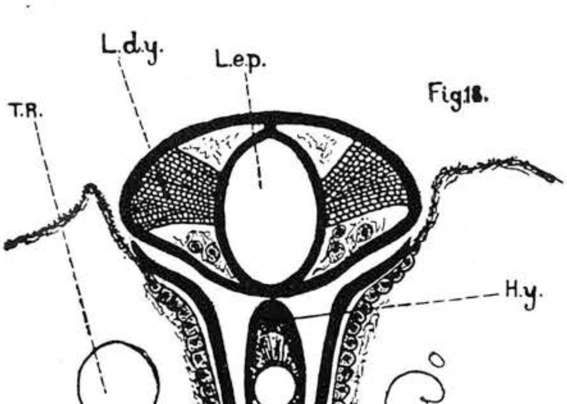
Fig. 12.



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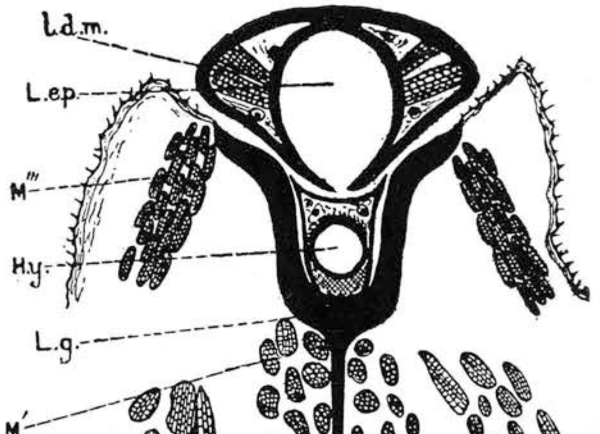

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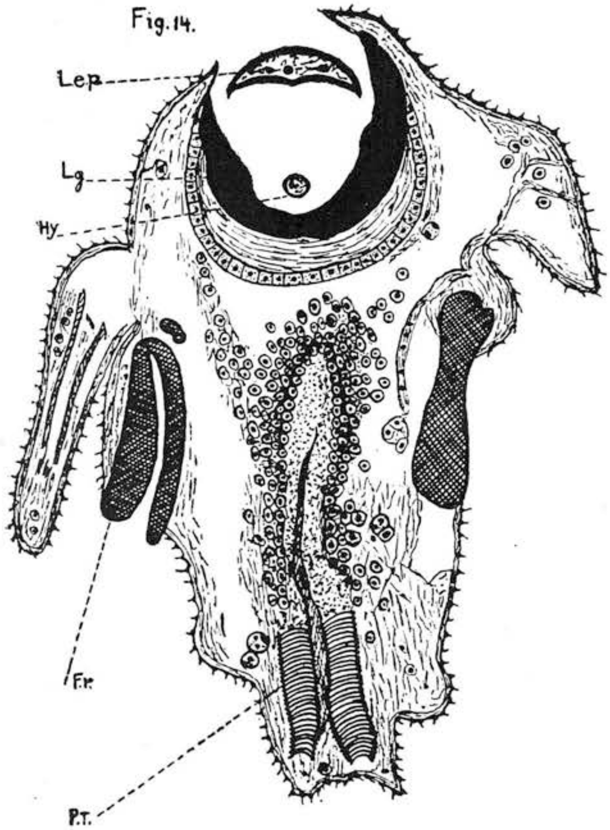
Fig. 14.



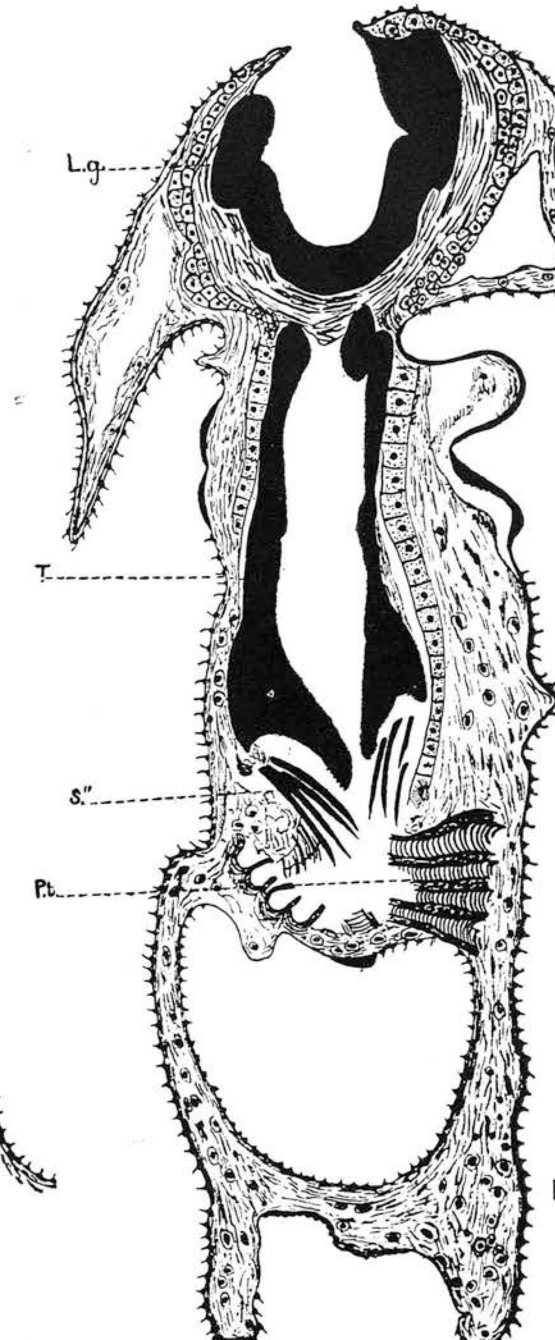
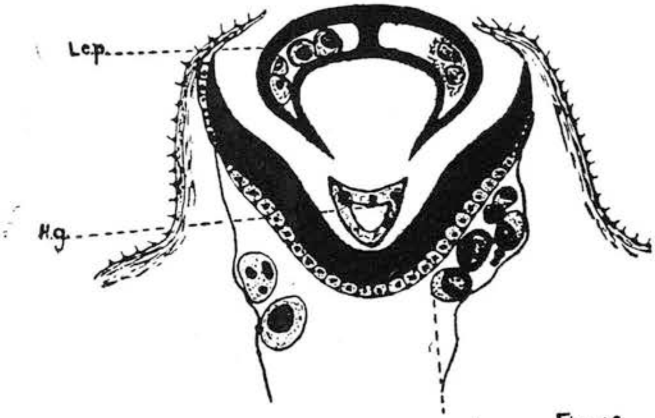


Fig. 13



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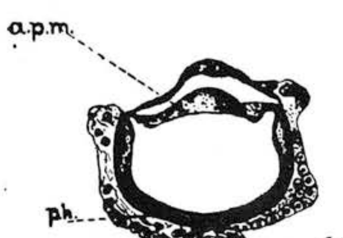

Fig. 20

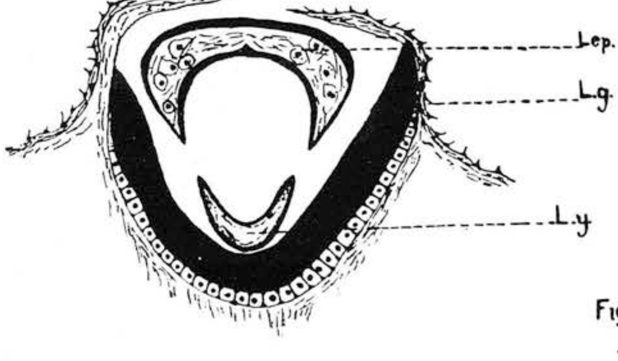

Fig 15

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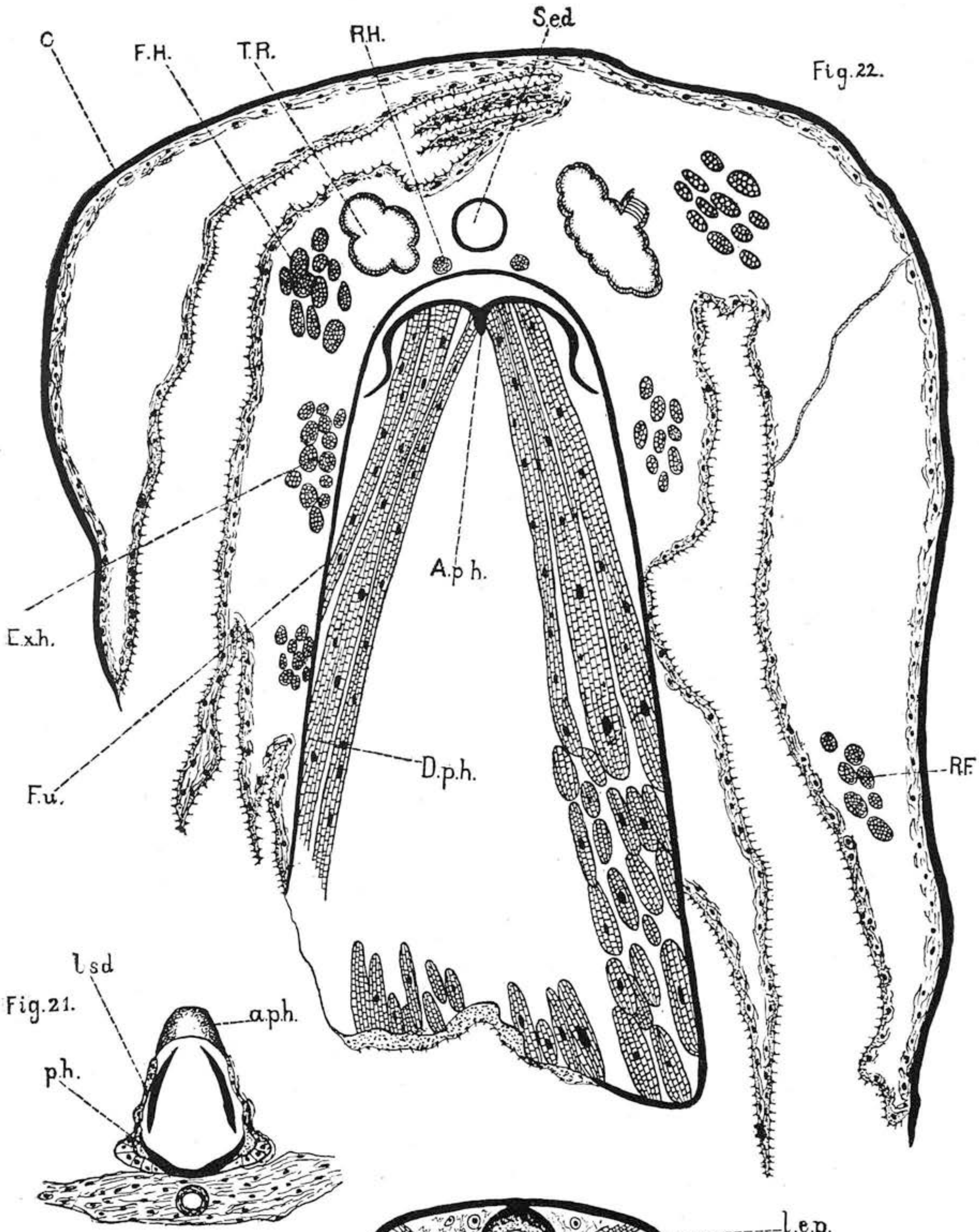

Fig. 22.

Fig. 21.

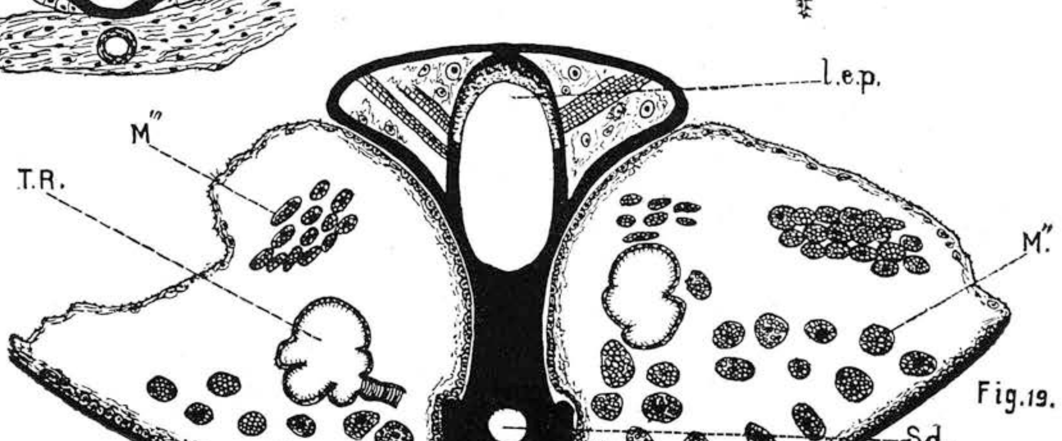

Fig. 19.

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Studies on the Mouth Parts and Sucking Apparatus of the Blood-Sucking Diptera.

No. 2.

Some Observations on the Morphology and Mechanism of the Parts in the Orthorrapha.

SINCE the discovery of the practical importance of the blood-sucking Diptera the attention of investigators has to a large extent been concentrated on the study of their binomics, distribution and classification, to the neglect of the problems which attracted the older entomologists, and the study of the homology of the parts and of the mechanism by which they act have received little attention. Much of this neglect is due, no doubt, to the fact that so large a proportion of the recent work has been done by medical men and others to whom entomology was of interest mainly as an applied science, and these problems, fascinating though they are to the zoologist, have no apparent connection with the rôle played by insects in the transmission of disease. It is not unnatural that such a restricted point of view should have led to misconceptions, and more especially since the mosquito, which, on account of its great economic importance, has been more studied than all the rest of the group together, happens to be a very highly specialised form. Moreover, most of the common mosquitoes are small and delicate flies, and are not at all easy to dissect, and it is not to be wondered at that many points in their anatomy and physiology should have been missed, when a comparative study was not attempted. In such a compact natural group as the Diptera, in which, although the variation in form is very great, the general principles of structure are maintained throughout, questions of the homology and of mechanism are intimately bound up with one another, and it is of the first importance to compare the separate parts in one fly with those, often markedly different in appearance, which fulfil the same function in the others. The comparative method, indeed, is not only the one by which the more strictly zoological side of the question is to be attacked, but it is of great assistance in elucidating the physiology of the proboscis, a matter of importance to the parasitologist.

I do not propose to attempt in the following pages any comprehensive review of the subject, not having at hand the necessary literature, but to discuss some of the more important points of structure and their bearing on the mechanism of the proboscis. At the outset it will be well to emphaize the fact that the process by which a blood-sucking fly obtains blood from the host is essentially a mechanical one, in the sense that it is governed by the ordinary principles of muscle movement and of physics. Any explanation of the process which is not in accord with the anatomy of the parts, or which takes no account of ordinary physical laws, must be rejected. One may add, that any hypothesis which would attribute to an organ in one fly a function which it does not possess in another is to be regarded with suspicion, and that due regard is to be given to the observed habits of the insect, when the size of the fly and other circumstances permit of observation. A critical examination of the method of feeding with these points in mind will show that the subject is by no means so simple as at first appears, and that many of the statements current, especially with regard to the mosquito, are vague and inaccurate.

It will be convenient to discuss the subject in two parts, the making of the wound and the sucking up of the blood.

The Biting Apparatus and its Mechanism.

The biting apparatus in the orthorraphic flies is ordinarily described as consisting of the paired mandibles and maxillæ, the labrum-epipharynx, and the hypopharynx. The orthorraphic biting flies are sharply distinguished from those of the Muscid group by the fact that the labium does not enter into the wound at all, functioning mainly as a sheath for the other parts.

The first question which attracts one's attention is as to the nature and origin of the force by which the "piercing stylets" are driven into the skin of the host. Most accounts of the mouth parts of the mosquito simply state that the piercing parts are thrust into the skin, without attempting to explain how this is done, though Nuttall and Shipley go so far as to say that the mandibles enter the skin when the labrum is thrust in, by means of the "same elastic force which induces the sharpened end of a piece of whale-bone to pierce a soft body if the other end is pushed towards the surface," and they note the presence of muscles for the retraction and protrusion of the maxillæ. Annett, Dutton and Elliot state definitely that "the piercing of the skin is brought about by muscular force directed from the body of the insect, the muscles attached to the bases of the stylets serving to keep them rigid." Actual observation does not help us much in the case of any of these flies, for all the parts concerned are small and concealed by the labium. The position of the fly while in the act of feeding is, however, of some importance. If it were simply a question of *vis a tergo*, then one would expect that the piercing parts would be brought into line with the long axis of the body, for it is obvious that the muscles concerned would act at a great mechanical disadvantage if they had to propagate a force through an angle. But this does not occur as a general rule. The only striking case in point is that of *Hæmatopota*, which when in the act of feeding raises the posterior part of the body so much that it makes with the surface of the skin an angle of nearly half a right angle. The posterior surface of the head and the anterior surface of the prothorax are moulded to fit one another, and, as the neck is a very short one, it is probable that some force at least can be propagated from the thorax, though not, it should be noted, through the neck. But even in this case it is improbable that the force from behind enters largely into the mechanism, for in *Tabanus* and the allied genera, although the mouth parts are almost identical, the position assumed by the fly is such that the body is parallel with the skin and the proboscis perpendicular to it. *Ceratopogon* assumes a position similar to that of *Hæmatopota*, but as the proboscis is perpendicular to the long axis of the body the manœuvre cannot possibly bring the two into the same straight line. In *Anopheles* the proboscis is directed straight forwards in the position of rest, and to reach the skin at all the insect has to raise the hind end of the body and to depress the proboscis, thus doing away with the apparent advantage of its attitude; as a matter of fact the proboscis is bent downwards very nearly to a right angle, as shown in Nuttal and Shipley's admirable drawing.

The attitude assumed by the fly when feeding therefore renders the operation of a force propagated from the thorax unlikely. We have next to consider how far the anatomical arrangements are adapted for such a force. So far as the muscles are concerned the question is a simple one. In all cases the feet are provided with claws admirably adapted to enable the fly to take a firm hold on the skin, and it might be supposed that the extension of the joints of the middle and hind legs would result in a forward thrust of the thorax and head of the fly. The ends of the piercing organs being then applied to the skin, they must enter or else bend forward, and we know that the latter, at least in the case of the mosquito, where the piercing stylets are readily seen when they are separated from the retracted labium, does not occur: in any case mere bending would not be of advantage, unless we adopt the view noted above for the mandibles, that the potential force produced by their flexion is used up in piercing the skin. A moment's consideration will show that this explanation will not suffice, either for the mandibles alone or for the piercing parts as a whole, for it would follow that the cutting edges of the blades must be directed forwards, while as a matter of fact those stylets which have cutting edges at all have them directed in the lateral plane.

Bending and elastic rebound are therefore out of the question for any of the mouth parts. There remains the simple thrust, which is rendered unlikely by the attitude of the fly. But a forward thrust cannot be propagated without some rigid structure through which it can act, and in this case the necessary rigidity would have to be ensured by the neck. As a matter of fact the neck of these flies is not at all adapted for such a purpose. Its length varies a good deal in the different forms, being very short in the *Tabanidæ*, and comparatively long in the mosquito. But in no case does it possess an amount of rigidity sufficient to permit of the propagation of a force capable of driving the stylets into the skin. By far the greatest portion of the wall of the neck consists of a soft and flexible membrane, attached in front to the borders of the occipital foramen and behind to the opening into the thorax. In this there are developed thin plates of chitin, one on each side, usually free from one another, but approaching in the middle line ventrally. These cervical sclerites are loosely articulated with the epicranium in front, but in none of the species which I have examined do they take part in a definite articulation with the thorax. In the *Tabanidæ* the cervical sclerites are displaced backwards out of the neck, and are found at the sides of the thoracic inlet, two of the three pairs being entirely free from chitinous attachments. The cervical sclerites, in fact, are mere strengthenings of the integument of the neck, and fill no other functions than those of affording additional support in the cases where the neck is long, and of providing attachments for the muscles which move the head. The neck is a soft canal, capable of distension as blood flows through the œsophagus, a point well shown in Nuttall and Shipley's drawing of the mosquito in the act of feeding.

The motive force must then lie in the head or the neck. The latter may be disposed of in a word or two. The muscles it contains are very small, and are merely the representatives in this region of the fibres which connect adjacent segments elsewhere in the insect body. Their function can be no more than to move the head on the neck, the looseness of the membraneous wall permitting of a certain amount of retraction and rotation, easily seen when a mosquito is beginning to feed and is searching for a suitable spot for the puncture. It is impossible to conceive of any arrangement of muscles by which the neck could be extended in such a way as to drive the mouth parts into the wound, nor can any such muscles be found by section or dissection.

The argument brings us to the conclusion that the muscles which make the wound are situated in the head of the fly. Before going further it will be well to consider for a moment the origin of the several organs ordinarily described as the piercing stylets. The *labrum-epipharynx* (Text-figure 2, page 27) is the result of the fusion of the labrum, which is an extension downwards of the clypeus, and in other insects connected with it by a freely moveable joint enabling it to act as a true upper lip, with the epipharynx, an outgrowth of the stomodæum, and in these flies easily traced upwards to its termination in the first part of the sucking apparatus. The fusion between them is not so close that the two become welded into one organ, for the epipharynx in all forms retains the shape of a nearly closed canal ; the labrum may, as in the mosquito, adapt itself to the shape of the epipharynx, or it may remain flattened and blade-like. There is in all the forms which I have examined evidence of a joint between the labrum and the clypeus, at the situation of the corresponding joint in insects such as the cockroach, which have a freely moveable upper lip, and in the region of this joint the labrum and epipharynx are much less firmly united than elsewhere. The *hypopharynx* is usually described as an outgrowth from the lower lamina of the stomodæum, corresponding to the epipharynx, but it would be more accurate to describe it as consisting of two laminæ, the upper one of which is derived from the stomodæum, the lower from the labium, the two enclosing between them the salivary duct. The distinction between the two laminæ can be made out by dissection in the larger *Tabanidæ*, in which it is quite easy to pull away the lower lamina still attached to the base of labium, and to leave the upper lamina, along with the salivary duct, still attached to the first sucking chamber. In all these biting flies, which must of necessity introduce the saliva into the wound, the lower lamina of the hypopharynx is completely separated from the labium, but in very nearly allied forms, and even in the males which do not suck blood, as in the case of the mosquito, the lower lamina remains attached to the labium. The separation is evidently due merely to the necessity of introducing the saliva into a comparatively deep wound, into which the labium does not enter.

The *mandibles* (Text-figure 1, page 13) represent the appendages of the fourth segment of the insect head, and are homologous with those of other insects, such as the beetles, in which they act as cutting and tearing weapons. Similarly the *maxillæ* correspond to the appendages bearing the same name, but with much more obvious functions, in other arthropods. They are the only appendages in the *Nematocera* which retain at all closely the primitive form.

Now, to repeat the statement made in the opening paragraph, we should regard with suspicion the supposed function of the labrum-epipharynx and hypopharynx as piercing organs, if for no other reason that they are homologous with structures which do not ordinarily possess such a function, whereas we would confidently expect the mandibles and maxillæ to play a prominent part in the making of the wound. It is now necessary to examine the musculature and armature of these organs, to see how far they are consistent with this view.

There is only one muscle attached to the labrum-epipharynx, and this is found in the same place as that which in the cockroach lifts up the upper lip.

It is conspicuous in *Tabanus*, in which it has been figured by Meinert and Hansen, and occurs also in the mosquito, and is very clearly shown in Nuttall and Shipley's drawings. It lies immediately behind the articulation between the labrum and the clypeus, arising from the internal surface of the latter and finding attachment to the proximal extremity of the labrum at the point where it is only loosely attached to the epipharynx; it is difficult to decide its exact point of insertion, or its function. Meinert regarded it as a depressor in *Tabanus*, while Nuttall and Shipley describe it in *Anopheles* as an elevator. Whatever its function may be, one thing is clear, that it cannot act as an extensor of the labrum. It is of constant occurrence in the Nematocera.

The hypopharynx has no muscle attached directly to it, so we have to pass further back, to the sucking chambers to which the epipharynx and the hypopharynx are so intimately attached. Here we find another proof, incidentally, that the forward thrust of the body of the fly cannot act as a motive power, as far as these two organs are concerned, for in no member of the group is there any chitinous connection between the wall of the head capsule and the sucking apparatus. Force transmitted to the head from behind can only be propagated to the labrum, and through it to the epipharynx by the attachment of the labrum to the clypeus, and to the hypopharynx by means of its loose basal attachment at the proximal end of the labium. There are, however, certain muscles attached to the sucking chambers which undoubtedly have the power of raising and lowering them, and with them the stylets which arise from them. These muscles can only be made out as definite bundles in *Tabanus*, in which they have been figured by Meinert. There are two sets, one of which is inserted at the upper end of the first sucking chamber, and by pulling in an upward direction retracts the chamber and with it the labrum-epipharynx and hypopharynx; the second set are attached about the same place but pull in a downward direction, and will therefore thrust the stylets into the wound. In *Simulium* the retractor muscles are present, as figured by Meinert, but the protractors do not exist as a distinct bundle. In *Anopheles* the first sucking chamber is a very small one, and the protractor and retractor muscles are not distinguishable. It is possible that some of the fibres of the muscle termed by Nuttall and Shipley the elevator of the palate may act as protractors and retractors to a slight extent.

Whatever be the true function of these muscles it is evident that they are not essential to the act of insertion of the proboscis, for they do not occur in an equal degree of development throughout the group, and are not to be distinguished in the mosquito, the piercing apparatus of which is at least as efficient as that of any of the other flies. In any case, it is almost inconceivable that such small muscles, acting at such a manifest disadvantage, could drive the labrum-epipharynx into the skin, even in the case of *Tabanus*. The extent of their action in protracting and retracting the labrum-epipharynx is limited to the amount of bending which can take place in the labrum at that portion of its upper end which is only loosely attached to the epipharynx. The utmost capacity of the protractor muscles can only suffice to stretch the proximal end of the labrum until it is in the same straight line as and in contact with the epipharynx. The amount of retraction is less easy to define, for it is limited only by the loose joint between the labrum and the clypeus, and there is nothing to prevent the first chamber, which in all cases is connected to the second by a membraneous canal, from being drawn up within the head, except the muscles which support it and connect it with the wall of the head capsule. It will be necessary to refer to this point later on, but for the present it will be sufficient to state, that the anatomy of the parts indicates that though a certain amount of retraction and protraction of the first sucking chamber can take place, the action is not a powerful one, and the limit of extension is such that the distal ends of the labrum-epipharynx and hypopharynx cannot extend further than the level of the ends of the mandibles and maxillæ. The fact that protractor and retractor muscles cannot be distinguished in the highly efficient mouth parts of the mosquito is a strong argument against their taking any prominent part in the making of the wound in the closely allied flies.

One other point occurs to one in this connection. No matter what the armature of the tip of the labrum-epipharynx may be, and as will be shown later it is ill adapted for piercing, it would work at a very great mechanical disadvantage if actuated by a simple forward thrust, without any lateral movement or rotation. If one attempted to drive a carpenter's augur through a piece of wood without the usual rotatory movement, the amount of force required would be infinitely greater than it normally is. Rotation of the labrum-epipharynx and hypopharynx is of course anatomically impossible.

It will be convenient to sum up the argument at this point. The driving force by which the piercing parts are inserted into the skin is not derived from the muscles of the legs or thorax, because the neck is too flexible and slender to transmit such a force. It is not to be found in the muscles of the neck, for these are sufficient only to move the head on the thorax in the adjustment of the proboscis to a position favourable for feeding, and there is no arrangement by which the neck could be forcibly extended so as to drive the stylets into the skin. The position of the proboscis in relation to the long axis of the body is a most unfavourable one for the exercise of any thrust from behind, as such a thrust would tend to bend the proboscis backwards towards the thorax.

The ingenious suggestion of Nuttall and Shipley that the mandibles enter the skin by means of an elastic rebound from a bent position will not hold for either the mandibles or the other stylets, for the cutting edges are invariably directed laterally, and moreover in most of these forms the stylets are flattened from side to side. The labrum-epipharynx and hypopharynx are capable of a certain amount of protraction and retraction, but the movement of protraction is limited to the amount necessary to bring their distal ends to the level of the tipe of the mandibles and maxillæ, and is in any case not a powerful movement, nor does it occur with such uniformity, at least as regards the degree of development of the muscles concerned, that one is justified in regarding it as an essential factor in the making of the wound.

There remain for consideration the mandibles and maxillæ, true appendages, homologous with those which are used by other arthropods to obtain their food, and those which, on general zoological principles, one would expect to find functioning as cutting organs.

In the mouth parts of insects there are many wonderful contrivances elaborated by nature to achieve her end, but nothing more remarkable than the adaptation of these appendages to their present function. Throughout the group, notwithstanding the individual variations, the mandibles and maxillæ preserve their distinctive character in such a way that one can readily discern in them the resemblance to the cutting and clasping appendages from which they have originated. So close is the resemblance that a general description will apply to any of the forms in the group. The mandibles are flattened and blade-like, terminating in a sharp point, slightly recurved after the manner of a sabre, and armed on the inner edge of the blade with a single row of fine serrations strikingly like those on the edge of a saw. The two mandibles are in the same plane, their inner edges being directed towards one another and almost meeting in the middle line in the position of rest. At the base of the blade the mandible is articulated to the edge of the gena, in a position corresponding to the ginglymus in other insects, and the articulation is such as to permit of an inward and outward movement of the blade, on the pivot formed by the point of attachment. This is very well shown in the larger *Tabanidæ*. The base of the mandible in these forms divides into a pair of stout cornua, the external one of which is articulated to the gena, the internal one free. To each of these cornua muscles are attached, by the contraction of which the mandible is alternately rotated inwards and outwards on its pivot, the muscles attached to the internal cornu acting as adductors of the blade, those attached to the external one as abductors. Now the cutting edge is internal, and this edge is not straight, but curved outwards, so that the motion of adduction does not merely displace the cutting edge inwards, but draws it obliquely through

Slip to be pasted with Scientific Memoir No. 58.

ERRATA.

Title page.—For "M.B." *read* "M.D."

Page 9, line 17.—For "Ashmorth" *read* "Ashworth."

the wound almost at the angle at which one ordinarily uses a knife. The action is very like that of a circular saw acting through a short arc.

With the exception of the mosquitoes, all the members of this group have well developed mandibles, and the variation found in the different forms is remarkably small. In *Tabanus* (figure 4) the serrations are extremely fine, although the blade itself and the edge bearing the serrations are quite strong. In *Simulium* (figure 2) the serrations are much larger and are continued round the tip of the blade to the external border. In *Ceratapogon* (figure 3) they are intermediate in size, and the inner edge of the blade is bent rather abruptly outwards, so that the teeth are directed inwards and forwards, and the point of the blade a blunt one.

In *Phlebotomus* the serrations are a little coarser than those of *Tabanus*, and are more widely separated; the blade is flattened. Newstead states that it is the outer edge which bears the serrations. I have not had the opportunity of making a sufficiently large number of preparations to express an opinion on the point, nor have I been able to consult Grassi's paper on this fly, though, thanks to the kindness of Dr. Ashmorth, I have obtained a copy of his drawings. In these I note that he represents, in a cross section of the proboscis, that the mandibles lie superimposed upon one another between the labrum-epipharynx and the hypopharynx, a most remarkable position for them to occupy, for they render it impossible for these two structures to form a closed food canal. Newstead, who offers no remark on this point, gives a drawing of the labrum-epipharynx and hypopharynx in apposition with one another, without showing the mandibles between them. Great difficulty arises in decided points such as these on account of the small size of the parts and the impossibility of separating the component parts of the proboscis without injuring some of them. In many of my preparations of *Ceratapogon* the serrated edge of the mandible appears to be external, and is in fact external to the edge of the labrum-epipharynx, but this is due to the two mandibles having crossed one another, and what appears to be the external edge of the mandible of the left side is really the internal edge of the one on the right. As already explained the direction of movement of the mandible is inwards and outwards in the lateral plane, and although there is no proof that they normally pass beyond the middle line, there is no reason, anatomical or otherwise, why they should not do so.

The *Culicidæ* show a certain amount of variation in the mandibles and it looks as if they were tending to disappear in that family. On account of the great elongation of the parts in the mosquito the cutting portion of the blade is limited to the distal end, which is slightly expanded. The serrations in *Anopheles* (figure 5) are excessively minute, and can only just be made out with a magnification of a thousand diameters, and in *Culex* it is difficult to be sure that they exist at all, nor is it possible in either case to say whether the serrations are on the outer or the inner side. In the male mosquito the whole appendage is missing. The muscles at the base of the mandible are not recognisible in this form, and one is justified in assuming that the appendage is of much less importance in the mosquito than in the other families. It would be interesting to know if the gradual disappearance of the mandible goes on *pari passu* with other changes in the different genera, and if there are any blood-sucking species in which the female is without mandibles.

The *maxillæ* are even more admirably adapted for the purpose of making a wound than the mandibles. The most remarkable feature about these appendages is the manner in which the primitive arrangement of the joints is maintained. The maxilla of a primitive insect, such as the cockroach, consists of five parts, the lacinia, galea, and palp, external organs, named from within outwards, and the stipes and cardo which are internal. Of these the palp persists and retains its sensory character throughout the Diptera; the galea becomes the cutting blade in the Nematocerous biting flies and the lacinia remains only as a small peg shaped projection at the base of the blade on the inner side. The stipes appears in these forms as a backward continuation of the blade, and passes through the interior of the head cavity in its lower part, external to and below the first part of the sucking apparatus, to a point almost as far back as the occipital foramen. Here it is attached to the wall of the head cavity by the interposition of the cardo, which is always very small and in the case of the smaller and more delicate flies may be absent. The maxilla is capable of movement on the joints between the stipes and the cardo, and between the cardo and the wall of the head capsule, into a small notch in which the cardo is fitted.

This arrangement is best studied in the large *Tabanidæ*. Here the cardo is easily seen as a wedge-shaped rod articulated in a small notch at the edge of the space occupied by the palatal membrane, and the method of action can be readily understood by an examination of the muscles which are attached to the stipes and cardo. As in the case of the mandible, there are two sets, termed by Meinert the adductor and abductor; the former arise from the internal surface of the head capsule near the occipital foramen, and run directly forwards in line with the stipes; the latter run in the opposite direction, arising from the anterior wall of the head capsule in the region of the gena, and are inserted into the cardo. The two sets are therefore antagonistic, and act on the joint between the stipes and the cardo, and on that between the cardo and the wall of the head, in opposite directions. The adductors would be more accurately described as retractors, and the abductors as protectors, for the action of these muscles must be to alternately protract and retract the stipes, and with it the cutting blade.

The armature of the maxillæ presents both a remarkable uniformity in all the flies included in the group, and a remarkable adaptation to the method of action of the muscles. In all cases the type is that of a rasp, on which most of the teeth are directed backwards, so that it cuts mainly when it is retracted. The cutting edge may be on the inner or the outer side, or both edges may be armed; the blade may be straight or a little curved.

Before going further the individual variations in the maxillæ may be noted. In the *Tabanidæ* (figure 10) the blade is stout and roughly quadrilateral, and is armed all round the distal end with strong spines which are only slightly raised from the surface of the blade; these spines are continued a considerable distance down the internal border, but only for a short distance externally. On the external border there is a row of extremely fine and closely set hair-like spines, the distal ones of which are enlarged basally to form regular spines like those on a rose tree. The blade is almost straight from apex to base, and is continued directly into the stipes. In *Simulium* (figure 1) the blade is flattened and triangular, and has down each side a single row of spines similar to those of *Tabanus*, but smaller. In *Ceratapogon* (figure 8) the blade is flattened and at the base is thicker on the external side than internally. Towards the apex the inner side becomes attenuated to a very thin and almost invisible edge, and the blade itself is twisted transversely, so the terminal portion of the internal edge is directed outwards. This terminal portion is armed with a row of extremely minute backwardly directed spines, set on the fine internal edge and somewhat widely separated from one another. In *Phlebotomus* (figure 12) the blade is similarly flattened and bent transversely,* but in this case both edges bear teeth. On one side there are six, all directed backwards and extending to the extreme tip, and on the other a row of very much smaller ones, not extending to the distal end, and directed upwards. In mosquitoes the blade is flattened and very much elongated. The inner side of the blade is thickened to a prominent ridge from the base and upwards, and the external edge is very thin and sharp, so that on cross-section the blade has a triangular outline. In cleared preparations the distal portion of the blade is usually bent outwards, but this is probably an artifact due to the different amounts of shrinkage in the thick and the thin edges. The blade is produced to a fine point, and in some cases, especially in the smaller forms such as *Anopheles maculipennis*, figured by Nuttall and Shipley and in

* The transverse bend may be an artifact.

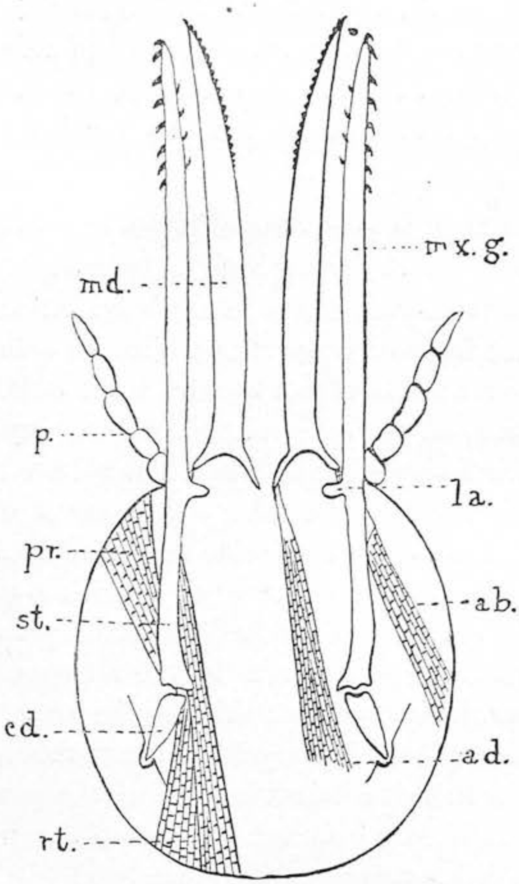
Culex fatigans, is slightly expanded. On this portion there is a single row of minute thorn-like teeth, all projecting backwards. In a large species of *Joblotia* (figure 3) I have seen a much more complex arrangement. The blade is the same as in the smaller forms, but at the tip it is armed on both sides. On the external side there are five comparatively large teeth, similar to those of the smaller mosquitoes. The distal one of these is situated some little distance from the pointed tip of the blade, and in the interval there are two much more delicate teeth with very sharp points, which point in the opposite direction to those above them, that is, towards the tip of the blade. On the internal edge there is a single row of short but stout teeth, seven in number, resembling those of *Tabanus*, and extending around the edge on to the two surfaces of the blade.

The stipes is readily seen in all these flies in cleared preparations of the head, as a stout rod running across the floor of the head cavity. It has been described in *Tabanus*, *Anopheles*, and *Phlebotomus*, in the latter two as the "apodeme" of the maxilla, and it presents very much the same appearance in *Simulium* and *Ceretapagon*. The cardo is less easy to distinguish on account of its small size, and I have not succeeded in distinguishing it in small species. In *Culex concolor* and in *Joblotia* it can be made out as a distinct piece at the base of the stipes. Its existence is not of course necessary for the mechanism of the maxilla, as it would suffice if the stipes were connected to the wall of the head capsule by the fibrous tissue, and I am inclined to think that this is the case in many forms, for one notices that the stipes remains adherent to the chitinuous wall in cleared preparations.

The muscles which act on these joints to produce the protraction and retraction are arranged in the same manner throughout, though it is a matter of some difficulty to make out their precise insertions in the smaller species. They are always to be found in transverse sections of the head, and I have found them in this manner in *Ceratapogon* after failing to dissect them. There is no doubt of the existence of a relatively large bundle of muscle fibres surrounding the stipes in all case, though one cannot always differentiate between the adductors and the abductors. The arrangement depicted by Nuttall and Shipley in *Anopheles maculipennis* is found also in *Joblotia* and *Culex concolor*.

The mode of action of the maxilla will now be evident. The extreme tip of the blade is pushed into the skin by the protractor muscles, and meets with very little resistance on account of the fineness of the point and the upward direction of the spines. It is then withdrawn by the retractor muscles, and as this takes place the rasps catch against the tissues and lacerate them.

Protraction and retraction follow one another rapidly, and each time the barbs are drawn upwards through the wound they enlarge it, so that at the next protrac-



TEXT FIGURE 1.

Diagram of the mandibles and maxillæ of the orthorraphic biting flies.

md., mandible.
ab., abductor muscle of the mandible, ad., its adductor.
mx. g., the galea, (the cutting portion) of the maxilla.
la., the lacinia.

p., the palp.
st., the stipes.
cd., the cardo.
pr., the protector muscle.
rt., the retractor.

tion the tip of the maxilla can penetrate, still against little or no resistance, further into the wound. When a certain depth is reached, the teeth on the opposite side of the blade, in the cases of *Joblotia*, *Tabanus* and *Phlebotomus*, also take part in the enlarging of the wound, acting, however, during the protraction of the blade, for the points of the barbs are directed towards the tip, and do not meet with resistance during retraction. The mandibles and maxillæ, acting together, the former as a saw and the latter as a file, bore a hole in the skin of the host, and as the hole is deepened the piercing mouth parts are lowered into it either by the movement of the head on the neck or by the flexion of the middle and hind pairs of legs, which results in approximating the body of the fly to the skin of the host. The retraction movement is a more powerful one than the protraction, and we find as a matter of fact, in the forms in which the muscles have been studied carefully, that the retractor muscles are of greater bulk than the protractors, as for instance in *Tabanus* and *Anopheles*.

The process is beautifully demonstrated in the case of *Joblotia*. In this fly the extreme tip is armed on the inner side only with small but stout teeth which do not project from the surface to any great extent, and the first three teeth of this row will be inserted before any resistance is met with in the protraction of the blade. At the level of the third tooth of this set the first of the two sharply pointed teeth on the outer side come into play, and at and beyond this depth both protraction and retraction result in enlarging the wound. When the puncture is so deep that the whole series of seven teeth on the outside and the two distal ones on the inside are introduced into the skin, the larger and blunter teeth on the outer edge come into play, and these are so shaped that they will cut in both directions, having two edges, of which, however, the one projecting backwards is the sharpest and strongest. In *Simulium* the case is much simpler than this, for the armature of the two edges is almost identical, and as all the barbs point upward the movement of retraction is the only one which is efficient in making the puncture. In *Tabanus* the resemblance to a file is very striking, for almost the whole surface of the distal half the blade is beset with powerful spines.

The analogy of the file must not, however, be carried too far. Except perhaps in the case of *Tabanus* and *Simulium*, the blade of the maxilla is not a rigid structure of the same thickness throughout, but is thinned out from the base upwards, and has its teeth set on the thinnest and most flexible portion. This is especially the case in *Ceratapogan* and *Phlebotomus*. In the case of *Joblotia* and *Anopheles*, the thickened internal border is continued to the tip of the blade, but the teeth are on the thin external edge. It might be urged, especially with regard to the mosquito, that the elongated stylets are too slender to bear the strain of this method of action, but the bending stress is not, when one considers the matter carefully, a very great one. On account of the direction of the barbs the greatest part of the resistance of the tissues has to be overcome while the blade is being withdrawn, and it will therefore tend to straighten rather than to bend the blade. The slight flexibility of the blade is in fact an advantage, as it will enable the point to travel to a certain extent in the direction of least resistance, and if in doing so the blade becomes bent, it will straighten itself on the return, the teeth meanwhile cutting their way through the resistant tissue. The extent of movement is of course a very short one, and is limited to the difference in length between the whole maxilla when the stipes and cardo are in the same straight line and when the stipes and blade form one side of a triangle and the cardo the base. In the most extreme case the excursion of the tip of the blade could not be greater than twice the length of the cardo, supposing the joint between it and the stipes were capable of moving through 180° (Figure 16). The joint between the proximal end of the cardo and the epicranial wall must of course move with the joint distal to it.

It is at first sight a little difficult to believe that these minute cutting organs, so small that even in the largest horse flies they are almost invisible to the naked eye, even though they are provided with such a perfectly adapted armature and muculature, should be able to pierce the thick hide of the larger mammals. And yet they not only do so efficiently, but the larger flies make such a formidable wound that the blood continues to flow after the proboscis is withdrawn, and here, where such species as *Tabanus straitus* and *albamedius* are common, it is by no means rare to see the legs of cattle splashed with blood as if from a bad scratch, as a result of the attack of these flies. The wound made is in fact not a punctured one in the surgical sense, but a lacerated one, and if it happens to involve a capillary of some size the amount of bleeding may be enormous in comparison with the size of the instrument by which it was made. If the piercing parts were simply thrust in it is inconceivable that such minute lancets could draw blood at all.

With regard to the muscles which are concerned in the biting action, it is by no means difficult to believe that they are capable of adequately performing their function without other aid, when we remember the extraordinary rapidity of action of which insect muscle is capable. Marey, quoted by Packard, states that the wing of the fly is capable of making 330 strokes per second, that of the bee 190. This rapidity, probably unequalled in any other creatures, is indeed characteristic of insect muscle, and it seems evident that in the movements of the mandibles and maxillæ of these flies we have another and still more remarkable instance of it, applied in a highly specialised manner. In spite of the very short range of movement and the minute size of the cutting weapons, there is no mechanical reason why a comparatively deep wound should not be made in a very short time, provided the rate of action of the muscles is sufficiently rapid. The abdomen of a mosquito can be seen to begin to distend within half a minute or less from the time it settles down to feed, and it is of course probable that the mandibles and maxillæ continue to act even after the blood has commenced to flow, and are continually employed in deepening and enlarging the wound as required.

The Sucking Apparatus.

It will be convenient to discuss the sucking apparatus in accordance with its natural division into three parts, the canal in the proboscis, and the buccal and pharyngeal cavities. We may commence with the former, leaving till later the question of the nomenclature of the two cavities which function as sucking pumps.

The canal in the proboscis is formed by the apposition of the labrum-epipharynx and the hypopharynx, the former taking always the larger share in the circumference of the canal. When the labrum-epipharynx is examined in cross section it is seen that it consists of two distinct laminæ, which represent respectively the labrum and the epipharynx. The outer lamina gives its shape to the combined organ, whatever that may be in the individual case, and may be either circular with a gap on the under surface or flattened dorso-ventrally. The upper end of this lamina is attached to the clypeus, and is either quite free from the inner lamina or else more loosely attached than at the distal end. Attached to the internal portion of it, where it reaches the clypeus, there is a well developed muscle which arises from the inner surface of the clypeus. The inner lamina, or the epipharynx, is always circular in outline, or nearly so, and has, like the outer, a gap on its lower or oral side. The two laminæ are attached to one another by the margins which bound the gap, so that they enclose a space in which a small amount of cellular tissue is found, though there is no muscle in this situation comparable with that found in the house fly. The free side of the epipharynx forms the greater part of the food canal, its circumference varying roughly from two-thirds to four-fifths of a circle. The hypopharynx also consists of two laminæ, though they are not so easily distinguished from one another as in the case of the labrum-epipharynx, and no soft tissue can be seen between them. In form the organ is always flat and wide enough to fill up the interval between the lateral borders of the groove in the epipharynx, being in most cases almost as wide as the latter. The epipharynx is always directly continuous with the upper or anterior plate of the first sucking chamber and in a similar manner the upper lamina of the hypopharynx is continuous with the lower plate. The two laminæ are, in fact, simply outgrowths from the stomodæum and are homologous with those of other families of insects. The lower lamina of the hypopharynx arises on the other hand from the labium, and is therefore quite distinct in its origin from the upper, since it comes from an appendage of the exo-skeleton, and not from the stomodæum.

The most interesting feature of the food canal in the proboscis is the relation of its width to the size of the particles which have to pass along it. Unfortunately it is not possible to make exact measurements of the diameter of the canal in the normal condition of the parts, and any manipulation introduces such a large possibility of error that it is perhaps better to avoid exact figures altogether. In sections prepared by either the combined paraffin and celloidin method or by simple celloidin there is always a good deal of shrinking, and in attempting to measure the width of the canal in fresh or cleared preparations one is met with the difficulty of defining the exact edge of the inner lamina when it is seen in optical section. The width of the channel is only to a limited extent correlated to the size of the fly, and varies from approximately twenty-five microns in the larger Tabanidæ to fifteen or less in Ceratapogon and in mosquitoes; that is to say, it measures from once to twice the diameter of a human red blood corpuscle, it being of course understood that *all measurements are made at the narrowest part of the distal end of the canal* as in many cases there is a gradual widening of the channel from the tip upwards. There are two obvious results of the small size of the channel; in the first place, objects definitely larger than the measurements given will not ordinarily be ingested by these biting flies, a point of some importance to the parasitologist, and which would well repay further investigation, especially with regard to the transmission of filaria by mosquitoes; secondly, if such an object, larger than the canal could conveniently accommodate, were to gain access to the canal, or to become impacted at the opening, which is the narrowest part, there would be considerable danger that the fly would be unable to get rid of it and would consequently die. Now one would think that in such a lacerated wound as that which must be made by the saw and file action of the mandibles and maxillæ there must of necessity be lumps of tissue much larger than can be ingested, and yet it is inherently improbable that nature would allow such an accident to occur. The only conceivable method by which such an impacted object could be got rid of would be by regurgitation, which, since it implies a reversed peristalsis, is a most unlikely event. We must therefore enquire as to what are the possibilities of a defensive mechanism to prevent the ingress into the canal of particles too large to pass down its lumen.

I have already expressed the opinion that the labrum-epipharynx and the hypopharynx can take no part in the making of the wound in the skin, on account of the nature of their attachment to the wall of the head capsule and of their lack of the necessary musculature. In most of these flies, however, there are certain processes on the distal ends of these organs which certainly bear a superficial resemblance to teeth and have been repeatedly described as such, though I am not aware of any detailed description of the method by which they might be supposed to act. It is just in this situation that one would expect to find a filtering mechanism, and it is worth while to examine these structures in some detail to see if they fulfil the requirements.

Considered with regard to the armature of these organs the flies of this group fall naturally into three divisions, the first including *Simulium*, *Ceratopogon*, and *Phlebotomus*, the second the *Tabonidæ*, and the third the mosquitoes. These will now be examined in detail and compared with one another.

In *Simulium* (figures 15 and 14) the labrum-epipharynx and the hypopharynx, which are flattened and spatulate organs, terminate in gently rounded margins without any point, the middle portion being in fact almost straight. In the labrum-epipharynx there is on each side of the middle line a rather thick longitudinal band of chitin, extending nearly but not quite to the tip, the two bands lying on either side of the food canal. On this band there is a row of fine non-pigmented hairs, somewhat irregularly arranged and extending in an oblique line to the point where the lateral border joins the distal one. They are directed forwards, inwards, and towards the opening of the food canal, and those which are the most proximal in position are a little longer than those at the distal end. At the extreme distal end of the organs there are two sets of extremely minute hooks or teeth, one set on each side of the opening, and projecting beyond the distal margin. On account of their small size and position it is very difficult to be certain of the exact number and arrangement of these structures, which could only be examined satisfactorily in a preparation mounted with the long axis of the organ in the same line as the microscope, and the figure must be taken as approximate only. There appear to be three teeth on each side, each having the shape of a rose thorn, and radiating outwards from their bases. One on each side projects definitely beyond the distal margin. It is somewhat difficult to find a function for these peculiar structures; they cannot be used as cutting teeth, for they are incapable of movement on the labrum, having neither joint or muscles so far as one can see, neither do they appear at all suited for use as a filter. Possibly they are used to fix the organ in position when a suitable depth has been reached. The edge of the labrum-epipharynx on either side of these teeth is very thin and difficult to define in cleared preparations, and is membraneous and probably flaccid; it bears a few minute hairs similar to those on the thickened portion of the surface.

The hypopharynx terminates distally in a border which is parallel to that of the labrum-epipharynx. In this case, however, the organ is chitinous right to its extremity, and is highly modified. The margin on each side of the alivary duct is broken up into innumerable minute elongated processes, which form a fine fringe like the frayed edge of a piece of cloth, all the processes being directed distally. This fringe occupies the entire extent of the rounded portion of the distal end, and terminates where the lateral borders become parallel to one another. On the posterior or inferior surface of the hypopharynx there are a few small hairs similar to those on the anterior surface of the labrum, but smaller, and arranged in a loose row near the margin. These arise from the inferior or labial lamina of the organ.

In *Ceratapogon* (figures 6 and 7) we find a similar arrangement, but the serrated border is found on both organs. The labrum-epipharynx is gently rounded at its distal end, and has on each side of the curved distal margin a row of five flattened and blunt pointed processes. These are simply produced by indentations of the margin, and have no thickened bases such as are found in true cutting teeth; they point directly in the long axis of the proboscis and have no fine serrations on their edges; one side of the process is not thinner or sharper than the other. Between the two most internal ones of the two rows there are two other pairs of processes, set on each side of the extreme apex of the organ, where the food canal opens to an exterior. These are rounded, about twice as long as thick, and with slightly constricted necks, which are bent a little backwards so that the rounded ends of the processes hang over the opening of the food channel. The two innermost of the two sides are more distant from each other than any of the other processes, and internal to their bases there is a pair of minute thickenings in the chitin, and proximal to these a medial oblong thickening situated a short distance proximal to the tip of the organ.

The serrated margin of the tip of the labrum-epipharynx is not in the same line as that of the rest of the lateral borders, but is separated from it by a deep notch situated a short distance proximal to the proximal process. This gives the labrum a somewhat barbed appearance. It will be noted in the figures that, if we deduct the width of the slightly thickened margins which project beyond the notch on the two sides, the width of the labrum is almost the same as that of the hypopharynx, and the serrated margin of the former will therefore project beyond the margin of the latter in the natural superimposed condition of the parts.

The hypopharynx resembles the labrum-epipharynx in outline, but, as indicated in the last paragraph, it is slightly smaller. Its margin is also serrated in a manner very similar to that of the labrum-epipharynx, there being five indentations and five processes on each side. At the point where the salivary duct opens to the exterior there are four small finger-like filaments, which arise from the lower lamina and project distally. The upper or anterior surface of the organ is marked by five longitudinal dark patches, which commence at the bases of the processes in the margin, and pass inwards towards the salivary duct. The appearance suggests that the surface is traversed by oblique longitudinal grooves, with ridges between them, and that the dark patches represent thickened portions of the chitin, but the parts are too small to permit one to be certain of the point.

The parts in *Phlebotomus* are rather simpler. The labrum-epipharynx is produced to a narrower point, the curve of the lateral margins at the distal end being concave rather than convex. The narrowed portion is divided up into a number of minute processes, coarser than those of the hypopharynx of *Simulium*, but much finer than those on that of *Ceratapogon;* the two spine at the extreme apex are rather thicker than those at the sides, and project forwards almost parallel with one another. The hypopharynx has its edge serrated in a similar manner, but the indentations are not quite so deep or so numerous. In its outline the hypopharynx is not quite so much pointed as the labrum-epipharynx, and some of the processes on its margin overlap its edges in the natural condition of the parts.

In these three flies we find, then, that the distal ends of these organs are split up into rows of more or less elongated and pointed processes, varying in shape, but all exhibiting the same general structure, and all directed forwards in line with the proboscis. With the single exception of those on the labrum-epipharynx of *Simulium* they bear no resemblance whatever to biting teeth such as are found in the mandibles and maxillæ of these flies, nor do they resemble those found on the inner surfaces of the labella of the blood-sucking Muscids. Apart from the facts already insisted on, that a suitable motive force and articulation are entirely absent, the nature of the margin, when it is examine ed in a well cleared preparation, is a sufficient indication that it is not primarily intended for cutting purposes. On the other hand, the arrangement is admirably adapted to serve as a filter or sieve, by which large particles can be prevented from entering the canal.

The groove on the under surface of the labrum-epipharynx does not extend to the extreme tip of the organ, but terminates a short distance from it by broadening out into a flattened sheet of softer tissue which is not distinguishable from the anterior lamina, the space between the two being gradually reduced until they come in contact with one another; in other words, the epipharynx does not extend the full length of the combined organ as a separate structure, but is reduced in size and fused with the labrum to form a more or less flattened and tongue-like end. Normally this lies in front of the flat apex of the hypopharynx, and the opening of the food canal is therefore not a circular one, but a transverse fissure between two superimposed plates. The figure of the ends of the two organs given in Newstead's paper on *Phlebotomus* is most suggestive. He shows that there is a slight interval between the two, caused by a slight forward curve of the labrum-epipharynx and a corresponding backward curve of the hypopharynx. The "teeth" on the former organ are directed slightly backwards, and those on the latter slightly forwards, so as to meet one another and even to overlap to a slight extent, thus filling up the interval which would be left by the curvature of the two extremities. The blood has to pass through the opening guarded by these processes before it can reach the circular portion of the lumen of the canal, and it is evident that the presence of these spines must be a most efficient means of stopping any particle too larger for the lumen from entering it. I have seen a similar appearance in a preparation of *Ceratapogon* amounted on its side, but the evidence of Professor Newstead's drawing is all the more convincing in that it appears to be simply an instance of accurate observation and drawing, for he does not refer in the text to the possibility of the mechanism being a filtering one.

I think it probable that the filtering mechanism provided by these spines is not altogether a passive one, but that the space between the two flattened tips can be varied to a limited extent by means of the muscle situated at the base of the labrum. Probably in the resting condition the two plates are in contact with one another and the spines more or less interlocked, at least in the case of *Phlebotomus;* in other words the mouth of the fly, or rather the prestomal orifice, is closed. When the piercing parts are introduced into the skin as the wound is made, the labrum is raised up a little by means of its muscle, and the potential opening converted into an actual one through which the blood can enter. It is at least very suggestive that the epipharynx and hypopharynx show no sign of fusing together to form a complete tube, in any of these flies, indicating that a certain degree of movement between the two is advantageous for the insect, whereas one would expect that a complete tube would afford greater stability than is provided by the simple apposition of the two organs; since the epipharynx and the hypopharynx are of identical origin, both being outgrowths from the same part of the stomodæum, one would expect such a fusion if a simple tube to function as a food channel were all that were required, and such fusion does actually occur in the upper portion of the canal in the more highly specialised biting flies of the Muscid group.

The *Tabanidæ* (figures 18 and 19) show a different type of apparatus, in which the filtering mechanism is not quite so obvious. Here the labrum-epipharynx is a much stouter and broader organ than the hypopharynx, and it is also slightly longer, so that the tip of the hypopharynx falls a little short of the other stylets. The apex of the labrum-epipharynx is broad and truncated, and the lateral borders are quite free from serrations such as are found in the flies already discussed. On the distal margin there are three sets of tubercles, arising from slightly raised areas, and projecting beyond the distal margin. The two lateral tubercles, which are comparatively large, consist of ten or twelve short stout peg-shaped processes, and the middle set of two rows of five each. Their exact number and arrangement is rather difficult to make out an account of their position, the posterior ones being overlapped by the anterior. The tip of the hypopharynx is distinctly narrower than that of the labrum-epipharynx, and is therefore overlapped by it. The two, however, resemble one another in shape, and, like the labrum-epipharynx, the hypopharynx is devoid of any armature at its sides. In some of the large species, such as *Tabanus striatus*, a distinct flange can be seen at the opening of the salivary duct, and in some preparations the projecting edges of this flange look very like teeth set on either side of the opening. It is easily seen in fresh preparations that they are not teeth, and that the lateral borders of the organ are only very thinly chitinised, so that they do not present well defined edges, but are on the contrary somewhat wavy. The flange at the mouth of the salivary duct bears a few extremely delicate hairs, possibly sensory in function.

In these flies there is therefore no structure which could act as a cutting weapon, and we conclude that they have only to do with the ingestion of food. The tubercles at the apex of the labrum-epipharynx will act as a protecting fringe to prevent the ingress of large particles from the front and sides, but can be by no means so efficient as the well developed fringe found in *Phlebotomus* or *Ceratapogon*. The hypopharynx in this case probably plays the most important part in the mechanism. Its tip and sides are extremely thin and are very easily bent, from which it is justifiable to conclude that in the natural condition they are flaccid. Now Stephens and Newstead, in their description of the mouth parts of *Stomoxys*, make the suggestion that the soft tip of the hypopharynx functions as a valve to prevent the ingress of large particles into the mouth, and I think that the same thing happens in the case of the *Tabanidæ*. In the natural position of the parts the rounded tip of the hypopharynx lies just behind that part of the labrum-epipharynx which bears the tubercles, and since both organs are flattened at the tip they will be normally in contact with one another, except when the labrum is elevated by the muscle at its base. The negative pressure created in the food canal by the dilator muscles of the sucking apparatus will tend to draw the two portions of the sucking tube together, and will act with the greatest effect on that part which is the most flaccid and the least supported, that is, it will tend to close the prestomal orifice by drawing the apex of the hypopharynx towards the tip of the labrum-epipharynx. The organ is sufficiently rigid to prevent this happening to such a degree as would completely close the orifice, and one must conclude that there is a nice adjustment between the flaccidity of the tip of the hypopharynx and the force tending to approximate it to the labrum-epipharynxe, so that an aperture of the correct size is left between the two.

In the mosquitoes the mechanism by which ingress of large particles is prevented is similar to that in the *Tabandæ*, but on account of the small size and delicate nature of the parts it is much more difficult to follow. The distal end of the labrum-epipharynx (figure 17) varies a good deal in the different forms, but so far as I am aware it never bears any armature which could be used for cutting or piercing. In shape it differs a little from any of the forms so far considered, for the main portion of the labrum-epipharynx is always rounded to the extent of almost four-fifth of a circle, and the transition from this round tube to the flattened tip gives the organ the appearance of being obliquely truncated, something after the shape of a quill pen. In Nuttall and Shipley's monograph on *Anopheles maculipennis* the tip of the organ is shown to be provided with two pairs of fine tooth-like processes, one pair at the extreme point and another pair a little distance behind them. These do not occur in all species of *Anopheles*, and I have not found them in any species of *Culex* which I have examined, even in *Culex concolor*, where they would be easily seen if present on account of the large size of the parts. In a species of *Joblotia* I have found the distal margin indented so as to produce four teeth on each side, the indentations being deep but the spaces between the teeth extremely narrow. There seems to be a considerable amount of variation in the method of termination of this organ, but all forms agree in the essential points, *viz.*, that there are no cutting teeth and that the end of the organ is flattened and fairly thick and rigid.

The tip of the hypopharynx presents a characteristic appearance in the large forms. If one examines the organ in the fresh state under a magnification of at least a thousand diameters and with as small a diaphragm as possible, one sees that the organ does not terminate in a well-defined point as ordinarily depicted, but in a very thin and apparently membraneous expansion, with a gently rounded margin (figure 9). In view of what has already been said with regard to the probable mechanism in the *Tabanidæ* the mechanism in this case will be obvious. The extremity of the hypopharynx lies a little above that of the labrum-epipharynx, so that when the sucking action commences blood can only enter from the posterior aspect, and in doing so will impinge on the soft tip of the hypopharynx and tend to drive it against the more rigid labrum-epipharynx, the stream of blood being aided by the negative pressure in the food canal, which will also tend to draw the two organs together. The entrance to the food channel is not a fixed and rigid one, but varies in size according to the distance between the labrum-epipharynx and the hypopharynx, this being regulated by the muscle at the base of the labrum. The adjustment is a very fine one, for the more powerfully the pharyngeal muscles contract the more will the two parts of the tube be drawn together, and more the valve-like end of the hypopharynx will tend to close the aperture.

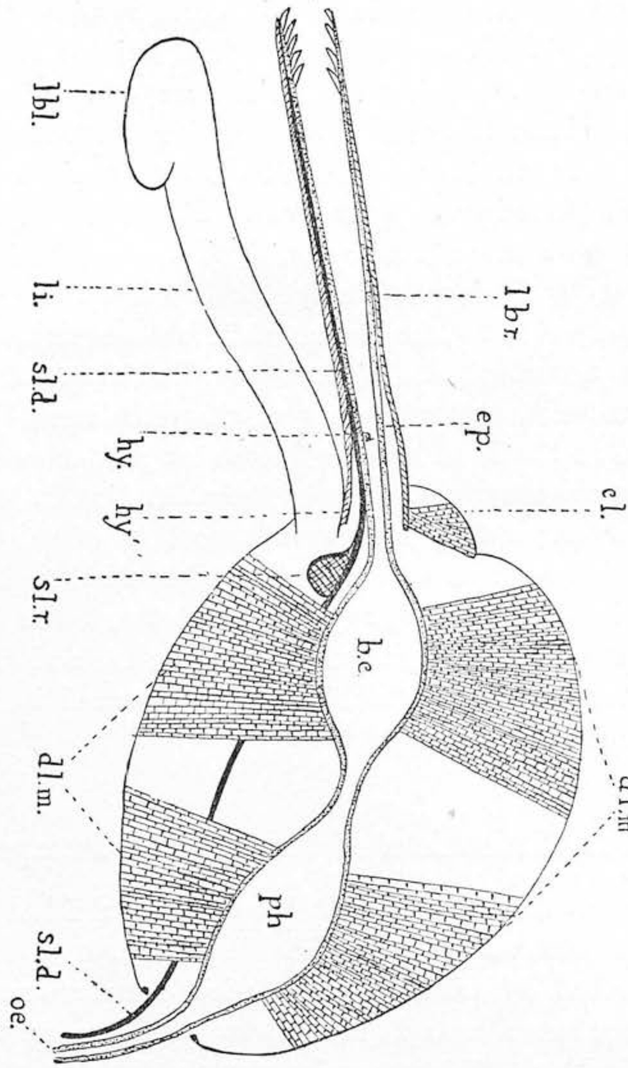
A word is necessary with regard to certain minute spines found in the in- ernal surface of the groove of the labrum-epipharynx. I have only found these in *Tabanidæ* and in *Simulium*, but it is likely that they also occur in the other members of the group. They are short, stout, and gently curved structures, arising from expanded and globular bases which lie in the substance of the chitin of the epipharynx, and are seen as clear spaces when the structure is examined in optical section. The base of each of these spines is perforated where it projects into the space between the labrum and the epipharynx, and with careful focussing a fine canal can be seen in the lower part of the free portion of the hair. They closely resemble the spines described in a corresponding situation in *Stomoxys* by Hansen and by Stephens and Newstead, and one is inclined to regard them, from their situation, as organs of taste, though of course there is no direct evidence as to their function. Possibly it may be through them that communication between the prestomal orifice and the muscle of the labrum is established for the purpose of regulating the flow of blood. Their occurrence in such a widely separated flies as *Simulium* and *Stomoxys* is suggestive.

The mechanism of the labium appears to have escaped the notice of workers on this subject. It is generally stated that when the mosquito feeds the labium becomes bent backwards like a bow, and the labella separated to allow the piercing parts to pass between them, but no mention is made of the forces which bring about this change in position, and one is left to assume that the labium is simply pushed back because it cannot enter the skin. The process can be readily watched in the mosquito, and is faithfully depicted in Nuttall and Shipley's drawing. In all the other flies without exception the same thing must take place, since the labium and labella are always long enough to conceal the mouth parts in the condition of rest. There is no reason to suppose that there is any such haphazard bending as that indicated above, for the labium has its intrinsic muscles, some arising within the head capsule and some within the cavity of the organ, which are inserted into its integument at the distal end and into the labella. These are familiar from the many diagrams of the cross-section of the proboscis of the mosquito, and are of course figured in the classical papers of Meinert and Hansen. In most Nematocerous flies the labium and labella are separated from one another by a loose joint in which there are lateral transverse bars of chitin, very conspicuous but not described in detail in the mosquito, which are probably homologous with the furca in the muscid flies, and some of the muscle fibres can be traced to these in the large mosquitoes. We have here all that is required for the retraction of the labium and the eversion of the labella which can be seen to take place when the fly feeds. The muscle fibres arising within the cavity of the labium and inserted into these transverse rods evert the labella to allow the piercing parts to enter the skin, exactly as is the case in *Tabanus* where the labella are large and important structures with a function of their own with regard to feeding. The retraction of the labium and the bent position it assumes are the result of the contraction of its muscles and of the peculiar structure of its wall. The mentum of the mosquito is a long chitinous gutter, straight or slightly curved, and of fairly uniform diameter throughout; its anterior open side is filled in by a soft membrane homologous with the labial gutter of other flies. The chitin of which it is composed is not, as generally represented, a continuous sheet, but is in its upper portion composed of a large number of separate narrow transverse plates, set very closely together and united by the membraneous ground work. These are very minute, and are only revealed by the examination of well-cleared preparations under a high magnification. They are found at just that portion of the labium which is bent acutely when the piercing parts are inserted into the skin, and the arrangement is, of course, one with which one is familiar in other situations in which a certain amount of rigidity has to be combined with flexibility.

The Sucking Chambers.

The nomenclature of the sucking apparatus in the Diptera is unfortunately in a most confused state, and it will be well before going further to fix a terminology and to point out the significance of the terms employed by different writers. It is agreed by all that the sucking apparatus is formed from the first part of the stomodæum, and is therefore an invagination at the anterior end of the fly, lined with chitin which is continuous with the exoskeleton. In all the Orthorrapha this invagination is dilated into two chambers, each of which, in the species which have been examined closely, is provided with a set of muscles which pass between the outer sides of the walls of the chamber and the walls of the head capsule. By means of these muscles the chambers can be dilated, so that their potential cavity becomes an actual one, into which the fluid food is sucked by a simple pumping action. The two chambers appear to be always separated by a narrower channel, which may be surrounded by a sphincter muscle, so that they work alternately, the posterior chamber drawing the blood from the anterior one, and passing it onwards into the alimentary canal. It is with regard to the respective names of these two chambers that the confusion exists, and this has arisen chiefly through the differences in degree of development of the two in different families, and to attempts to follow too closely the terms employed in general anatomy. Meinert, in his description of *Tabanus*, termed the first of these, which in that family is rather more prominent than the second, the pharynx, and then divided the succeeding part into the first and second parts of the œsophagus, the first part being a large and dilatable chamber, the second a simple tube passing through the brain to the neck. In the mosquito it is the second chamber which is the most conspicuous, and this is universally known as the pharynx, at least at the present time, subsequent to the description of Christophers. Nuttall and Shipley term the first portion the buccal cavity and the second the pharynx in the mosquito, and I think it would be of advantage to retain these terms throughout the group. The word œsophagus is chiefly used in zoological nomenclature for a simple channel, and there is no special advantage in retaining it to signify a part of the sucking apparatus. This nomenclature has the advantage that it is equally applicable to the Cyclorraphic Diptera, in which there are also two parts to the apparatus, only one of which, the upper one, is a functional pump. It must be remembered, however, that that pharynx in *Tabanus* and in the mosquito, the two most divergent members of the group, possess this difference, that they are on opposite sides of the brain, the pharynx of the former—the first part of the œsophagus according to Meinert—being anterior, and that of the mosquito posterior. In what follows, then, the first chamber will be termed the *buccal cavity*, corresponding to the pharynx of Meinert and Dimmock, and the second the pharynx, corresponding to the first part of the œsophagus of the same authors, and homologous with the fulcrum in the house fly as described by Kraepelin, and the pharynx of Lowne. The simple tube which connects the pharynx with the alimentary canal in the thorax may be termed the œsophagus. The duct which unites the buccal cavity and the pharynx hardly needs a special name.

It is to be understood that this nomenclature has no precise embryological significance, and that the pharynx in one fly is not necessarily strictly homologous with that of another. We may imagine that in a very primitive insect of this type the whole of the outer wall of the stomodæum would be united with the wall of the head capsule by strands of muscle fibre, so that it formed one continuous dilatable chamber, in which a sucking action could be produced by the peristaltic contraction of the muscles, the anterior one contracting first, and then relaxing, so that a wave of dilatation



TEXT FIGURE 2.

Diagram of the sucking apparatus of the orthoriaphic biting flies. lbr., labrum. ep., epipharynx. cl., clypeus.

hy., hy'., the anterior and posterior laminæ of the hypopharynx. sl.d., the salivary duct. li., labium. lbl. the labella. sl.r., the salivary reservoir.

b. c., the buccal cavity. ph., the pharynx. dl. m., the dilator muscles, passing from the wall of the head capsule to the sucking chambers. oe., the œsophagus, entering he neck.

passed along the chamber, carrying the food with it onwards to the digestive portion of the canal. In course of time, as the various genera were differentiated from one another, certain portions of the muscle disappeared, and the chamber became divided up, until in the present forms two main dilatations were left, a small portion of the stomodæum in the head remaining as a simple duct. The condition found in the different families depends simply on the particular portions of the primitive chamber which have retained the original character, and it is quite possible that these are not always the same. One is not perhaps justified in speculating further on this subject in view of the little that is known of the larval characters of these flies, but it is interesting to note in passing that there are points which suggest that the pharynx of the mosquito is developed from a part of the stomodæum much posterior to that from which the pharynx of *Tabanus* arises, although the chamber here referred to was regarded as the first part of the œsophagus by Meinert. In the first place, the second chamber of the mosquito is posterior to the brain, while the corresponding chamber in the *Tabanidæ* is anterior. In *Tabanus* we find also that there is a well-defined pair of muscles, the retractors of the œsophagus, which run from the posterior wall of the head capsule in the neighbourhood of the occipital foramen to the œsophagus, and though their function is probably correctly indicated by their name, they represent a portion of the once continuous band which united the whole of the wall of the canal to the head capsule. They correspond in position, with regard to the brain, to the large and powerful dilator muscles of the pharynx of the mosquito, and it certainly looks as if the part of the canal to which they are attached is homologous with the pharynx of the mosquito.

The Mechanism of the Sucking Pumps.

In the numerous descriptions that have been published of the pharynx and its muscles, no account seems to have been taken of the necessity that exists for some method by which the distended chamber can be closed again, and the plates once more brought in contact with one another in readiness for the next contraction. It is generally assumed that the recoil of the plates takes place by virtue of their elasticity, an assumption that does not seem to be justified by the facts of the case as far as they are known. Chitin is certainly to some extent flexible when it is in thin sheets, and the chitinous mouth parts when bent will as a rule return to their original shape, but it by no means follows that the elasticity of the chitinous plates of the sucking chambers is sufficient to bring about their return, for it must be remembered that such a degree of elasticity would have to be overcome by the dilator muscles when the chamber were expanded. It is of course as difficult to prove that the plates are not elastic as it is easy to assume that they are, and I will not go further than to say that the assumption is an unnecessary one. Let us consider what must happen when the chamber is dilated. In the first place, if the head were entirely separated from the body, the total contents would be increased, and either some of the cranial contents would have to be compressed or the capacity of the head increased by distension; the difference in size between the cavity of the pharynx of the mosquito when it is empty and when it is full is considerable, when compared with the total size of the head. The only compressible substance in the insect head is the air in the air sacs, and the only substances which can be displaced from the head by simple pressure are the air in the air sacs and the blood in the hæmatocœle of the head. If these are displaced by the expansion of the sucking chamber they will pass through the neck and increase the total contents of the body. There are therefore two possible ways by which the chambers can be emptied after dilatation, *viz.*, by blood pressure or air pressure. Of the two the latter is the more likely, both on account of the structural peculiarities of the head and by reason of the analogy of the method by which the retractile proboscis of *Musca* is known to be thrust out. The head of the fly, and particularly of these blood-sucking flies, contains a remarkably large amount of air, contained in air sacs with relatively thick walls—very thick in the case of the *Tabanidæ*. The air in these sacs is in communication with the rest of the tracheal system by means of tracheæ which pass through the neck, and so with the thoracic spiracles. That the insect is capable of distending the air sacs of the head by means of respiratory movements we know from the case of *Musca*, so thoroughly studied by Kraepelin, and I think that the dilatation of these sacs offers a far more rational explanation of the means by which the plates of the pharynx and the buccal cavity are brought together, than the assumption that the chitin has of itself sufficient elacticity to accomplish it.

The Intracranial Tunnels.

In all the flies of this group there exists a pair of hollow tunnels which pass through the lower part of the head from front to back, and open on to the anterior and posterior surfaces. They have been described and figured in *Anopheles* by Nuttall and Shipley, and by myself in *Hæmatopota*. Similar tunnels occur also in *Chironomus* (Miall and Hammond) and in *Asilus*. They act as supporting buttresses to counteract the tendency of the dilator muscles of the sucking apparatus to pull the walls of the cranial cavity together, and, as I have pointed out in connection with those of *Hæmatopota*, the fact that they are hollow is in accordance with the mechanical principle that a hollow cylinder is stronger, weight for weight, than a solid rod. They also act as an additional surface for muscle insertion, and several muscle bundles can be traced to their posterior ends. The anterior end of the tunnel opens in all cases just below and at the outer side of the antenna, and the posterior a little in front of the occipital foramen. The interesting point about these structures is their constant occurrence and their connection with the sucking apparatus.

The Oesophageal Diverticula.

It does not appear to be fully recognised that the presence of an œsophageal diverticulum is a constant feature in Diptera, and that the form in which it occurs in the mosquito is merely a modification of a structure well known not only in this order but throughout the whole class *Insecta.* A good deal of the confusion is possibly due to the loose way in which many names, more or less applicable, are used for the different forms in which the structure occurs. Many of them are open to objection; probably it would conduce to clearer ideas on the subject if the term "crop" were adopted for all, though it is of course rather too late to attempt to change the term in such common use in connection with mosquitoes. The words "œsophageal diverticulum" are, however, somewhat misleading. The real relations of the two parts are best seen in a longitudinal section of the anterior part of the thorax of a Tabanid, or in a series of transverse sections. The duct of the diverculum passes in a straight line backwards through the neck, lying between the salivary glands; in front it is directly continuous with the œsophagus, and there is nothing to indicate where the one ends and the other begins, as they are precisely similar in the structure, and form one continuous duct extending from the intracerebral part of the œsophagus in the head to the small sac-like diverticulum in the second or third segment of the abdomen. At a point a little distance behind the inlet of the thorax the proventriculus is seen lying below the duct and between the salivary glands, and it has an aperture on its upper surface by means of which it opens into the lower surface of the duct. The junction between the two is therefore at a right angle to the line of the gut, and it is, in the *Tabanidæ*, surrounded by a few circular muscle fibres which may function as a sphincter muscle. It is clear that in view of this it is literally incorrect to speak of the sac as a diverticulum of the œsophagus. The term " sucking stomach" is open to the even more serious objection that it is not a stomach, in the sense of an organ in which digestion takes place, and that it is not a sucking organ. On the whole the term crop is the most applicable of any of he words in use, as it indicates the function fairly closely, and has the advantage of emphasising the homology between the apparently different structures in the mosquito and the house fly.

The crop is primarily the chamber into which the blood first flows from the pharynx, and is intended, no doubt, as a reservoir to contain the food until the digestive portion of the midgut is ready for it. The different degrees of development which it attains are dependent on the amount of food the midgut can deal with at one time. In a full-fed mosquito killed immediately after feeding one finds the three divisions of the crop all filled with blood, and very little in the midgut, while in a horse fly the crop is empty and the midgut distended with blood. In the former case we may regard the crop as a true reservoir, as was pointed out by Nuttall and Shipley, while in the latter the function appears to be merely to pass on the blood slowly from the pharynx to the midgut. The wall of the crop is composed of a very fine basement membrane and an interlacing network of delicate muscle fibres, and the degree of the development of the muscle gives one support to the observations made on the fly in dissections. In the *Tabanidæ* the muscle fibres are very well developed, forming a network which can easily be seen in unstained preparations, and the sac is thus able to pass on at once the whole of the blood received by it to the gut, contractions of the wall of the sac following relaxation and emptying of the pharynx. I have dissected for various purposes several hundreds of Tabanids of various species, and at varying times after feeding, and have never found fresh blood in the sac in any case. In flies killed immediately after feeding one often sees the wall of the sac displaying rather rapid peristaltic movements, such as would result in driving the blood out of the sac and up the tube into the proventriculus. In flies killed some time after feeding the sac is either empty or contains a few granules of blood pigment. In the *Tabanidæ* the crop is therefore to be regarded as functionally a part of the sucking apparatus, its task being to receive the blood from the sucking pharynx and to expel it again into the midgut, while in the mosquitoes it is a true reservoir, retaining the blood at the time of feeding and passing it on to the gut as it is required later, the contractions not necessarily taking place immediately after the blood is received and not being correlated with the contractions of the pharynx.

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Description of Plate.

The figures were drawn with the aid of a camera lucida.

Figures 1 to 15 are on the same scale as that to the right of figure 1 and figures 17 to 19 on the same scale as that at the right lower corner of the plate. The divisions in the scales in each case represent hundredths of a millemetre.

Figure 1. The edge of the maxilla of Simulium.
Figure 2. The edge of the mandible of Simulium.
Figure 3. Ditto Ceratapogon.
Figure 4. Ditto Tabanus.
Figure 5. Ditto Anopheles.
Figure 6. The distal end of the labrum-epipharynx of Ceratapogon.
Figure 7. Ditto hypopharynx do.
Figure 8. Ditto Maxilla do.
Figure 9. Ditto hypopharynx of Joblotia.
Figure 10. The edge of the maxilla of Tabanus, showing some of the teeth.
Figure 11. Three red cells and a large mononuclear cell of human blood drawn for comparison of size.
Figure 12. The distal end of the maxilla of Phlebotomus.
Figure 13. The distal end of the maxilla of Joblotia. The curvature is probably an artifact, *vide* page 11.
Figure 14. The distal end of the hypopharynx of Simulium indicum.
Figure 15. Ditto Labrum-epipharynx do.
Figure 16. To indicate the extent and direction of the movement of the maxilla in Tabanus Diagramatic.
Figure 17. The distal end of the labrum-epipharynx of Joblotia.
Figure 18. Ditto hypopharynx of Hæmatopota.
Figure 19. Ditto labrum-epipharynx do.

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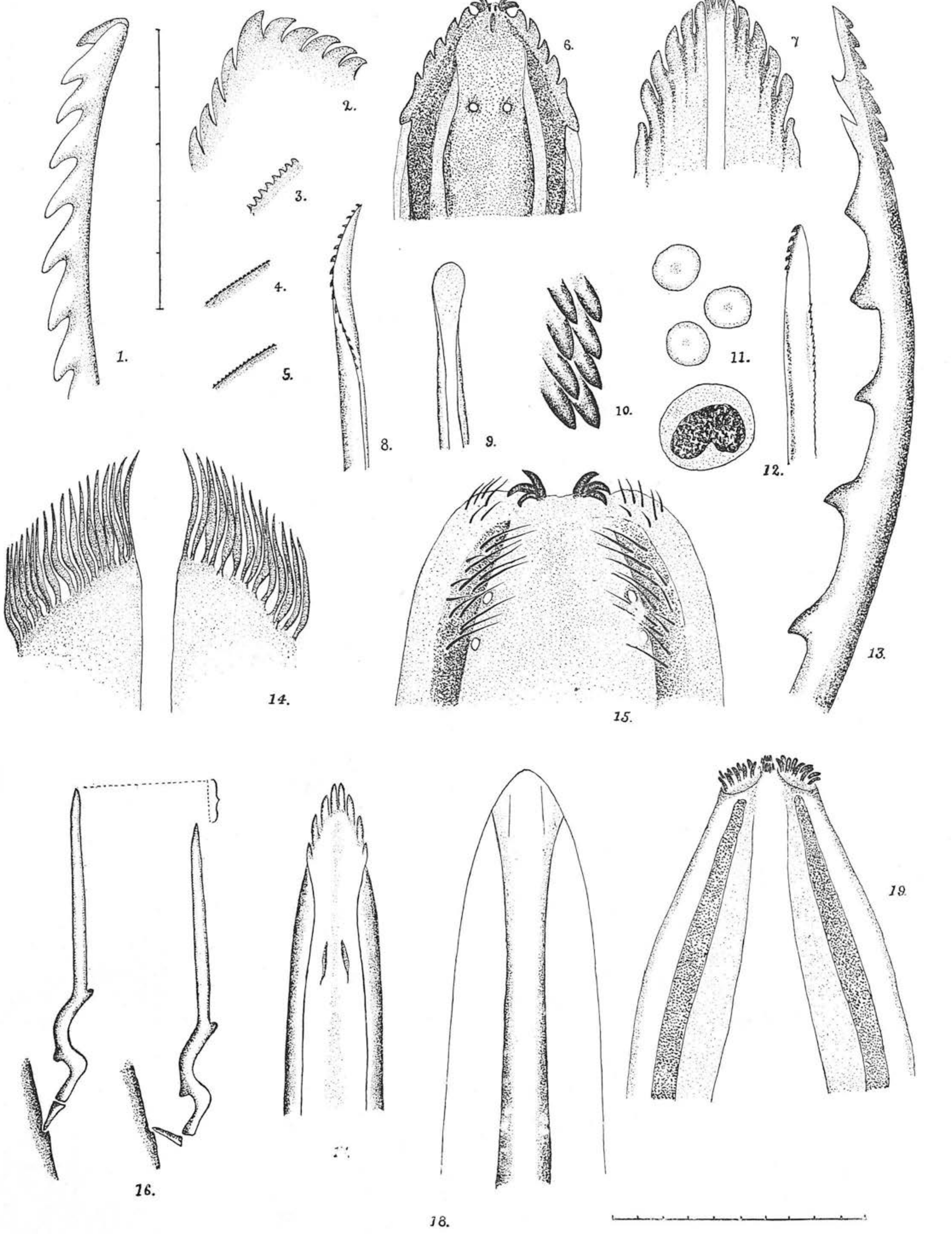

F. W. C DELET.

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Studies on the Mouth Parts and Sucking Apparatus of the Blood-Sucking Diptera.

No. 3.

Lyperosia minuta, Bezzi.

ALTHOUGH the mouth parts of *Musca* and its non-biting allies have been a favourite subject of research, especially among the older entomologists, the blood-sucking members of the group do not appear to have attracted much attention until the advent of the modern era of parasitology. Since the recognition of the rôle played by the blood-sucking arthropods in the transmission of disease the subject has come to have, in addition to the academic interest attaching to it, a certain practical importance, for it is through the proboscis that the infective stage of the blood parasite must pass when it is transmitted from one host to the other. A knowledge of the anatomy of this region, and of the mechanism of the complicated structures concerned in the act of feeding, is therefore essential to those engaged in the study of insect-borne disease.

The only recent accounts of the proboscides of the blood sucking Muscids are those of Hansen, who gave brief descriptions of *Stomoxys* and *Glossina* and of Stephens and Newstead, who described and figured the external mouth parts of the same flies in much greater detail, and the present writer's account of *Philæmatomyia insignis*. The descriptions of both on *Stomoxys* and *Glossina*, though they are accurate as regards the anatomical details, are incomplete, these authors having unfortunately had access only to dried and preserved material. This is a most serious handicap, for it is only by the examination of fresh material that one is able to study satisfactorily the complex mechanism of the proboscis, and this is one of the most important points. The suggestions regarding the nature of the biting action offered by the above authors are a good deal wide of the mark.

According to Austen the genus *Lyperosia* is intermediate between *Stomoxys* and *Glossina*. As regards the structure and general appearance of the proboscis it closely resembles *Stomoxys*, such differences as there are being only in matters of detail. The two are at once distinguished by the length of the palpi, which in *Stomoxys* are short, and in *Lyperosia* project almost to the tip of the proboscis. The internal structures show a rather greater degree of specialisation than seen in *Stomoxys*, thus corresponding with the external characters. Notwithstanding the similarity of the two forms, however, I propose to give a detailed description of *Lyperosia*, for my observations differ in many points from those of the authors cited, and my view of the mechanism is so essentially different that a complete account will be necessary to ensure lucidity. The homology of certain of the parts with those of *Musca* will be pointed out in passing, leaving the details of this interesting branch of the subject to be dealt with in a further paper, which I hope to publish shortly.

Methods.

The parts were studied first by the examination of cleared preparations, in order to become familiar with the chitinous skeleton of the proboscis. It was found convenient to place a large number of specimens in potash solution at the same time, and to remove them at intervals, so that preparations showing different degrees of transparency could be obtained. Dissection is most conveniently done after the preparations are cleared in clove oil, for many of the parts, for instance the labella, are so small that one runs great risk of losing them if they have to be subjected to any manipulation after removal from the rest of the organ. It is so difficult to mount such small objects in the desired position that it is best to mount a large number at the same time and preferably on the same slide, so as to increase the chances of getting the desired point of view. Dissection was performed under a Zeiss binocular microscope, with a magnification of from twenty to forty diameters. Carefully ground needles with various shaped points are essential. The dissection of fresh specimens is of the greatest importance in the study of the mechanism, for one often can decide what is the function of a muscle by pulling on it when one cannot be absolutely certain of the exact point of its attachment. The examination of flies recovering from a dose of ether is also very instructive, as one can actually see the same movements of the proboscis as are performed during the act of feeding, though they are, of course, convulsive and irregular.

For serial sections the combined paraffin and celloidin method was used. It is best not to attempt to cut a whole series from one preparation, but to cut away boldly one end of the specimen, so as to allow the fluids to penetrate freely. The chitinous walls themselves are practically impervious to the ordinary reagents, and it is advisable to perforate them with a needle at some unimportant point, in addition to making a free opening at one end. Bles's fluid was used as the fixative, followed by rapid dehydration in several changes of absolute alcohol; the shorter the time chitinous objects are left in absolute alcohol the more likely one is to get unbroken sections.

General Account.

The proboscis (Fig. 1, Plate 1) consists of three parts, corresponding to those found in *Musca*, and more or less freely moveable on one another. The rostrum is hidden from view on the under surface of the head in the position of rest, and is much smaller than that of *Musca*. The haustellum, or proboscis proper, on the other hand, is elongated and narrowed, and projects horizontally forward in front of the head. It is not fixed in this position, but is capable of forward and backward movement, and elevation and depression, in exactly the same manner as that of *Musca*, though to a smaller extent. It consists of the usual parts, *viz.*, the labrum-epipharynx, hypopharynx, and labium, the latter forming the main bulk of the haustellum and concealing the other two in a groove on its upper surface. The labium is typically spindle shaped; its greatest breadth, about one-third of the total length, is situated at its proximal end, this portion being termed by Stephens and Newstead the "bulb." At the distal end the labium is divided into a pair of labella, which are completely separated from one another in the middle line in front and distally, but united in the proximal part of their posterior surface. They project beyond the labrum-epipharynx and hypopharynx. The wall of the rostrum is entirely membraneous and flexible, that of the haustellum chitinous and rigid, except at the place where the labium divides into the two labella, the chitin being here partly replaced by a soft membrane. That portion of the labellar wall which is external in the position of rest is chitinous.

The palps arise from the anterior surface of the rostrum about its middle. They are clavate, slightly flattened from side to side, and have a few short stout bristles scattered over the surface, and a coat of very fine recumbent hairs. Their length is about equal to that of the haustellum. At the base of each palp there is a small area extending downwards in which the membrane is chitinised. In the resting position the palps lie in front of and in contact with the proboscis, but when it is in use they move forwards and upwards so as to become almost perpendicular to it.

It will be well to refer here to the relation of the several parts of the proboscis to one another in the position of rest, and to the range of movement as seen in the living fly, comparing *Lyperosia* with *Musca* as regards these points. The most obvious difference between the two is that while in *Musca* the proboscis is completely retractile, in *Lyperosia* the haustellum in the position of rest remains completely visible and in a horizontal plane. The labella are not folded backwards on the lower (or posterior) surface of the haustellum, but remain fixed in the same line with it. The joints between the head and the rostrum and between the rostrum and the haustellum may be compared to the human shoulder and elbow, if one imagines the shoulder joint to be capable of movement only in the same plane as the elbow joint. In *Musca* the position of rest is equivalent to that in which the upper arm is bent backwards horizontally behind the body, and the forearm flexed so that the two are in contact ; in *Lyperosia* the amount of flexion of the upper joint is not quite so great, and the haustellum, which remains in a horizontal plane, makes an angle of about sixty degrees with the rostrum. The difference in appearance is simply due to the increased length of the haustellum in *Lyperosia*, and to the incompleteness of the retraction.

From this position movements can be performed which are in every respect similar to those of *Musca*, except that they are more limited in extent. The proboscis is extended by the straightening out of the two joints in the same way that the arm can be extended from the position indicated above until it is thrust out in front of the body. The two joints act together, but not always to the same degree, so that the tip of the proboscis may come to lie in any position within a quadrant of a circle the centre of which is the joint between the rostrum and the head, and the radius the line between this and the tip of the proboscis when fully extended; the upper limit of the quadrant is the horizontal line in which the proboscis lies in the position of rest, and the lower limit in the vertical line, that is, in the position of full extension in *Musca*. The range of movement from the periphery of the circle is of course limited to a distance less than twice the length of the rostrum. In the act of feeding the position occupied is about midway between the upper and posterior sides of the quadrant, and a short distance from the periphery, or, in other words, one of incomplete extension of both joints, whereas in *Musca* and in *Philæmatomyia* there is complete extension, a position only occasionally seen as an agonal phenomenon in *Lyperosia*. By means of these two joints the fly is enabled to move its proboscis about on the skin of the host, while selecting a suitable place to insert the biting parts, and in doing so it is assisted by the lateral and rotatory movements of the head and neck. It will be obvious at once that the whole arrangement of joints is adapted to ensure mobility, and that the proboscis is by no means the fixed organ it is sometimes assumed to be. It follows also that there can be no question of *vis a tergo* in the method of making the wound. The mechanism of these movements will be discussed when the anatomy of the parts has been described.

The Rostrum.

The rostrum has the shape of an inverted and truncated cone, the length of which is slightly greater than the breadth. The relative lengths of the rostrum and haustellum are approximately as one to two, while in *Musca* the two parts are about equal. In the position of rest the rostrum is retracted and can only be seen when in profile. Its wall is entirely composed of a tough but flexible membrane, attached above to the margins of the aperture in the head capsule, and below to the upper end of the labium and to the broadened upper end of the labrum. When the proboscis is fully extended the wall of the rostrum is smooth and taut, and presents four surfaces, anterior, posterior, and two lateral, but when retraction takes place the organ collapses and the wall is thrown into numerous folds, mainly on the posterior surface.

The rostrum is, strictly speaking, a part of the head which can be protruded, and is not composed of the true mouth parts. The internal structures consist of the pharynx, the salivary duct, certain important tracheal sacs, and the muscles which act upon the joint between it and the head and on the haustellum in the movements of extension and retraction. All these correspond with similar structures in *Musca*, but show certain modifications which must be noted.

The pharynx is contained within a chitinous fulcrum which is proportionately smaller than that of the non-biting forms, and narrower in proportion to its length. The lateral plates arise from the middle third of the lateral borders of the posterior plate, and their upper borders, which are much thicker than the rest of the lateral area, pass almost directly forwards to the anterior arch, which therefore lies more nearly opposite to the middle of the posterior plate than in *Musca*. The upper cornua are rather long, and turn slightly forwards at their terminations. The anterior plate of the pharynx, which with the posterior plate encloses the potential cavity of the pharynx, presents an interesting peculiarity in the arrangement of the sensory hairs. There are two sets, a lateral one corresponding to those described by Kraepelin in *Musca*, and a median set situated on the sides of the ridge in the middle line. The lateral set consists of eleven hairs, the position of which is easily seen under a low power on account of the circular clear areas on which they are set; they are arranged in pairs, but only irregularly so, for those of the left side are slightly distal to those on the right and the right hand member of the third pair is absent. The first (distal) pair is much larger than the others, and the second pair smaller, and placed nearer to the first than to those of the third; the median set are small and are just visible as clear spaces at the sides of the ridge, though of course on the opposite surface. There are two nearly opposite one another between the first and second pairs of the lateral set, and three others at irregular intervals proximal to this. This irregularity in structures which one would expect to be symmetrically arranged is rather remarkable.

The lower end of the fulcrum (Figures 11 and 12, Plate II), at the inlet of the pharyngeal cavity, is very different to that of *Musca* or *Calliphora*, being specially adapted to receive the duct which connects the pharynx with the food canal in the haustellum. The lateral diameter of the fulcrum contracts until a four sided channel is formed, bounded in front and behind by the anterior and posterior plates of the pharynx, and at the narrowest point the anterior and posterior walls of the channel cease, while the lateral walls expand downwards and diverge from one another so as to form a sort of funnel, incomplete in front and behind, the concavity of the plates increasing as they diverge.

As described above, the length of the fulcrum is proportionately less than it is in *Musca*, and there is a considerable interval between the lower end of the pharynx and the end of the labrum-epipharynx. This interval is bridged over by a flexible duct, which is continuous with the food canal at the distal end of the haustellum, and terminates above between the lateral funnel-like expansions at the end of the pharynx, which I have just described. This duct corresponds in position and in function to the hyoid sclerite of *Calliphora*, and to the " chitin kapsel " of Kraepelin. Something of the kind appears to occur in all the flies of the Muscid group, and it will be of advantage to adopt for it a term which will be applicable to all. In the above flies, which are certainly more primitive than *Lyperosia*, it resembles a miniature pharynx, having the form of a cavity, communicating in front with the food channel between the labrum-epipharynx and the hypopharynx, just behind the point correctly regarded by Kraepelin as the mouth of the fly. It corresponds exactly with the first of the two cavities of the sucking apparatus of the Nematocerous Diptera, except that it has no dilator muscle and can take no active part in the mechanism of feeding. As it is always sound to name a structure common to many different forms from its appearance in the simpler rather than the more highly specialised forms, I suggest the name " buccal cavity " for this structure, a term which has the double advantage of referring precisely to its position and emphasizing its homology with the corresponding part in the more primitive Diptera.

The buccal cavity in *Lyperosia* (Figure 1, Plate 1, and Figure 30, Plate VI), then, has the form of a tube, which extends from the distal end of the haustellum to the inlet of the pharynx, and has length equal to about one-third that of the fulcrum. In the resting position it is bent forwards at a sharp angle, the upper half being nearly vertical and in line with the pharynx, the lower half horizontal and in line with the haustellum ; in the extended position of the proboscis the tube becomes straight. The structure of its wall illustrates an arrangement commonly met with in insect anatomy in situations where strength and flexibility are required in the same structure. It consists of two laminæ, and internal and an external one. The internal lamina is soft and membraneous for most of its length, and is attached to the chitinous duct which is formed by the coalescense of the labrum-epipharynx and the hypopharynx at the distal end of the haustellum. At the upper end, where the duct is enclosed by the funnel-shaped expansion of the lower end of the pharynx, the membrane is replaced by thin but rigid chitin ; in this situation, of course, no flexion takes place. The outer lamina resembles, when seen from the side, a coarse tracheal wall. It consists of about thirty incomplete rings, very much thicker behind than at the sides, and open in front ; the open space between the rings in front diminishes towards the pharynx, and the terminal rings appear to be quite closed. The thickness of the posterior portion of the rings is so great that they come into contact with one another, and so have, when seen from behind, the appearance of a continuous band with a series of transverse ridges. The lateral portions of the rings in the lower half of duct terminate in minute forks, though those of the one side do not interlock with those of the other as do the more regularly arranged rings in the pseudotracheal channels of the house fly. The arrangement is admirably adapted to maintain the lumen of the soft inner duct, and at the same time to allow of flexion without occlusion.

The salivary duct (Figs. 30 and 31, Plate VI) lies in the middle line behind the pharynx and the buccal cavity. The distal portion is a simple chitinous tube with no cellular lining or differentiation of the wall, but after a short course this is replaced by a series of chitinous rings similar to that of the salivary duct of *Musca.* A short distance above the junction with the hypopharynx there is a small valve, acted on by a delicate muscle, precisely corresponding to that *Musca.*

The tracheæ of the rostrum play an important part in the mechanism of extension of the proboscis. There are two large lateral ones, rather of the nature of air sacs than true tracheæ, on either side of the fulcrum. In dissections of fresh flies one can often separate out these as white sausage-shaped bodies, filled with air ; in transverse sections they appear as irregularly crenulated circles much reduced below their natural size on account of the extraction of the air ; at the lower end of the rostrum they are reduced to the ordinary size and structure of tracheæ, and pass into the cavity of the labium.

The musculature of the rostrum is very difficult to study in so small a fly, and I have not succeeded in dissecting out all the separate bundles of fibres ; sections give one little help. The main bundles are however distinct enough, and do not differ from those described by Kraepelin in *Musca.* It is indeed remarkable how closely the arrangements correspond in the two forms. It will be convenient to discuss the separate movements and their musculature together. Starting with the proboscis in the position of rest, we have to consider first the nature of the mechanism by which the rostrum is extended on the head. The method by which this is accomplished in the house fly has been dealt with with such conclusiveness by Kraepelin that it would be unnecessary to go inte the matter further than to say that there is nothing to indicate that the action is different in this fly, if it were not that the most important muscle of the rostrum has had assigned to it by Hansen the function of extension, in his description of *Stomoxys*. According to Kraepelin, extension of the rostrum on the head is accomplished by the distention of the air sacs of the rostrum, and this is easily demonstrated, as I have pointed out in the case of *Philæmatomyia*, by pressing on the head with a needle. The rostrum is in fact blown out in the same manner that the top of the puparium is forced off at the time of emergence of the imago. Now there is a pair of large muscle arising from the internal surface of the head cavity just in front of the aperture to the margins of which the wall of the rostrum is attached, and inserted into the posterior cornua of the fulcrum, and therefore tending to pull the fulcrum forwards. According to Hansen, the course of this muscle is a backward and upward one, so that its contraction causes the fulcrum to rotate on the fixed point formed by the anterior margin of the aperture, and thus extends the rostrum on the head, an exactly opposite view to that taken by Kraepelin, who regards it as rotating the fulcrum in such a way that its ower end passes backwards, that is, as a retractor of the rostrum, acting in association with another pair which will be referred to below. The direction of rotation really depends on the relation of the fixed point on which the rotation takes place to the line of action of the muscle ; if the fixed point at any period of the contraction of the muscle is below the line of the muscle, then the rotation must take place in a backward and upward direction, and retraction will result. If, on the other hand, the fixed point is above the muscle, then the lower end of the fulcrum must pass forwards and the result will be extension. The action of this muscle might be compared to that of a piston rod acting on a wheel : the direction in which the wheel will revolve is determined by the initial position of the wheel, and if the rod were to be exactly across the middle of the wheel there would, theoretically, be no rotation at all, but the whole wheel would be pulled bodily backwards. In this case, however, the "fixed point" is not really a permanent one, but can be altered by the action of other muscles tending to raise the lower end of the fulcrum, so that the line of action of the muscle is by no means a constant factor. Kraepelin recognised this, and regarded the two movements of rotation and upward displacement as taking place together, the point on which the rotation occurred being constantly displaced upwards and backwards by the action of another muscle. It is quite possible that the divergent views held by Kraepelin and Hansen may each represent a part of the truth, and that this muscle may function as both an extensor and a retractor of the rostrum, the direction of rotation being determined by the action of other muscles ; but this is somewhat unlikely. The point depends really on the exact relation of the upper end of the fulcrum to the aperture in the head cavity in the position of rest, an anatomical detail on which it would be rash to speak with certainty.

The retraction of the rostrum takes place, like the extension, by means of rotation of the fulcrum on a fixed point formed by the apposition of the anterior arch of the fulcrum to the anterior boundary of the head capsule, and this is brought about by the contraction of the muscle discussed above. The pair of muscles which act in conjunction with it arise in the interior of the head, above the occipital foramen, and pass downwards through the whole length of the rostrum to be inserted into the upper end of the labium posteriorly. In addition to these comparatively large and definitely separated muscles, there are several other shorter bands of fibres, apparently corresponding to some at least of those described by Kraepelin and Hansen, but so small that it is impossible even in sections to make out their precise points of attachments. Some of these doubtless aid in the retraction of the rostrum, while others, inserted more anteriorly, appear to flex the haustellum on the rostrum.

The extension of the haustellum on the rostrum is accomplished mainly by a well-defined pair of muscles corresponding exactly to those described by Kraepelin as the "strecker der russel." They arise from the lower end of the fulcrum and pass upwards and outwards to the expanded upper ends of the labral apodemes, and will therefore thrust the labrum-epipharynx, and with it the labium, downwards and into line with the rostrum. The reverse action is brought about by a pair of muscles passing between the upper end of the fulcrum and the distal end of the apodemes, and lying in the front of the rostrum ; flexion is also probably assisted by some of the ill-defined groups of fibres situated, as indicated above, on the sides of the rostrum, some of which are inserted into the membraneous wall.

The Haustellum.

The haustellum of this fly is a much more solid and compact organ than that of *Musca*, a much greater degree of rigidity being necessary for the efficient working of piercing mouth parts. The wall is almost entirely chitinous, and, as in *Stomoxys*, the labrum-epipharynx and hypopharynx lie concealed in a deep and thick "labial gutter." The external appearance has already been described.

The labrum-epipharynx is an elongate slip of yellow chitin of equal diameter throughout the most part of its length, thereby differing from that of *Musca*, which tapers from base to apex. Its upper surface is evenly rounded, and its lower surface deeply grooved to form, with the hypopharynx, the food channel. On cross section it is seen to consist of two laminæ, the outer one, which represents the labral element, having a heart-shaped outline, while the inner lamina, which is the epipharynx, is oval. The two unite at the borders of the groove, and enclose between them a U-shaped space in which there is a small amount of loose cellular material, but no fan-shaped muscle similar to that found in *Musca* and *Philæmatomyia*. At the upper end of the channel the walls become much thicker and the space between them at first increases, so that the whole organ is a little broader than elsewhere and the food channel of a slightly greater capacity. Immediately beyond this point the channel undergoes transition into a closed duct, in the following manner. The outer and inner laminæ approach one another until they come in contact, and fuse to form one thick layer of chitin, the space between them being entirely obliterated; at the same time the edges of the groove formed by the epipharynx approach one another and unite, so that closed canal is produced. This point is therefore the true mouth of the fly, and lies anterior to the position of the mouth in *Musca*. The canal is at first oval in outline, being broader in its transverse diameter than in its vertical one, but in a short distance it becomes circular. The duct is produced upwards a short distance beyond the end of the labrum, and projects into the rostrum. Here it joins the duct already described as the buccal cavity.

The labral apodemes are so similar to those of *Stomoxys* that they call for no remark. They are attached to small pits on the lateral aspect of the labrum at its thickened upper end, the method of attachment being such as to permit of movement inwards when the apodemes are brought into line with the haustellum in the movement of extension. In the resting position the angle between the two apodemes is about fifty degrees; in the position of extension they are almost parallel.

The distal end of the labrum-epipharynx (Fig. 3, Plate 1, and Fig. 23, Plate 4) is modified in a very curious manner, which all the more calls for a detailed description in that no explanation of its function can be offered, though the structure is obviously a purposeful one. When seen from above, the lateral edges approach one another in a gentle curve, to form a point like that of a two-edged sword. The area between the converging margins and that portion of the blade immediately proximal to it has a totally different appearance to the rest of the blade. The upper surface remains as before described, an evenly rounded one, but on the under surface there is developed a conspicuous elongated elevation, about four times as long as it is broad, a little narrower in the middle than at the two ends, and equal in width at its narrowest point to one half the width of the whole organ. When seen in section the organ has at this point a complete rounded outline, with no trace of a groove. The upper half of the section is more pointed than the lower, and the two are separated by a prominent groove, due to the fact that the raised portion of the under surface is constricted at its base. At the proximal end of this elevation the groove on the under surface of the rest of the labrum-epipharynx ceases abruptly in what is apparently a cul de sac, the margin of the raised portion being slightly concave backwards. This margin is situated at the junction of the middle third of the elevation with the upper third, and the elevation proximal to it consists of raised flanges on either side of the termination of the groove, which end abruptly as a pair of blunt tubercles projecting into the food channel. Proximal to these tubercles the margins of the groove show a slight concavity, and thereafter run parallel to one another in the ordinary manner.

The distal end of the elevation extends to within a very short distance from the extreme tip of the organ; at its broadest point it reaches almost to the limit of the converging margins. Beyond it, and reaching to the distal margin, there is a hollowed out tongue-shaped depression on the under surface. The lateral margins of this are raised and overlap the central portion in the middle third, and converge towards one another so as to form a narrowed portion which might be compared to the handle of a racket. The narrowed portion projects into the elevation of the under surface for nearly one-third of its extent, and has at a point just distal to its termination a pair of short curved tubercles set on either side of a slight expansion of the lateral diameter.

It will be seen that the groove of the epipharynx falls considerably short of the end of the organ, being separated from it in fact by the whole length of the elevation. At first sight one is apt to think that the purpose of the tongue-shaped depression at the extreme end must be to direct the food into the channel, and that the elevation is due to the union of the two lateral margins of the epipharynx in the same way that they are united at the upper end of the organ, and that the elevation is a hollow one through which the food passes. Examination of preparations under a very high power tends to confirm this view, for distinct clear space can be seen by focussing down through the elevation. Sections, however, do not confirm this, for they show only one continuous outline, with a little shrunken cellular tissue inside it, and no trace of even a membraneous inner tube, and it is clear that the food channel does actually end at the concave transverse ridge in the upper third of the elevation.

The only suggestion that occurs to one as regards the function of this remarkable structure is that it, in connection with the hypopharynx, acts in some manner as a valve to regulate the flow of blood into the food channel. It can have nothing to do with the making of the wound, for the tip of the organ is far too thin and flexible to have any perforating power, and moreover—and this is an important point which will be referred to later—the labrum-epipharynx does not reach to the tip of the proboscis.

The sensory hairs of the labrum-epipharynx resemble those of *Musca* and *Stomoxys*. There are two opposite to one another at the level of the tubercles which project into the lumen at the distal end of the canal, and several others at irregular intervals along the course of the canal. Each consists of a short stout cylindrical base, projecting into the lumen of the channel and a very fine hair arising from the apex of this. The hairs are all bent downwards in the direction of the canal.

The hypopharynx (Fig. 23, Plate 4, *et seq.*), like the labrum-epipharynx, is a much finer and more delicate organ than that of *Musca*. It is a thin flat slip of yellow chitin, containing in its middle line the salivary duct, and also serving by its apposition with the labrum-epipharynx to close in the food channel. Its distal end, which falls a little short of that of the labrum-epipharynx, is quite simple; it is not produced to a point, but terminates in a very much attenuated margin, in the middle of which the salivary duct opens. At the upper end of the haustellum the hypopharynx fuses with the labial gutter and disappears as a separate organ, only the salivery duct being left. Where the lateral portions of the organ cease the walls of the duct become much thicker and also become adherent to the closed canal formed by the union of the lateral margins of the epipharynx (Fig. 29, Plate 6). The salivary duct thus projects at the upper end of the haustellum below the commencement of the buccal cavity.

The Labium.

The labium consists of two separate parts, the mentum and the labial gutter, which together form a cylindrical chamber enclosing the muscles and other structures. The shape of the labium in *Lyperosia* is intermediate between that of *Stomoxys* and that of *Glossina*, that is to say, the " bulb " is more pronounced than that of the former, and the whole not quite so pointed as that of *Glossina*. Distally it is divided into two labella, which differ so much from the rest of the labium that they constitute a distinct organ.

The mentum (Fig. 1, Plate 1) composes by far the largest part of the labium. It has the form of a spindle, composed of a plate bent to the shape, and evenly rounded except on the anterior surface, where there is an interval in which lies the labial gutter. The truncated upper end is continuous with the membraneous wall of the rostrum, and the lower end with the external wall of the labella. The groove on the anterior surface is a deep one, the edges of the mentum turning backwards as well as inwards, and leaving an interval between them, in which the labrum epipharynx and the hypopharynx lie. There is no thickened lateral border such as is found in *Philœmatomyia.* On the external surface there are a few scattered short bristles, irregularly distributed. The whole length of the organ shows a series of transverse ridges and furrows, deeper and more numerous at the narrower part of the spindle, similar to the "striations" in *Stomoxys*; as will be seen later, these are of great importance in the mechanism of the proboscis. The lower end of the mentum is obliquely truncated from in front backwards and upwards, in such a way that the distal portion of the posterior border is in advance of the anterior border to an extent equal to the diameter of the labium at this point.

On the posterior surface of the distal end of the mentum there is a pair of small but stout chitinous sclerites, termed by Stephens and Newstead the *ventral sclerites* (Fig. 2, Plate 1). They are homologous with the forked rods at the end of the mentum in *Musca.* Each is wedge-shaped, with the broad end of the wedge directed distinctly, and forming a support for the U-shaped rod which separates the labium from the labella. This rod, termed by Stephens and Newstead the "fork," is the homologue of the rod commonly known as the furca in *Musca.* It has the shape of a wide U, and embraces the posterior half of the labium at its junction with the labella. In the resting position of the parts it is directed obliquely downwards and forwards across the external surface of the labella, reaching a little more than half-way across the surface. The middle portion of the furca is moulded to articulate with the ventral sclerites, on to which it is pressed by the action of the muscles inserted into it. A short distance external to the ventral sclerites, there is on each side, proximal to the furca, a small rod of chitin, attached to the edge of the receding margin of the mentum, and closely approximated to the posterior border of the furca, though not fused with it. This represents the second or distal division of the fork of the mentum as seen in *Musca,* where it is as long as and similar to the first division, and only separated from it by a slight thinning of the chitin. The furca and its "lateral sclerites" are not internal structures, as stated by Stephens and Newstead, but are thickenings of the external wall of the labella, the articulation lying between it and the ventral sclerites.

The distal end of the mentum has been described as being obliquely truncated, the posterior portion, which articulates through the ventral sclerites with the furca, being produced beyond the anterior. In this way a space is left between the border of the mentum and the furca, where there is no chitinous wall to the labium. This interval is filled in by a membrane which is attached to the border of the mentum, and anteriorly becomes continuous with the external wall of the labellum; it has developed in it two thin chitinous plates, roughly oval in shape, and placed one behind the other on the anterior border of the organ. The plates are mere thickenings in the membrane, and have no chitinous attachments, and are much thinner than the chitin of the wall of the labium.

The labial gutter forms the bottom of the groove in the anterior surface of the labium, and supports the labrum-epipharynx and the hypopharynx. In its general features it resembles that of *Stomoxys*; it is, of course, the homologue of the shallow chitinous groove on the anterior surface of the labium of *Musca*, but on account of the great development of the muscles of the bulb it has come to have additional functions. It is a stout chitinous groove, U-shaped in the distal portion, but becoming more V-shaped towards the upper end. It extends the whole length of the labium, from the termination of the labrum and the formation of the closed portion food canal to the level of the lateral portion of the furca in the position of rest. As for the most part of its course it lies between the overlapping edges of the mentum it cannot be seen even in cleared preparations, but at the distal end it projects beyond the anterior border of the mentum and forms the anterior boundary of the membraneous space between the furca and the truncated end of the mentum, and can easily be distinguished through the thin wall in this situation. Throughout its length its lateral borders are attached to the adjacent borders of the mentum by a stout membrane, which, however, is of very limited extent, its width being just sufficient to fill in the sides of the space occupied by the labrum-epipharynx—a marked contrast to the corresponding membrane in *Musca*, which is very loosely arranged. At the distal end of the proboscis it is attached to the furca by means of a continuation of the same membrane, in the triangular space already referred to.

The sheet of chitin projecting into the cavity of the labium from the posterior surface of the labial gutter, and aptly termed by Stephens and Newstead the "keel," is present also in this fly, in a slightly modified form. It commences a little distance behind the end of the gutter, as a ridge equal in height to the depth of the groove, and of about the same thickness as the rest of the gutter. This extends for about one-fourth of the length of the gutter, and then becomes thinner, and approaches the base of the gutter again. The keel does not, however, cease at this point, but broadens out again and passes still deeper into the cavity of the labium as the latter becomes of greater diameter towards the bulb, until it almost reaches the posterior surface of the mentum. This upper part of the gutter is only a very thin sheet of chitin, easily bent in dissection, and difficult to see in cleared preparations.

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ERRATUM.

Title page.—For "M.B." *read* "M.D."

ADDENDA.

The magnification of the figures is as follows :—

Fig. 1 × 160.
Fig. 2 × 520.
Fig. 3 × 850.
Fig. 4 × 733.
Fig. 6 × 2,000.
Figs. 7, 8 and 9 × 380.
Figs. 11 and 12 × 500.
Fig. 13 × 900, about.
Figs. 14, 15, 16, 21, 22, 23 × 1,250. The accompanying figures on a slightly larger scale.
Fig. 26 × 750. The accompanying figures larger.
Fig. 30 × 900.
Fig. 31 × 425.

At the upper end of the haustellum the labial gutter becomes much reduced in thickness, and becomes attached to the hypoharynx at the point where the latter is itself becoming narrower. Finally the two fuse together, and a few sections further up only the thickened salivary duct remains, and this, as previously described, becomes adherent to the food canal. This is precisely what happens in the case of *Musca*, except that in the latter fly the hypopharynx does not become adherent to the food canal. The two laminæ of the hypopharynx cannot be distinguished from one another, but this method of termination makes it probable that here, as in the Nematocerous flies, the salivary duct lies between one lamina which is a true outgrowth from the stomodæum and another which is derived from the anterior surface of the labium, that is, from the labial gutter. The chief difference between *Lyperosia* and *Musca* in this respect is that in the former the separation of the labial element from the labium has gone much further than in *Musca*. Separation of the hypopharynx from the labium appears to occur with the adaptation to blood-sucking habit, as one finds a similar state of affairs in the mosquito, where the hypopharynx, though not capable of taking part in the making of the wound, is completely separated from the labium in the female, and remains united with it in the male.

The distal end of the labial gutter (Figs. 4 and 5, Plate I, and Fig. 10, Plate II) is a somewhat complex structure, having become moulded in an intricate manner in order to take part in the articulation between the labium and the labella, and to assist in supporting them during the act of feeding. In the first place, the distal third of the gutter is much thicker than the remaining portion, and is curved a little downwards, that is, towards the furca. It forms a prominent chitinous bar bounding the upper side of the membraneous triangle in the region of the furca. Towards its termination it becomes separated into two distinct portions, with a narrow interval between them. The lower portion, coming from the bottom of the groove, retains the shape of a shallow gutter when seen in cross section, while the upper portion appears as a stout rod, flattened from side to side so that its vertical diameter is about twice its width. In other words, the gutter becomes deeper and at the same time its bottom portion becomes separated from its lateral walls. At the extreme end the lateral roads are slightly swollen, and terminate in blunt points. The lower portion is much more highly specialised. The most ventral portion is continued onwards to the level of the termination of the lateral rods, with a slight upward curve, but the lateral portions cease abruptly at the level of the swollen portion of the upper rods, so that when seen in profile the end appears as if it were sharply cut away from above, leaving a wide interval between the upper and lower portions of the gutter. Further details of the articulation between this pointed end and the discal sclerite will be reserved until the chitinous framework of the labella has been discussed.

The muscles of the labium are very well developed, as they have to actuate the biting apparatus. The most important one is the retractor of the furca. This large and powerful muscle occupies the whole of the cavity of the bulb, arising from the internal surface of the mentum and from the "keel" of the labial gutter, which separates the muscles of the two sides. As it passes forward a tendon is developed in its middle, and as the diameter of the cavity decreases the muscle fibres give place as to a large round bundle of fibrous tissue, very conspicuous in all sections of the narrower part of the proboscis. This tendon is inserted mainly into the inner and posterior surfaces of the tip of each lateral arm of the furca, but it also sends out numerous branching fibres to the internal surface of the external plate of the labellum in the neighbourhood of the furca. Intermingled with the most internal fibres of this muscle in the middle and distal portions of the labium there are other fibres having an oblique direction, and passing from the internal surface of the mentum inwards and forwards; this band of muscle corresponds to that described by Stephens and Newstead, but in *Lyperosia* it does not appear to be inserted into the labial gutter. It has no tendon at any part of its extent, so that it is difficult to trace it to its insertion, and in any case it is a very small band. In addition to this there is in the distal part of the labium, in the region of the thick part of the "keel," a definite band of fibres passing from the posterior surface of the mentum in the region of the ventral sclerites and also proximal to them, directly across the cavity of the labium, to the base of the labial gutter, so that the bands of fibres are cut in their long axis in transverse sections of the proboscis.

It will be well to note here the relations of these muscles to those of *Musca*, in order to be able to understand their function in connection with the mechanism of feeding when we come to discuss the complex structures on which they act. The large retractor muscles in the bulb are quite evidently similar in their origin and insertion to the retractor muscles of the furca in *Musca*, those termed by Kraepelin *retraktor der unteren Chitingabel*; they are, however, enormously enlarged. The second set of fibres appears to correspond to the retractors of the discal sclerites (*oberen Chitingabel* of Kraepelin), while the third is evidently the same as the transverse set in *Musca*. The three sets of muscles are therefore retained, but one of them has increased to a very great degree, while the other two sets are much less conspicuous than in *Musca*, or even in *Philæmatomyia*. In addition there are a few fibres in the middle and posterior portions of the labium, which pass from the lateral extremities of the gutter across the front of the cavity to the mentum; these do not correspond to anything found in *Musca*, and it is impossible to say what their origin may have been.

The only other structures to note in the labium are the nerves and tracheæ. As might be expected in so small a fly, one cannot trace them to their ultimate terminations, but there is one important point to note with regard to the tracheæ. From the end of the tracheal sac in the rostrum to the end of the proboscis the only tracheal structures to be found are a small pair of simple tracheæ, smaller indeed than one would expect to find, situated on either side of the keel of the labial gutter. These become very small in the distal part of the proboscis, and can only be distinguished in the labella by following them up in serial sections. There are no traces of anything resembling an air sac. The nerves pass down the cavity of the labium together with the tracheæ, and are remarkably large. They lie external to the tracheæ, one on each side, and at the upper end of the proboscis the two are of about equal size, but as they pass down the proboscis the tracheæ diminish in size much more than the nerves, so that at the junction of the labium and the labella the trachea appears in sections as a small clear area on the posterior surface of the nerve. It is evident that though the labella require a large supply of nerves, most of the tracheæ are destined for the supply of the muscles in the labium, and it will be a legitimate inference from this that the labella are very highly sensitive structures, and that the reflexes on which the control of the biting parts must depend are highly efficient.

The Labella.

The structure of the labella is so extraordinarily complex that it would be almost impossible to describe it intelligibly were it not that one can trace, in some at least of the parts, a homology between this fly and the simpler, or at any rate the better known, non-biting flies. It will appear in the course of the description that according to my interpretation of the anatomy and physiology of the proboscis, that of *Lyperosia* is not essentially different to that of *Musca*, but is a modification of it, all the parts found in *Musca* being present here and fulfilling for the most part the same functions.

Regarded from this point of view the first thing that strikes one is the great reduction in the size of the labella. The transverse diameter of the two labella is the same as that of the narrowest part of the labium, and the vertical diameter only a little greater. Secondly, the labella, in the position of rest, are not folded backwards on the labium, but are extended in the same line with it, and are, as a matter of fact, incapable of being moved into the position of rest of *Musca*. Further, the fringes of macro-chaetæ which are so conspicuous in the non-biting flies are not present in *Lyperosia*.

The labella are oval in shape, slightly longer than broad, and deeper in the vertical diameter than in the transverse. They are completely separated from one another on the anterior surface by a narrow fissure, which is continuous with the groove on the anterior surface of the labium. The fissure extends round the blunt apex to the posterior surface, but about midway between the tip of the proboscis and the furca it terminates, and from this point the two are continuous with one another. Each labellum consists of an external and an internal wall, united at the side of the fissure, except where the two posterior surfaces are continuous with one another. The external wall on each side consists of thin plates of chitin separated from one another by narrow fissures, which are filled in by membrane, the arrangement being adapted to ensure rigidity and at the same time to permit of movement. The internal wall is composed of the biting teeth, the discal sclerite, and the membrane uniting it to the external wall.

When seen in cross section (Fig. 14, Plate III) the external wall of the labella appears as a oval ring of chitin, the long axis being directed vertically; the ring is incomplete on the anterior surface throughout the length, and in the distal half of the posterior surface. When examined in cleared preparations the plates of the two sides, convex externally, show certain well-defined fissures. The largest of these is on the posterior surface, and commences on each side a short distance external to the middle line and just distal to the furca; from this point the two run parallel to one another up to and a little beyond the point where the two posterior walls diverge at the fissure. Proximal to the commencement of these fissures and anterior to the furca the chitin of the external wall is very thin and semi-membraneous. At the side of each plate there is a similar membraneous interval posterior and distal to the end of the furca. On the anterior border of each labellum the continuous plate ceases gradually and is replaced by a thin membrane loosely arranged, and of course continuous with the membrane bounding the triangular space behind the furca. The membrane is of the same nature as the one in the same situation in *Stomoxys*, that is to say, it is composed of a clear and transparent (in cleared preparation) ground set with small squamæ arranged so that the clear spaces between them form a fine network. The squamæ or thickened areas in *Lyperosia* are however much smaller and less conspicuous than in *Stomoxy*.

The distal limit of this external plate is not well defined, but merges imperceptibly into the membrane of the inner wall. It presents a gently rounded contour, on which there is a row of ten short bristles arising from small raised bases, and forming a terminal fringe to the proboscis. Except for a few much finer and shorter hairs, two pairs of which are situated just in front of the lateral end of the furca, and two more pairs, one internal and external to the membraneous interval on the posterior surface, near the termination of the median fissure, the external surface is naked.

The internal surface of each labellum consists of two distinct portions, one of which is freely moveable, the other being united with its fellow of the opposite side. The distal moveable portion corresponds to the inner surface of the labellum of *Musca*, while the fixed part is composed of the discal sclerite. It will be necessary therefore to describe these two parts separately.

The free portion of the internal surface of the labellum extends obliquely from the proximal limit of the median fissure on the posterior surface, forwards and upwards to the anterior surface, so that it occupies rather less than half the area of the labellum as seen from the side. It is entirely occupied by the biting teeth and their accessory structures, and is connected with the external surface by the thin and transparent membrane which forms the actual internal wall of the labellum in this situation.

The teeth (Fig. 6, Plate II) are very formidable weapons for so small a fly. There are in all eight on each side, three of the set being small and inconspicuous. All are roughly oblong in shape, slightly bent in an upward and forward direction, and with one exception, are bifid at the free end. Counting from the anterior or upper end of the set, the third tooth is the largest, the second and fourth equal in size and little smaller than the third, the fifth and sixth are of the same size and are smaller than the fourth, while the first is smaller still. The seventh and eighth teeth are rudimentary. The seventh resembles the others and is about the half the length of the sixth; the eighth, which is concealed in the angle formed by the two sets of teeth, is very small and its shape is difficult to be certain of. It is not bifid, but pointed, and has on each side of it two deep notches. All the teeth are united to one another at their bases by means of a stout but narrow ridge of chitin, into which the bases merge, so that the arrangement is not unlike that of the teeth of a comb. The ridge of chitin is gently curved along its proximal margin, in such a way that the cutting edges of the teeth are brought into the same straight line, the longest arising from the deepest part of the curve, the short ones from its two ends. The eighth and seventh teeth do not come into line with the others. When *in sitú* the cutting edges of the teeth form an oblique line running from the front backwards and downwards, in the same direction as the end of the discal sclerite.

The accessory structures of the teeth may for convenience be termed collectively the *interdental armature*. That of *Stomoxys* has been elaborately described by Stephens and Newstead and the appearances seen in *Lyperosia* are very much the same, although I have not been able to find some of the smaller structures. The armature consists of two sets of petiolated blades and one set of rod-like sense hairs. The proximal set of petiolated blades are delicate leaf-like processes arising in pairs between the teeth, one pair between each to adjacent teeth, and one pair external to the first tooth. Their length is about the same as that of the teeth next to which they lie, and they project distally so far that the tip of the tooth is opposite the middle of the blade. Each blade arises from the ridge of chitin to which the teeth are attached, at the point where the bases of the teeth join with one another. The pairs arising between the sixth and seventh and the seventh and eighth teeth are very much smaller than the rest. The surface of the blades is finely granulated, but they do not appear to have any coating of hairs. The distal set of blades are much larger and at the same time much more delicate than the proximal ones, and arise from longer stalks, so that their distal ends extend almost to the extreme limit of the internal surface of the labellum. On account of their extreme delicacy it is very difficult to make out their exact number and arrangement, for if one examines them in uncleared preparations the opacity of the other structures renders it impossible to trace them to their terminations, and in cleared preparations they become almost transparent. There appear to be seven pairs, of which the second to the sixth are equal in size, the first rather smaller, and the seventh less than half the size of the others. In shape they are similar to the blades of the proximal set, their length being rather greater than that of the teeth, their breadth about equal to that of the fifth and sixth teeth. The blade ceases at a little distance beyond the apices of the teeth, and they are presumably connected with the ridge of chitin at the bases of the teeth by a stalk, but this is either hidden from view by the blades of the first set or else is so exceedingly delicate that it becomes invisible in cleared preparations.

The rod-like hairs resemble those of *Stomoxys* and *Philæmatomyia*, but are relatively larger, being in fact the most conspicuous objects on the inner surface, next to the teeth. Each arises from a short but broad cylindrical base, and runs forwards and inwards so that it is raised a little from the surface of the membrane, above the level of the teeth. One side of the hair is deeply grooved, and the tip is bluntly rounded. I have not succeeded in finding the nerve ganglion at the base of the hair, but doubtless it exists.

The membrane which forms the internal wall of the labellum, and on which all these structures lie, is an extremely delicate and transparent one, and is apparently structureless. It corresponds to the pseudo-tracheal membrane in *Musca*, but since distension of the labella with blood no longer pays an important part in the mechanism of feeding, and since the size of the labella has been so very much diminished with the adaptation to a blood-sucking habit, its extent has been reduced to the minimum, so that it now exists merely as a narrow sheet connecting the external wall with the ridge of chitin formed by the fusion of the bases of the teeth. There is of course no trace of the pseudo-tracheal channels, but, as I hope to show in a future memoir, there is reason to believe that the petiolated blades are derived from the rings of the pseudo-tracheæ, and moreover continue to fulfil the function of the channels so far as their filtering action is concerned.

We have next to consider the fixed portion of the internal wall. This is evidently derived from the discal sclerite, but the alteration has proceeded to such a degree that it will not be advisable at the present juncture to attempt to separate it into its component parts, since its homology only becomes evident when we trace it through the intermediate forms. The term discal sclerite may then be accepted provisionally, in place of the nomenclature used by the authors cited above.

The discal sclerite is composed of two plates of chitin, lying in the antero-posterior plane, united to one another below, and with their inner surfaces concave towards one another in their middle thirds. The distal margins of these plates are articulated to the teeth, and the proximal ends to the labial gutter. Its structure is so complex and at the same time so important in connection with the mechanism of the proboscis that it must be described in detail.

When a well-cleared preparation mounted on its side is examined, the teeth, discal sclerite, and the end of the labial gutter can be readily seen through the thin external wall of the labellum (Fig. 4, Plate I). One obtains a still better view if by a fortunate dissection one contrives to remove the external plate of one side and to leave the rest of the structures *in sitú*. From this aspect one sees that the apices of the teeth form a line parallel to the distal margin of the labella, and that the ridge of chitin formed by their united bases lies about the junction of the distal and middle thirds of the labella, measured from the furca. The remaining two-thirds are occupied by the discal sclerite, which is closely apposed to the bases of the teeth in front and extends to the end of the labial gutter behind. It does not occupy the whole of the vertical depth of the labella, but only about one-third, and is situated much nearer the upper than the lower border. Its shape when seen from the side is as follows. It is roughly oblong, its long axis being in the long axis of the labella ; the distal end is wider than the proximal, and is parallel to the distal margin of the labella, that is to say, it is directed obliquely downwards and backwards. It is also slightly concave downwards to correspond with the convexity of the distal margin of the united bases of the teeth, which are so closely pressed against it that the two appear united; there is however no chitinous union between them, and they are readily separated by dissection in potash preparations. The upper or anterior border of the sclerite is straight for its distal two-thirds, and in its proximal third dips suddenly downwards so as to leave a shallow notch, in which the lateral portion of the end of the labial gutter rests. The lower border of the sclerite is concave downwards, but its two ends lie equidistant from the border of the labellum. The proximal end is most irregularly shaped, on account of the complexity of the joint between the sclerite and the end of the labial gutter; its ventral third projects upward beyond the dorsal portion, and is bounded by a thickened ridge of chitin continuous with the concave lower border of the sclerite. This thickened portion, equal to about one-third the total width of the sclerite, terminates abruptly by bending again forwards, and from the slight projection thus formed a few strands of fibres can be seen to pass towards the lower angle of the sclerite in front, thus separating the lower portion of the sclerite, bounded by its concave margin, from the remaining portion. The part of the posterior border above this projection is ill-defined, as the chitin is here thinner than elsewhere. It has already been stated that the upper border dips suddenly downwards in its posterior third, where it is overlapped by the lateral part of the labial gutter; at its proximal limit it dips again downwards to join the projecting portion just described, and so forming a sharp angle. This angle is situated exactly in line with the sharply cut away distal end of the lower part of the labial gutter, and by careful focussing one can see that the sharp end of the gutter, which projects forward beyond the angle, in the manner already described, lies between the two sides of the discal sclerite, in fact, it projects into the interior of the sclerite for at least one fourth of its length; the ends of the lateral and lower divisions of the labial gutter are at the same level, but the former is outside, the latter inside, the sclerite.

One more point is well brought out by examination from the side. The wall of the sclerite is not of equal thickness throughout, but is thickened along the upper and lower borders, and at the articulation with the labial gutter. There is also an apparent thickening along the distal margin, but it is difficult to make out whether this is a part of the discal sclerite or if it is the ridge at the bases of the teeth. The thickening along the lower border, and the upturned end of the posterior border continuous with it, form a conspicuous hook-like piece, the significance of which will be seen later.

The discal sclerite when seen from the side appears to be a flat structure, and this is confirmed when we examine it from the front. It is not, however, a simple flat plate, as has already been hinted, but is composed of two plates with a narrow interval between them. This will be better understood if we describe the appearance as seen in a cleared preparation mounted anterior side uppermost.

In the first place one must note that the two labella are not in contact with one another, but that they diverge from behind forwards, leaving a comparatively wide fissure between them. This is, I think, to be regarded as an artifact, due to the shrinkage in the making of the preparation; the two labella are in all probability closely apposed to one another in the natural condition of rest. Allowing for this in the interpretation of the appearance seen, the two sides of the discal sclerite appear from this point of view as parallel or slightly diverging ridges, the edges of the plates. By careful focussing one can make out that the two plates are concave on their opposing surfaces, bounding a cavity open only on the anterior surface, and probably closed in the natural condition of the parts by the apposition of the anterior edges of the plates (Fig. 7, Plate II). The joint between the sclerite and the labial gutter is seen by careful focussing in a well-cleared preparation. At the most anterior (dorsal) point one can distinguish the two lateral rods derived from the end of the labial gutter, overlapping the most proximal portions of the upper borders of the sclerite, and lying a little to their outer side. At a lower level the projecting pointed end of the lower part of the labial gutter comes into view (Fig. 8, Plate II), and it is seen that the poin corresponds to the middle third of the floor of the gutter; when seen from above it is not unlike a J pen in shape. At either side of the base of this point the edges of the gutter are transverse. It is clear from this that the middle portion of the gutter does actually project into the cavity between the two walls of the sclerite. At this level there comes into view a stouter piece of chitin, at the distal end of the sclerite, which marks the point where the two labella are united on the posterior surface, and by focussing a little lower than this (Fig. 9, Plate II) one sees that it forms the point of a long and narrow triangle, the base of which is situated proximal to the joint between the labial gutter and the sclerite. The base, which is a well marked transverse band, lies at a lower level than the apex, and, as one may infer from the fact that the lateral portions come into focus before the middle portion, is itself so bent as to be convex downwards. The significance of this apparent triangle will be evident by comparing it with the lateral aspect. It is, in fact, the lower triangular portion of the discal sclerite. The pointed apex is the most distal limit of the lower border of the sclerite, a point where the two lateral walls are attached to one another, and the base is the upturned edge of the lower border, which when seen from the side appears as a hook-like projection.

To confirm the above observations it is necessary to examine the labella in serial section.

Figure 14, plate III, represents a section through the distal portion of the labella, at a point where the two are still separate. The external chitinous plates of the two sides form an oval outline, with the long axis in the vertical plane. Inside this there are seen the two sets of teeth parallel to one another in the long axis of the labella, and separated from one another by a narrow interval, which, by the way, is probably an artifact due to shrinking. At the upper end the teeth are united to the external plate by a strong membrane, which is thrown into numerous folds; at the lower end the junction is less definite, being formed by loose strands of fibres. At the lower end of the section one sees some of the rod-like hairs cut into irregular but recognisable fragments, and some of strands of yellow chitin which are probably the stalks of the petiolated blades. The free portions of the teeth are shaded lightly, and show an irregular outline due partly to fractures and partly to the teeth of the two sides not being cut in exactly the same plane; in the sections they are of a bright canary yellow colour, like that of the piercing stylets of the Nematocerous Diptera. The more deeply shaded portion into which the teeth merge is stained a deep purple by Delafield's hæmatoxylin, and is of a fibrous nature. It forms a continuous band which unites the bases of the teeth to the edge of the discal sclerite, and it is by virtue of the flexibility and strength of this band that, as will appear later, the teeth are retained in position and yet can be turned completely backwards on the edge of the sclerite.

Sections distal to this have much the same appearance, except that they show the fringe of hairs on the distal border of the labella, and in these one can note the central canal which perforates them, and the enlarged base, which bears the same relation to the hair as the basal joint of the antenna does to the rest of the appendage. The rod-like hairs do not show a central canal, nor can one recognise in them the groove which they appear to have when examined in cleared preparations.

As the teeth are traced upwards the darkly stained band of fibres at their bases becomes more regular in outline until it forms a continuous band on either side of the labella, and after a few sections the bands of the two sides unite on the lower side. The membrane on the external aspect of the labella then becomes continuous from side to side and the labella are open only on the anterior aspect.

A few section above this we have the appearance represented in figure 15, Plate III. The teeth have disappeared, and in place of them we find only the discal sclerite, composed here of two lateral plates in the vertical plane, united at the lower end only. In the upper and lower thirds the two plates are almost parallel to one another, but in the middle they diverge so as to present opposing concave faces, limiting a circular space. In the interval between the two at the lower end there appears a separate piece, oval in outline, pointed at its ends, and almost filling up the interval between the two lateral walls in this situation. In the next few sections this piece enlarges, becomes more rounded, and is more and more closely approximated to the lateral plates, until it fuses with them. The distal end of this free piece is situated at the point where the two labella fuse with one another on the posterior surface, and it can be seen in this situation in cleared preparations. As it broadens out distally the two lateral halves become a little separate from one another, and a small amount of loose cellular tissue appears in the space.

In the sections proximal to this point there is a rapid change in the appearances, once we pass to the upper end of the discal sclerite. Figure 16, Plate III, represents a section just behind the point where the free median plate has fused with the lateral plates. We see here that the external plate has undergone a considerable change and now presents an irregular outline, marked by two furrows on either side of the middle line; the median portion of the sclerite is now fused to the lateral portions, and shows some loose cells in its interior. The two plates of the sclerite are now divided into an upper and a lower portion. A few sections distal to this the division commences at the upper limit, and passes down as we progress from the labella to the labium. In the middle of the lower portion of the section there appears another free piece anterior to the one already noted, as shown in the figure. We have therefore two lateral and anterior portions, a U-shaped lower or posterior plate, and a middle piece fused in the angle between them, and now another piece of solid yellow chitin anterior to this. The two lateral pieces are the ends of the upper portions of the labial gutter, the anterior piece in the middle is the end of the middle portion of the gutter, and the rest belongs to the discal sclerite. As we pass upwards from this point the discal sclerite becomes steadily reduced in size while the labial gutter comes to occupy more and more of the section. In the next figure (Fig. 17, Plate III) we see that the anterior middle piece has increased in breadth and in depth, and the vertical extent of the lower U-shaped piece has become much less, and at the same time it is wider. The gutter rests on two notches on the inner sides of the sclerite, which is here rather V-shaped. In the next figure, which represents the next proximal section, the middle portion had definitely assumed the shape of the gutter, and has become connected with the ends of the lateral portions, while it is embraced by the now rather wider part of the sclerite. Still higher up the sclerite becomes much thinner and recedes behind the gutter, where it appears as a wide arch. A few sections higher up it appears only as a narrow arched hand behind the gutter, the two portions of which remain quite separate from one another. Above this it ceases, and at the level of the furca (Fig. 21, Plate IV), the two halves of the gutter unite with one another by bands of fibres. Proximal to this the keel of the gutter begins to appear and the section passes through the ventral sclerites.

In the distal portion of the labella, then the food canal commences between the teeth. As we shall see later, the vertical portion of the interval between the two sides at this part of the proboscis does not exist in the state of action, but the true permanent canal begins at the distal sclerite, about the point depicted in figure 23, Plate IV. Its commencement is bounded by the two sides of the discal sclerite, and above this by the labial gutter. The labrum-epipharynx and hypopharynx do not appear in the section till we reach a point just proximal to the thick ends of the vental sclerites.

The Hæmatocœle of the Labella.

So far only the inner and the outer walls of the labella have been described. Distal to the point of fusion on the inferior surface each labellum has a complete inner and outer wall, as shown in figure 14, Plate 3, and throughout the labella are separated on the anterior surface of the labium. The space seen in the sections between the inner walls of the two labella in the position of rest is probably an artifact due to the different degrees of shrinkage between the chitinous and membraneous portions; the two inner walls, normally in contact with one another in the resting state, correspond to the pseudo-tracheal membrane of the house fly. The potential space between them represents, as will be seen presently, an invagination of the distal end of the proboscis, which can be done away with by the retraction of the outer wall. Between this inner wall and the chitinous outer wall there is a space, which is continuous with the hæmatocœle of the labium and through it with that of the rest of the body; this space, as shown in the sections, which are accurate drawings traced with the aid of a camera lucida, contains a number of large and irregularly shaped cells, which are the corpuscles of the blood of the fly. In the drawing they are depicted as actually seen in the preparations, and show obvious shrinkage and deformity, due of course to the drastic treatment which is necessary to get even tolerably good sections of such a resistant and impermeable region. Most of the cells are free in the space, while others, which are probably of different origin, appear to be attached to the inner and outer walls. The number and distribution of these cells differs a good deal in different preparations, but they are generally most numerous in the distal part of the labella. From the point of view of the parasitologist, the existence of this blood space in the labella is of some importance, on account of the opportunity it offers for the passage of any parasite which once becomes free in the body cavity to pass into the wound made by the fly. The only obstacle to be encountered is the thin inner wall of the labellum. The connection of this blood space with the mechanism of the proboscis will be discussed later, but it should be noted here that this very small and definitely bounded space represents the wide interval between the inner and outer wall which is found in the labella of the non-biting flies, when the labella are distended.

The Mechanism of Feeding.

Having now described the anatomical structure of the proboscis, we are in a position to consider the mechanism by which it acts in the making of the wound and in the absorption of the blood. It will be evident that such extraordinarily complex structures as are found in the labella must have an equally complex method of action, and it will be well at the outset to state that since the difficulties in the way of observing the actual working of the organ, or producing the actions by artificial means, have proved insurmountable, the explanations offered hereafter are in the nature of working hypothysis, and do not pretend to be a complete account of all the factors which may come into play when the insect feeds. So many remarkable features have appeared in the course of the investigation that one hesitates to assume that the subject is exhausted, and although what has been found agrees in the main principles with what occurs in other flies, one must be prepared to find that further study will reveal yet more complications.

So far the whole description of the anatomy has referred to the parts in the position of rest, and all the sections are drawn from specimens fixed in that position. Sometimes, however, one can succeed in fixing a proboscis in another position, which, there is reason to believe, is that into which it passes during the process of feeding and, as I hope to show, it is the change from the one position to the other that it is the essential act by which the wound is made. It will be necessary to describe the appearance of the labella in this position (Fig. 13, Plate II); the attitude taken up by the haustellum and the rostrum has already been dealt with.

The specimens which I have obtained fixed in this position were got by pressing forcibly on the head while the fly was immersed in the fixative, and mounting without clearing. I have found that the action of the potash in dissolving the soft structures always results in bringing the proboscis back to a position of rest, and that unfortunately precludes any detailed examination of the chitinous parts. It enables one to assume, however, that the position is attained, and retained by the action of the muscles, and that when the muscles relax, as happens when they are dissolved by the potash, the position of rest is again assumed.

In the position of action, as we may provisionally term it, the appearance of the labella is totally changed. The internal surface becomes external, and the length of the organ is reduced. In other words, the distal end of the proboscis is evaginated. The two labella now present a rounded appearance, with no trace of the fissures on the anterior and posterior surface, and all the structures which in the position of rest lie on the internal surface and point distally now lie on the external surface and are directed backwards. The distal margin of the organ is formed by the bases of the teeth, which, it should be noted, form a concave border directed downwards and backwards, not in the direct transverse axis of the proboscis. At each end of the tooth plate there is a short forward projection, and if one focusses carefully one sees that these are the two ends of the anterior border of the discal sclerite, which lies immediately behind the united bases of the teeth. The teeth themselves arch upward and backward from their bases, so as to point in the direction of the long axis of the proboscis, and the petiolated blades and rod-like hairs lie in line with them. Behind these there lies the fringe of hairs, which in the resting state form the distal fringe. They are now, however, directed backwards well out of the way of the teeth. The external plate of chitin is displaced backwards so as to reach the furca, and it, and the smaller plates of chitin which lie in the triangular space between the end of the labial gutter and the furca, are very loosely arranged, and ruckled up. The position of the furca is important. Instead of being arranged as a transverse arch, it is rotated backwards so that it makes an angle of half a right angle with the long axis of the labium, pointing upwards and towards the head. The lateral arms of the furca are thus displaced backwards for a distance equal to the length of the external plate. With regard to the labium, the transverse ridges and furrows are much more conspicuous than they are in the resting condition. As I have been unable to obtain cleared preparations fixed in this position the position of the labrum-epipharynx and hypopharynx cannot be defined, but it is evident that their distal ends must now be much nearer the distal end of the proboscis than they are in the resting position.

We have now to discuss the possibilities of the proboscis as a biting and piercing organ, and in doing so it will be convenient to clear the ground by noting certain limitations under which the organ is placed by reason of its anatomical structure. In the first place, the labrum and the hypopharynx are placed at once out of court; they do not reach to the end of the proboscis, and even supposing that they could reach it in the evaginated condition, they could not project sufficiently far to be effective unless the discal sclerite were already inserted into the wound. Moreover, they are not provided with cutting ends, but are more or less flaccid.

The arrangement of the joints of the proboscis is such that it is not adapted for the propagation of force from the body of the fly, as any pressure from behind would tend to fold up the organ. This point has already been dealt with.

The cutting weapons must therefore be the teeth, and the teeth only, and the question to decide is as to the particular motion by which they act. Stephens and Newstead, in their account of *Stomoxys*, have suggested that they cut by a semirotatory motion, after the manner of a carpenter's auger, the muscles involved being those which pass between the gutter and the wall of the labium. This hypothesis cannot stand, for it would necessitate the presence of a joint adapted for a rotatory motion between the teeth and the rest of the proboscis, and such a joint does not exist and is not described by them; indeed, the only joint which would be of use for such a method of action would be one between the base of the labial gutter and the mentum, assuming the teeth to be firmly fixed on the end of the discal sclerite and that the sclerite was firmly fixed on to the end of the labial gutter. Rotatory motion of any sort would be a very extraordinary deviation from the type of motion possible in *Musca*, and in the case of *Lyperosia*, as in *Stomoxys*, it is put entirely out of the question on account of the nature of the articulations.

The one motion about which there is no doubt is that of the eversion of the labella and the upward displacement of their outer walls. One can see this take place under ether, and can produce it by pulling on the muscles of the bulb in dissections. These muscles are by far the largest in the proboscis, and one would naturally expect them to play an important part in the mechanism of the making of the wound. By their contraction they cause the furca to be rotated in an upward direction, on the fixed point provided by its articulation with the ventral sclerites, in such a way that its lateral arms are displaced from their transverse position to one in which they make with the long axis of the labium an angle of about half a right angle, the ends of the furca pointing towards the head, and as the rotation takes place the chitinous external wall of the labellum is also displaced, both on account of its intimate connections with the furca and because it receives directly some of the fibres of insertion of the tendon of the muscle of the bulb. Now the internal walls of the labella are firmly attached to the distal end of the discal sclerite, and the sclerite itself is practically a fixture on the end of the labial gutter, so that what happens when the full amount of traction is exercised on the outer walls is that the invagination is undone, and the end of the discal sclerite becomes the most distal point of the proboscis, as is shown in figure 13. As this unfolding takes place the teeth, which are firmly attached to the end of the discal sclerite, are rotated through about half a circle, so that their serrated points come to point upwards instead of downwards.

This movement of the teeth constitutes, I believe, the essential act in the mechanism of the proboscis, and it is by a repitition of this movement that the wound is made. I have referred in a previous paper to the rapidity of action of which insect muscle is capable, and the action of the muscles of the bulb in undoing the invagination at the end of the labella, and so causing the teeth to press upwards, appears to me to be another instance of it. The muscles which are inserted into the furca are not only much larger in this fly than they are in *Musca*, but they are proportionately very much larger than those of the anterior set, and are undoubtedly the dominant motive force in the proboscis.

Retraction of the furca is not the only result of the action of these muscles. It has already been pointed out that the labrum-epipharynx and the hypopharynx do not reach to the distal end of the proboscis in the resting position. In fact, they are so much shorter than the combined labium and labella that their distal ends only appear in sections about the level of the furca, and distal to them there is the whole length of the discal sclerite. Now the discrepancy in length is partly compensated for by the retraction of the labellar walls, by means of which the distal end of the discal sclerite becomes the terminal point of the proboscis, but even this is not sufficient, as is clearly shown by actual measurements of cleared proboscides, to bring their distal ends into such a position that they can perform their functions, and further shortening is required before they can reach the wound. This is accomplished by the shortening of the whole of the mentum. In the early part of this paper it was stated that the whole of the chitinous wall of the mentum is traversed by a closely set series of ridges and furrows. Now these do not present the same appearance in all preparations, and a careful comparison of those in proboscides which are in the position of rest and those in the position of action shows that the more the lateral arms of the furca are displaced backwards the more marked the ridges and furrows become, and it follows that in each individual specimen the more marked the furrows are the shorter the mentum will be, for the crinkling of the wall must reduce its length. I have been unable to obtain a cleared preparation in which complete evagination has occurred, but I have no doubt that if one could obtain one it would show that the evagination of the labella and the crinkling of the mentum taken together had reduced the total length of the labium just sufficiently to bring the labrum-epipharynx and the hypopharynx to the distal end of the proboscis. The muscles of the bulb, the retractors of the furca, bring this about by pressing the furca on the ventral sclerites, so that the movement of the furca is an actual displacement as well as a rotation on its fixed point.

The labrum-epipharynx and the hypopharynx are of course quite incapable of being moved on the labium, owing to the close attachments at their proximal ends. The labial gutter cannot move on the mentum, for, although there is no firm chitinous union, they are closely held together by means of the membrane which unites their lateral borders throughout their length, and at the proximal end the attachment is still more close. When the mentum is shortened the labial gutter must therefore remain of the same length, and it is a little difficult at first to see how this difficulty is to be overcome, for if the two remain in the same plane retraction of the mentum alone will not affect the relations of the discal sclerite and the terminations of the labrum-epipharynx and the hypopharynx. Two points which have already been mentioned help to solve this difficulty. In the first place, the proboscis when in use is not held perpendicularly, but points a little forward, and the distal margins of the discal sclerite form a line parallel to the surface of the skin of the host when the proboscis is held at this angle, as will be seen from figures 1 and 5, Plate 11. If the angle at which the labella make with the labium in the position of rest be compared with that in the position of action, it will be seen that in the latter case the angle is considerably greater, that is to say, the retraction of the mentum is accompanied by a flexion of the joint between the labial gutter and the discal sclerite. The amount of flexion is small, but it is enough to materially shorten the distance between the base of the labium and the opening at the distal end of the discal sclerite. This flexion is produced by the action of the retractors of the furca, acting through traction on the inner walls of the labella.

By means, therefore, of the contraction of the retractor muscles of the furca, the most powerful muscles in the proboscis, the furca is rotated so that its arms pass in the direction of the head, and so carries with it the external wall of the labella, which are turned inside out, the teeth being drawn through the wound and exercising their obvious cutting function as they go ; it is also displaced bodily upwards, room for it being made by the actual shortening of the mentum. The discal sclerite is at the same time flexed on the end of the labial gutter, and in this way the distance between the proximal and distal ends of the labium is so shortened that the labrum-epipharynx and the hypopharynx come to be at the same level as the end of the discal sclerite. They are thus in a position to form the tube up which the blood can be sucked, and the hypopharynx can transmit its saliva directly into the wound. We have next to consider how the parts pass from the position of action thus attained to the position of rest, in order to be able to repeat the movement. There is obviously no muscle which can directly invaginate the end of the labella, and undo the furrowing of the mentum, and we must look for some indirect method by which this can be accomplished. Here a comparison with *Musca* helps considerably. In *Lyperosia*, as in *Musca*, there is a well developed transverse muscle, situated, as already described, in the distal portion of the labium, and the simple acceptance of the similarity of function between this and the corresponding one in the non-biting flies provides a rational explanation of the method by which the labella are returned to the position of rest. In *Musca*, according to Kraepelin, the contraction of this muscle drives the blood into the space between the inner and outer walls of the labella, and thus assists in distending them so as to bring the pseudotracheal membrane into action. In *Lyperosia* the relations of the labellar walls to the labium are considerably altered on account of the fixation of the organ in a definite position, the backward and forward rotation of the discal sclerite being very limited, but the distension of the intralabellar space can still occur, and is brought about by the same mechanism as in *Musca*, that is to say, respiratory movement, aided by the transverse muscle. The result in this case is that when the blood is forced down into the labella the invagination at their distal end is reproduced, and the two internal walls come again in contact with one another, and at the same time the contraction of these fibres, by reducing the transverse diameter of the labium, must increase the longitudinal diameter, and thus undo the furrowing of the wall. The eversion of the teeth, which is the essential feature of the action of the proboscis, is thus accompanied by evagination of the labella, and the passage back again to the position of rest by a corresponding invagination; evagination being a reduction, and invagination an increase, in the length of the labium. The fixed point from which the labellar walls can be forced out, and back to which they can be drawn, is the distal end of the discal sclerite, to which they are attached.

There remains only to consider the mechanism by which the discal sclerite is returned to the position of rest. Again a comparison with *Musca* affords valuable assistance. We have seen that the discal sclerite is articulated, in a most complex manner, with the end of the lanial gutter, and that there is in *Lyperosia* a small bundle of muscle fibres which correspond with the anterior and mesial set in *Musca*, the retractors of the discal sclerite. The exact point of insertion of these fibres, which have no terminal tendon, is difficult to make out, but they can be traced to the proximal end of the sclerite. Whether they are actually inserted into the sclerite or to the membrane in its vicinity will not affect the action, for the fibres are definitely anterior to the larger muscle of the bulb, and must act on the joint in an opposite direction. The joint between the discal sclerite and the end of the labial gutter having then been flexed by the indirect action of the retractor muscle of the furca, it can be straightened again by the anterior muscle fibres, and these two actions follow one another each time the teeth are drawn through the wound at the eversion and closing of the labella. Eversion of the teeth is of course carried out against the resistance offered by the skin of the animal on which the fly is feeding, and consequently the muscles which bring it about are very highly developed, while the closing of the teeth is carried out without any special resistance, and the muscles are not more developed than in *Musca*. We may suppose that after each contraction the labella are thrust a little deeper as the wound is made, until blood is reached. When this occurs the proboscis is probably held in the fully retracted position, so that the labrum-epipharynx and the hypopharynx are in the most advantageous position for collecting the blood.

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EXPLANATION OF REFERENCE LETTERING.

a. a., axial apophysis, or ventral portion of the discal sclerite.
a. f., the fissure between the two labella on the anterior or dorsal surface.
ap., apodeme of the labrum.
b., the bulb.
b. c., the buccal cavity.
c., blood cell, in the hæmatocœle of the labellum.
c. p., the distal chitinous plate in the membraneous area of the labella.
c. p., the proximal ditto.
c. s., the cul de sac at the end of the labrum-epipharynx.
d. ph., the dilator muscle of the pharynx.
d. s., the discal sclerite.
e. f., the external fringe of hairs on the labella.
ex. h., extensor of the haustellum.
ex. p., external plate of chitin in the labellar wall.
ev., elevated area on the ventral aspect of the labrum-epipharynx.
f., the fulcrum.
f.', the anterior arch of the fulcrum.
f.", the funnel-shaped lower end of the fulcrum.
f. b., strong fibres uniting the upper end of the labial gutter and the lateral borders of the mentum.
f. c., the food canal.
f. t., fibrous tissue uniting the teeth to the discal sclerite.
fu., the furca.
fu. f., fibrous band connecting the two lateral arms of the furca internally.
hy., hypopharynx.
k., keel of the labial gutter.
lb., labella.
l. ep., labrum-epipharynx.
l. g., labial gutter.
l. g.', the dorsal portion of the labial gutter, forming the sides of the groove.
l. h., labral hairs.
l. r., lateral rods, corresponding to the distal portion of the fork of the mentum in *Musca.*
m., membrane forming the wall of the rostrum.
m. a., membraneous area between the chitinous walls of the labella and the mentum.
m.', the transverse muscle of the labium.
m.", the anterior and mesial set of muscles, which act on the joint between the discal sclerite and the labial gutter.
m'''., the retractor muscle of the furca, with its tendon.
m. a., membraneous area between the labium and the labella.
mt., the mentum.
n., nerve.
p., the palp.
p.', the distal petiolated blades.
p.', the small proximal set of petiolated blades.

ph., the pharynx.

r., the ridge of chitin which connects the furca with the external chitinous plate of the labella.

r. r., retractor of the rostrum.

r. h., rod-like hairs.

s. d., salivary duct.

t., teeth.

tl., t. 6., the first and sixth teeth, counted from the dorsal side.

tb., tubercles at the distal end of the labrum-epipharynx.

tr., trachea.

v. sc., ventral sclerites.

PLATE I.

Figure 1.—The proboscis in profile, drawn from a potach preparation. The position is one of slight extension, and only the structures of one side are drawn. Note the extent and position of the membraneous area near the furca, and the transverse ridges and furrows on the mentum.

Figure 2.—A view of the posterior surface of the labella, to show the furca and its attachment to the external wall of the labella on each side, and its articulation with the ventral sclerites.

Figure 3.—The ventral aspect of the labrum-epipharynx at its distal end, to show the curious nature of the termination of the food canal, which ends in the cul-de sac. c. s.

Figure 4.—The end of the labium and the labella in side view. The middle portion of the external wall is shown as cut away to disclose the discal sclerite *in situ*, with its attached teeth.

Figure 5.—Outline of the labial gutter at its distal end, where the lateral dorsal and the middle ventral portions are separated.

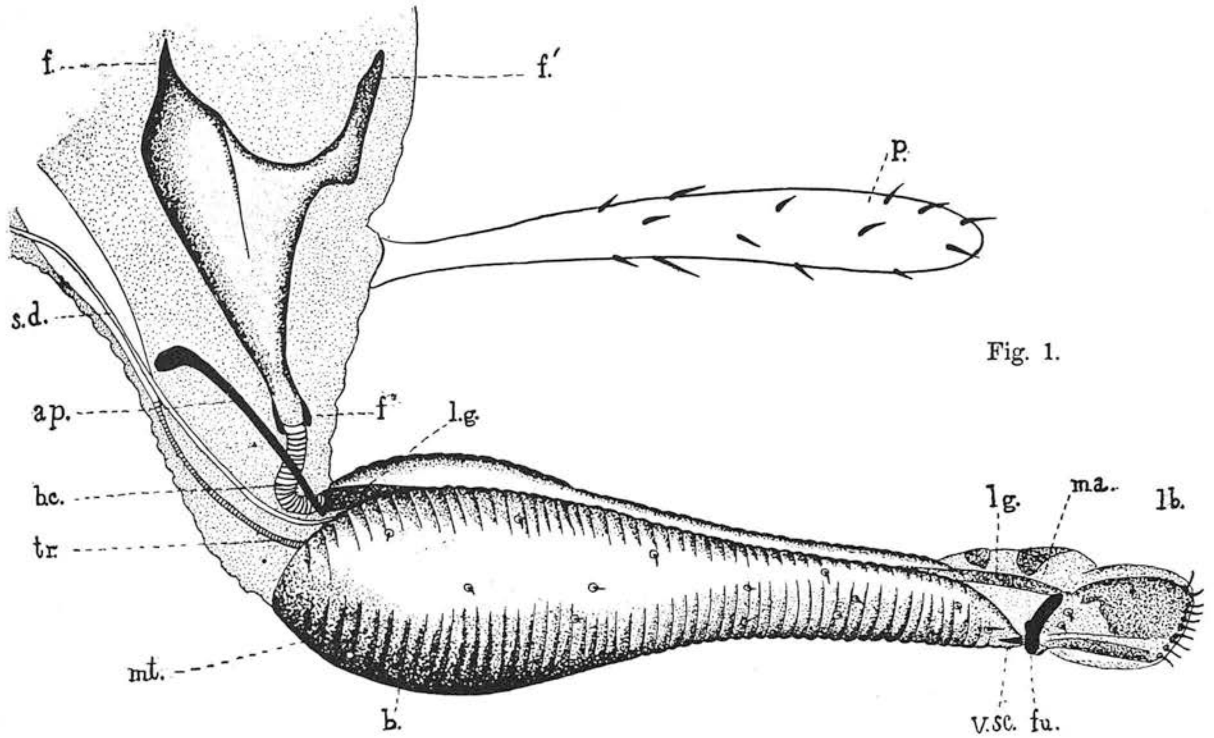


Fig. 1.

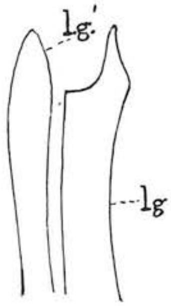


Fig. 5.

Fig. 2.

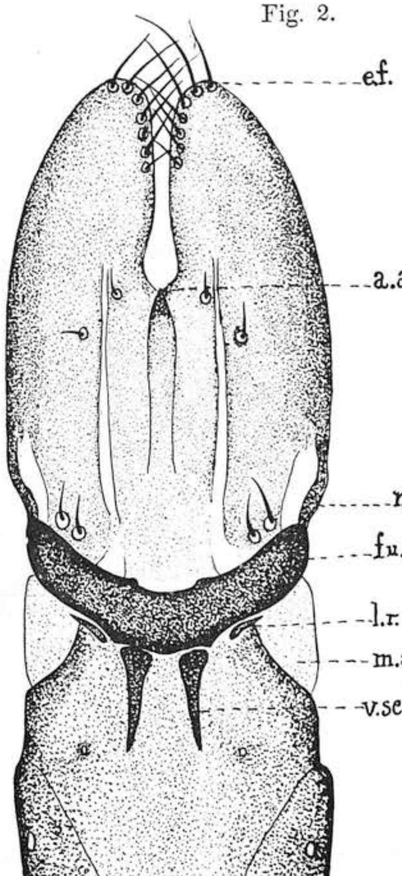
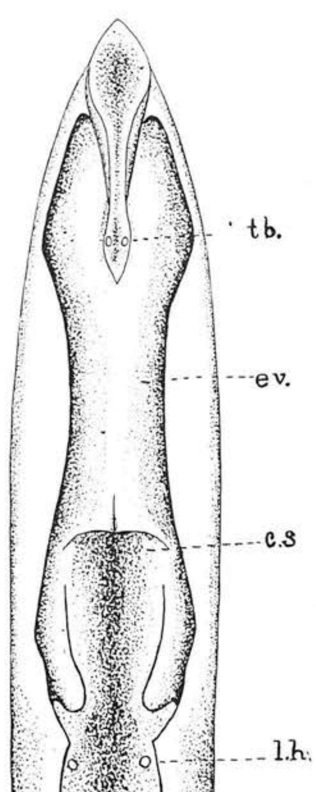


Fig. 3.



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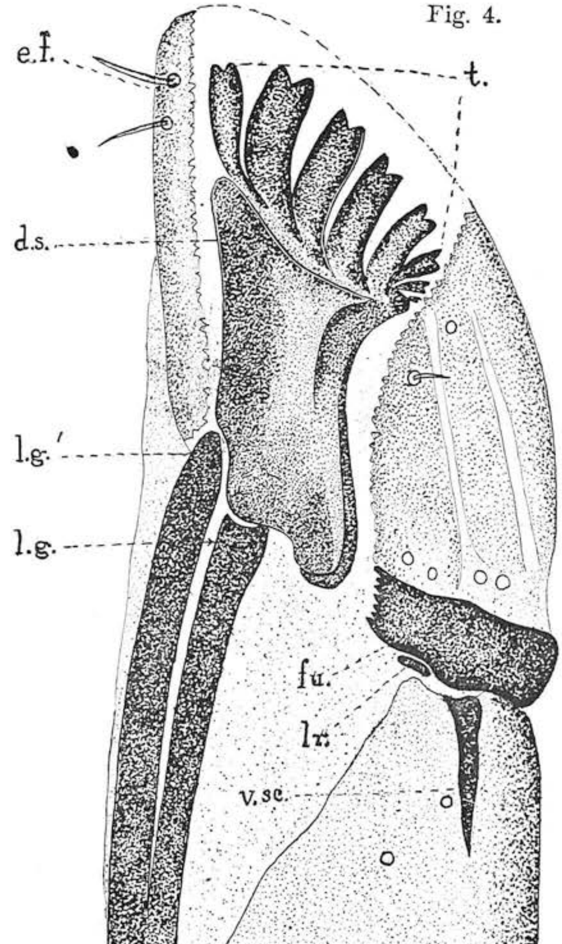

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PLATE II.

Figure 6.—The teeth and their accessory structures, dissected off the discal sclerite. Note that, although the teeth differ in size, their cutting ends are brought into line by the curvature of the attached ends.

Figure 7.—The labella as seen in a well cleared preparation, mounted dorsal side uppermost. In this drawing the portions nearest the microscope were in focus.

Figure 8.—The same preparation, at a slightly lower focus. Here the ventral portion of the labial gutter is shown, and the lateral arms of the furca, which arch forwards from the posterior surface so as to come into focus.

Figure 9.—The same preparation, at a lower focus. Here the furca is seen from the front, and the whole length of the triangular axial apophysis is in view.

Figure 10.—The distal end of the labial gutter, as seen in a dissection. Note the separation of the dorsal and ventral portions.

Figure 11.—The distal end of the fulcrum, showing the funnel-like expansion and the buccal cavity.

Figure 12.—The proximal end of the food canal in the haustellum, showing the tube formed by the fusion of the epipharynx and the stomadeal portion of the hypopharynx as it projects from the haustellum into the rostrum.

Figure 13.—The labella in the position of action.

Fig. 6.

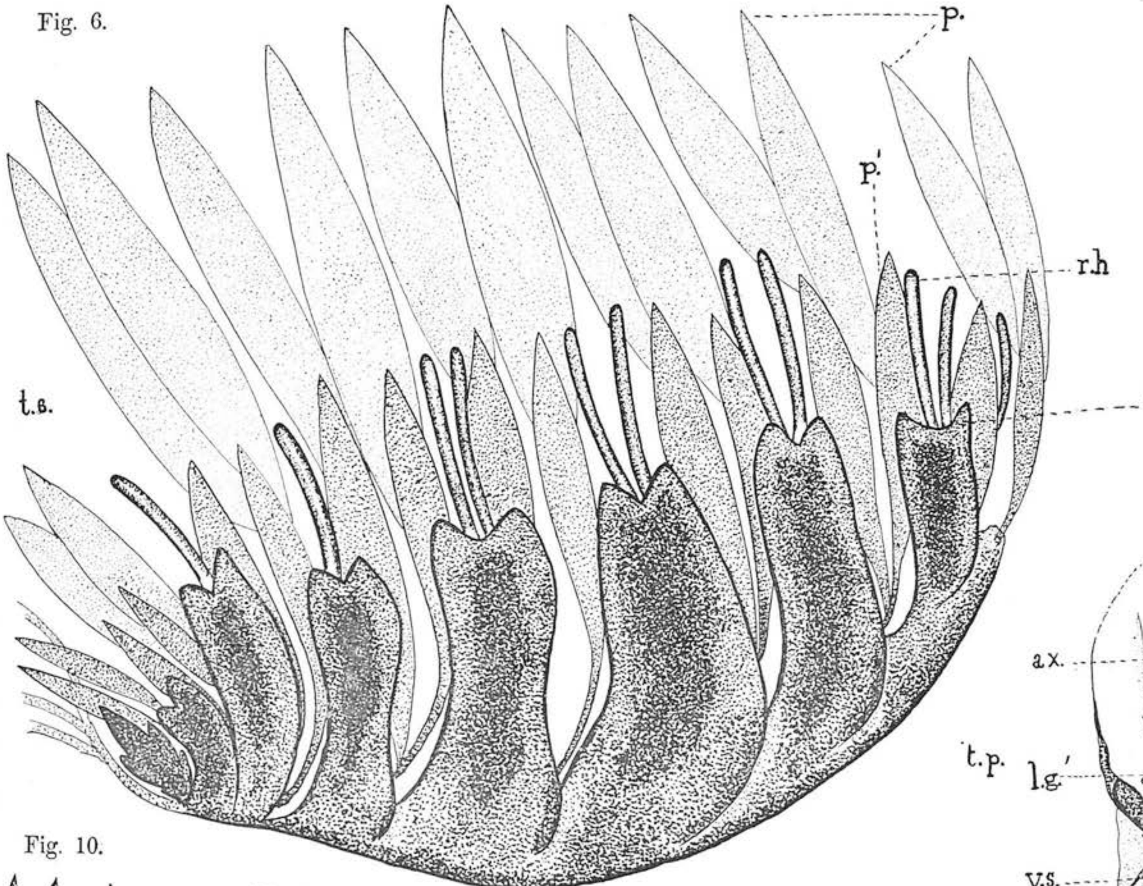


Fig. 9.

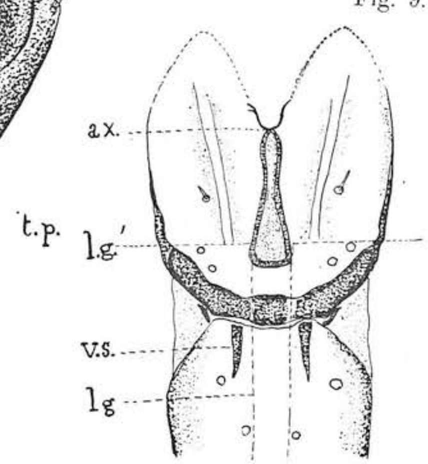
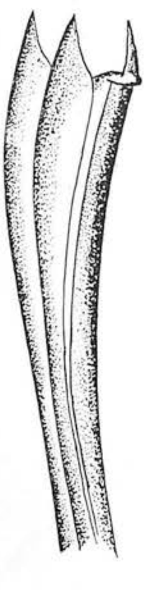


Fig. 10.



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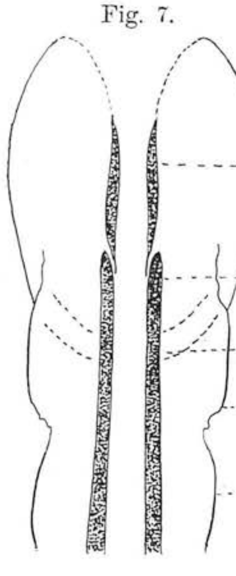

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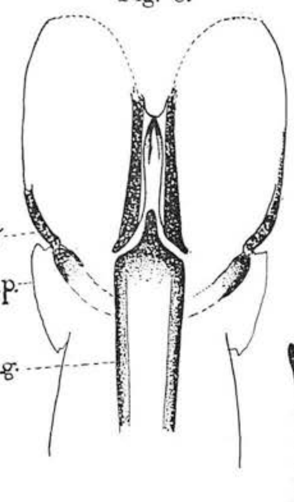

Fig. 11.

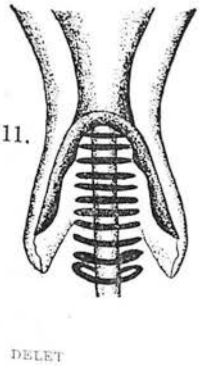

Fig. 12.

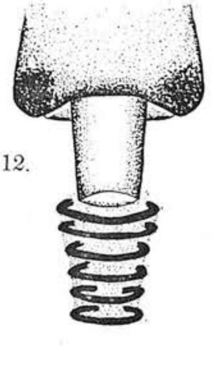

Fig. 13.

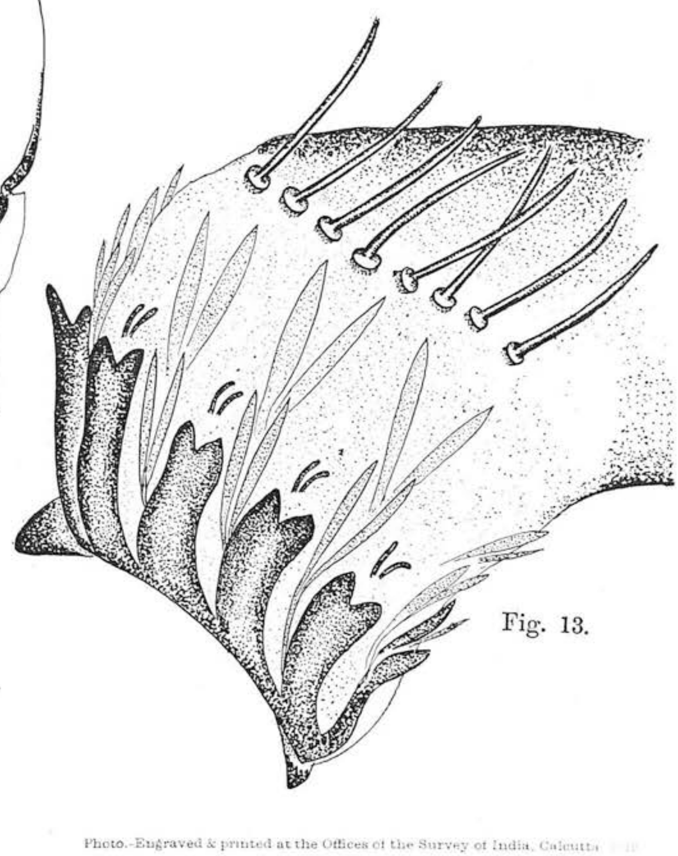

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PLATE III.

Figure 14.—Transverse section through the labella in the position of rest, at the level of the teeth. The space in the middle between the labella is an artifact due to shrink age. The irregularity in the outline of the teeth is due to the slight obliquity of the section.

Figure 15.—A transverse section a little higher up than the last figure, passing through the discal sclerite and the tip of its axial apophysis. Note the fusion of the two posterior walls of the labella at this point.

Figure 16.—A transverse section above the level of the teeth. The ends of the labial gutter are seen in the upper part of the section, projecting in front of the discal sclerite as seen in figure 4, Plate I. The axial apophysis is here united to the rest of the discal sclerite, occupying the ventral angle. Note the strong bands of fibrous tissue which unite the two external walls in this situation. Also compare the size of the tracheæ and nerves with those in figure 24, Plate V.

Figure 17.—The next proximal section. Only the joint arrangements are shown in this and the next three figures. Note the disappearance of the axial apophysis and the appearance of the ventral portion of the labial gutter, which is however separated from the dorsal portion by the intervention of the dorsal and lateral part of the discal sclerite.

Figure 18.—The next section, showing the widening of the labial gutter, and the approach of the ventral and lateral portions. The ventral portion of the gutter rests on two lateral projection of the discal sclerite.

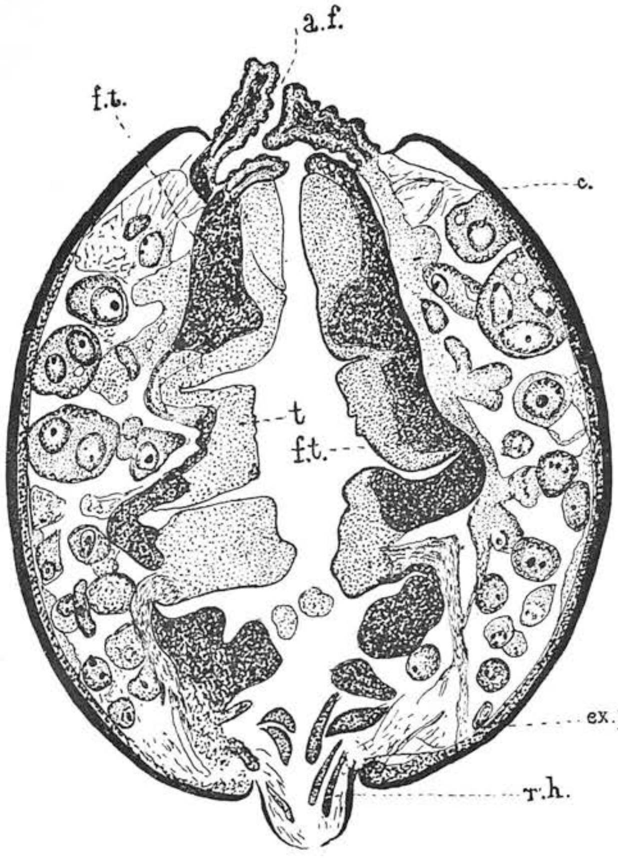


Fig. 14.

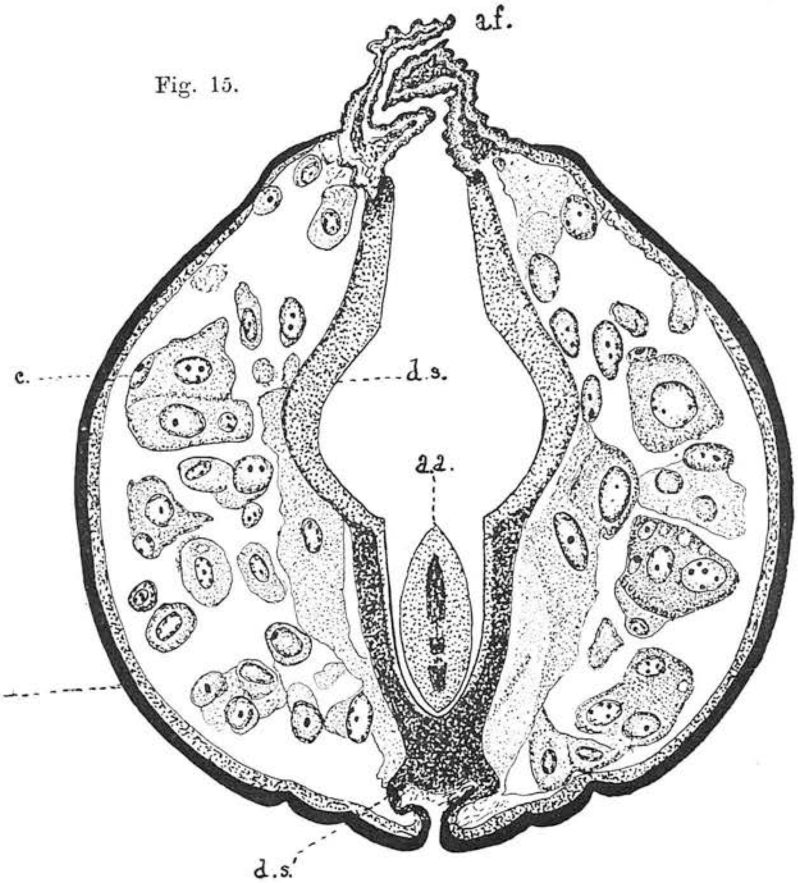


Fig. 15.

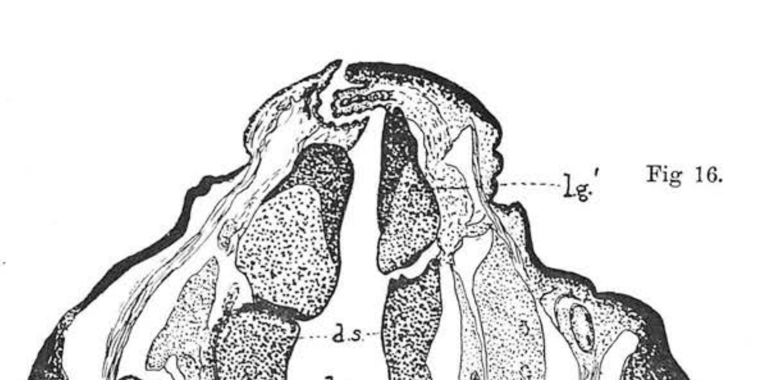
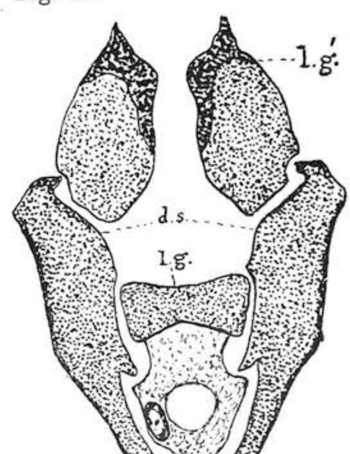


Fig 16.

Fig. 17.



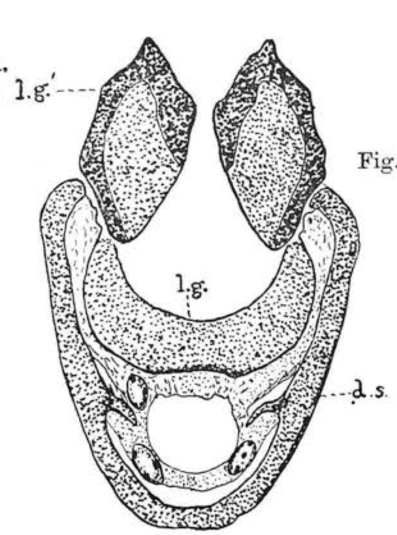


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PLATE IV.

Figure 19.—A transverse section a little higher up. Here the discal sclerite is very much reduced in size, and has passed altogether behind the labial gutter.

Figure 20.—The next section. This has passed through the upturned end of the discal sclerite, as seen from the front in figure 8, and from the side in figure 4.

Figure 21.—Section through the region of the furca. Note that the discal sclerite has completely disappeared, that the two portions of the labial gutter are united by fibrous tissue, and that the keel of the labial gutter is not present at this point. There is a well-marked band of fibrous tissue passing across the labella at the level of the furca.

Figure 22.—Section a little higher up than the last, showing the first appearance of the keel. The dorsal half of the labium at this point is bounded by membrane only. Compare other drawings of this area, figures 1, 4, 7, 8, 9. The ventral sclerites make their appearance at this level.

Figure 23.—Section at the level of the first appearance of the labrum-epipharynx and the hypopharynx. This section passes through the 'elevation' on the tip of the labrum-epipharynx.

PLATE IV.

Fig. 21.

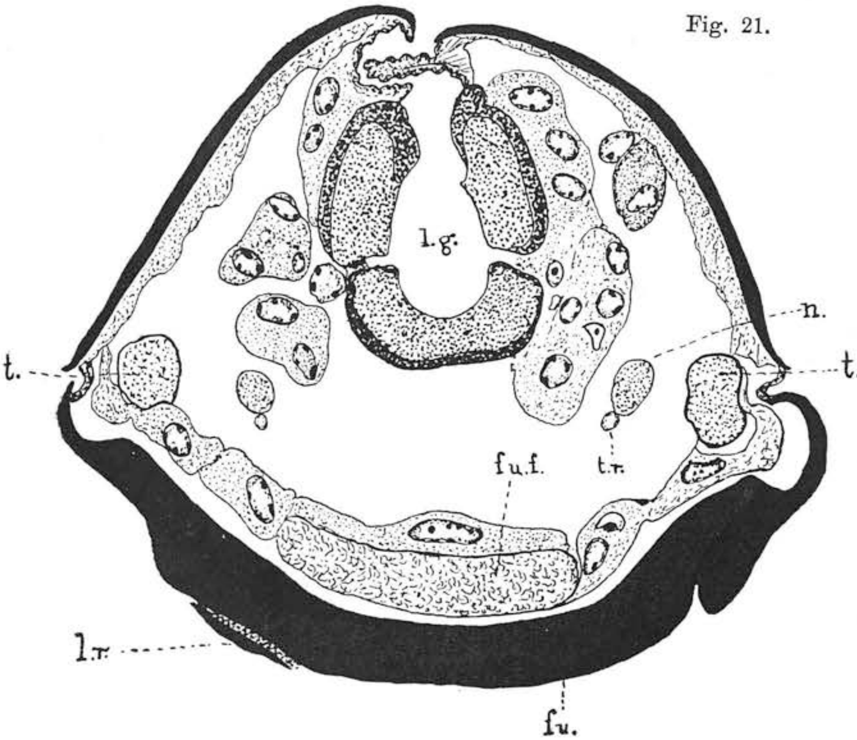

Fig. 19.

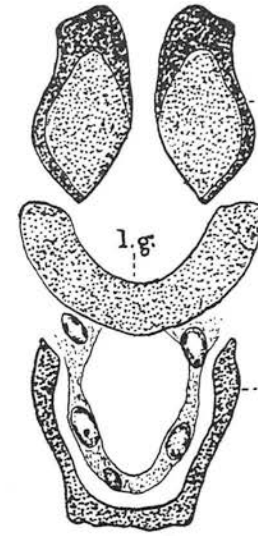

Fig. 20.

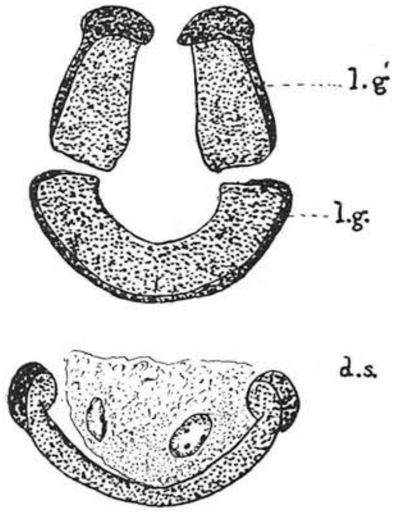

Fig. 22

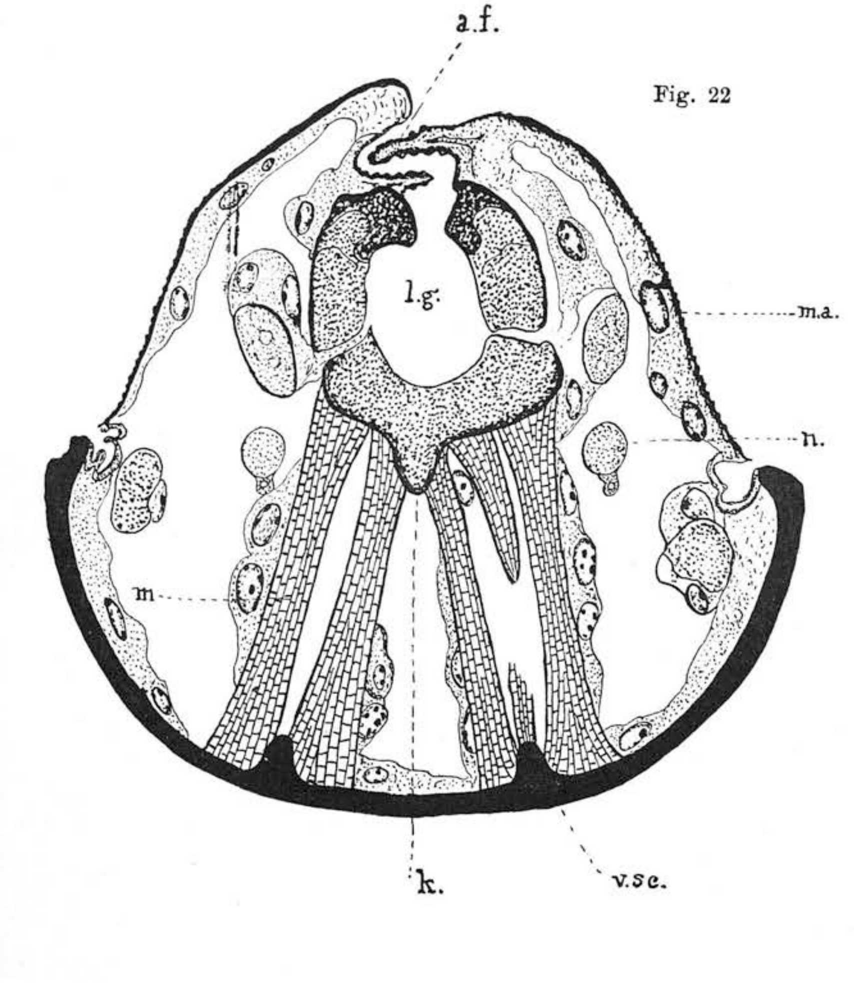

Fig. 23

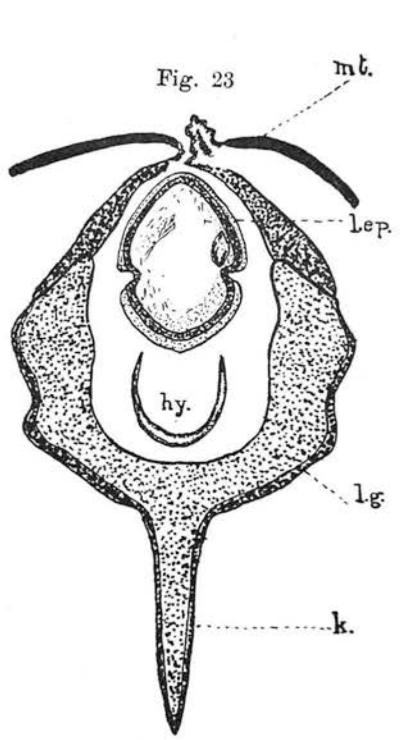

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PLATE V.

Figure 24.—The next section above the last, showing the commencement of the food canal, between the labrum-epipharynx and the hypopharynx. The two divisions of the labial gutter are completely united. The appearance of a central space in the labrum-epipharynx and the hypopharynx is an artifact due to shrinkage. Probably the division of the concavity in the under surface of the former organ has been produced in the same way, as no trace of it can be found in fresh preparations.

Figure 25.—The food canal in the labial gutter, as seen in the greater part of the length of the labium. Note the firm fibrous membrane which unites the borders of the labial gutter with the mentum.

Figure 26.—A transverse section of the haustellum about the middle of its length. As in the other sections, allowance must be made for the shrinkage in the interpretation of the appearances seen. The spaces between the muscle fibres are artificial, and are due to the unequal shrinkage of the chitinous wall and the softer contents. Only a very small portion of it represents true hæmatocœle.

Figure 27.—The food canal in the upper end of the haustellum. The outline of the labrum-epipharynx is altered, and the salivary duct has thicker walls. The membrane connecting the labial gutter with the mentum is here replaced by a thin sheet of chitin.

Figure 28.—A section a little above that of the previous figure, and at the extreme upper end of the haustellum. The labrum and the epipharynx are here separating, the labrum to fuse with the membraneous wall of the rostrum, which is above continuous with the clypeus, and the epipharynx to unite with the upper lamina of the hypopharynx to form a closed canal.

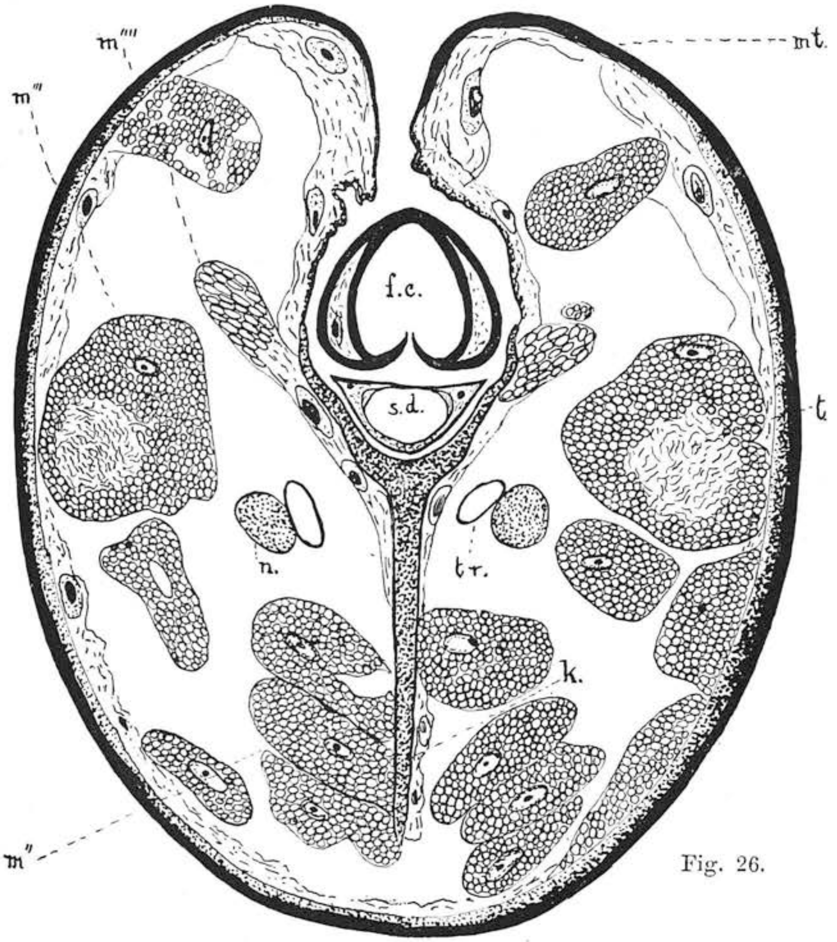

Fig. 26.

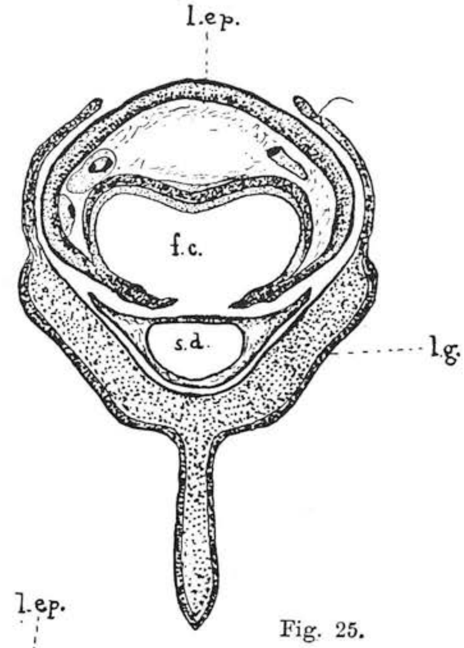

Fig. 25.

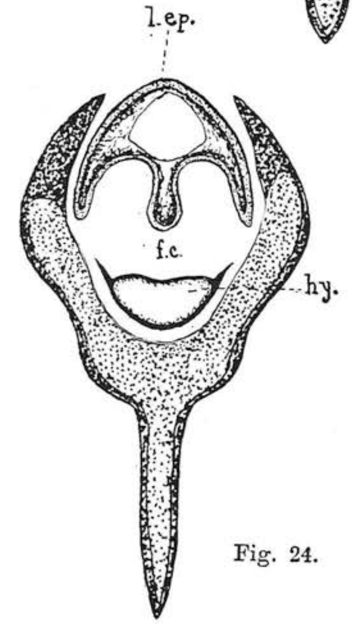

Fig. 24.

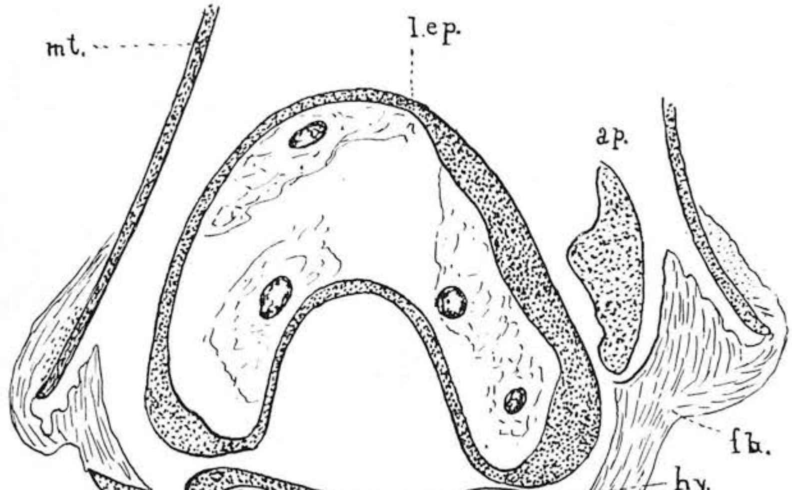

Fig. 28.

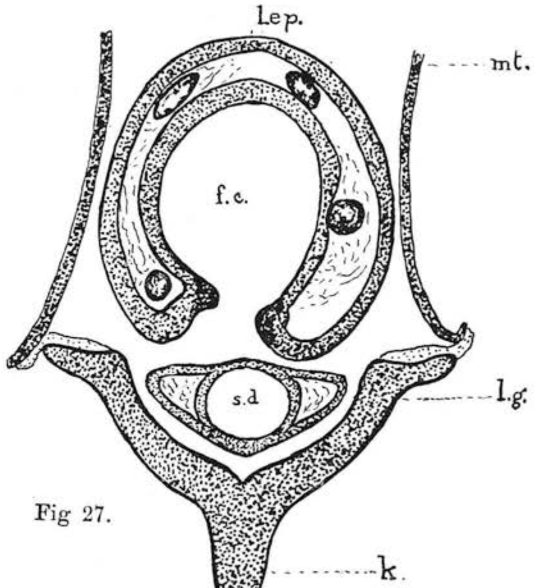

Fig 27.

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PLATE VI.

Figure 29.—This shows the closed canal formed by the union of the epipharynx and the hypopharynx. The lower lamina of the latter has fused with the labial gutter above this point.

Figure 30.—A section through the lower end of the rostrum, showing the separation of the food canal and the salivary duct, and the apodemes of the labrum. The rostrum was distended when the specimen was fixed, but the subsequent treatment has dissolved out the air from the air sacs, and left an empty space of considerable extent, in this section and the next.

Figure 31.—A section through the middle of the rostrum, showing the pharynx. The salivary duct has receded to the posterior part of the rostrum.

Fig 29.

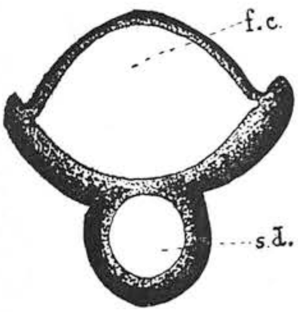


Fig. 30.

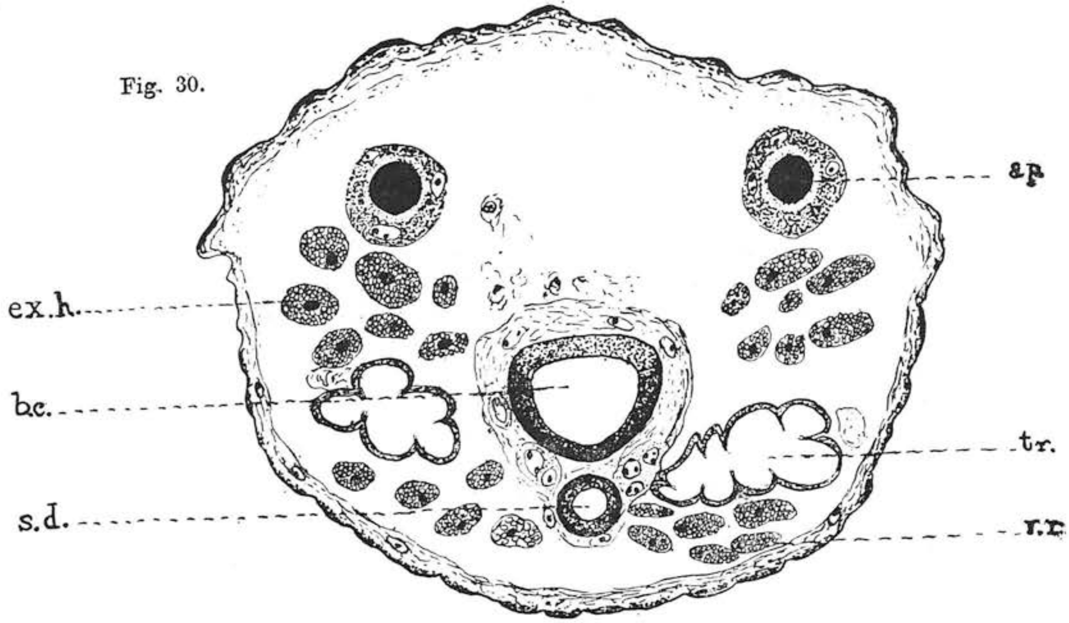
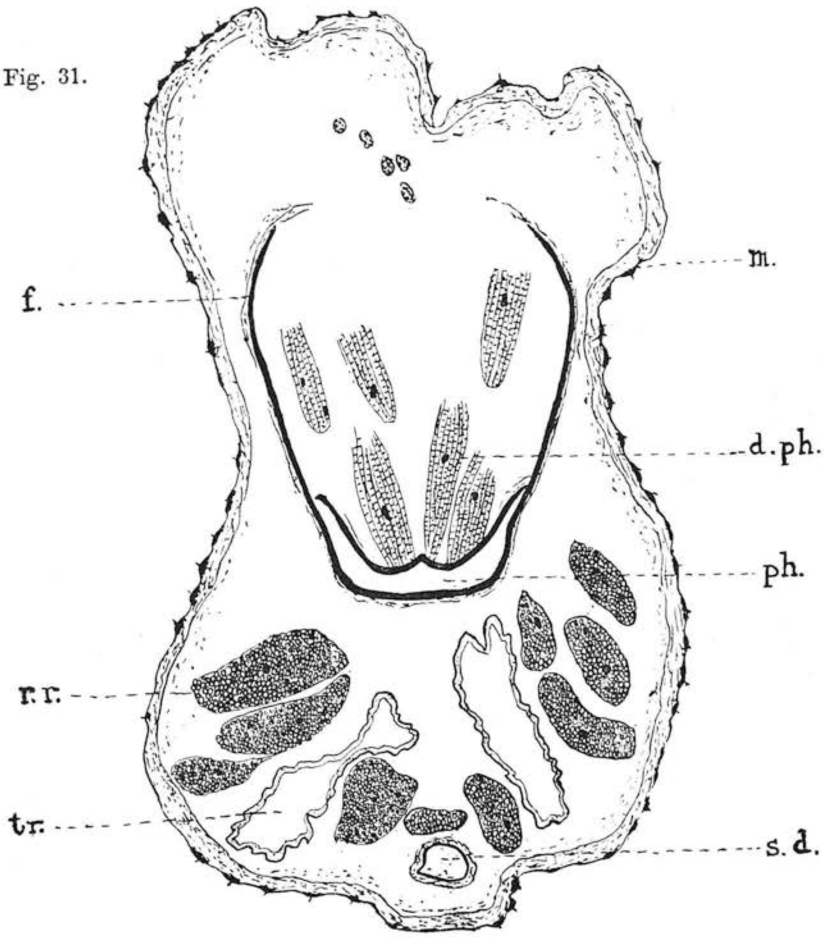


Fig. 31.



F. W. C. DELET.

Photo.-Engraved & printed at the Offices of the Survey of India, Calcutta, 1912.

Studies on the Mouth Parts and Sucking Apparatus of the Blood-Sucking Diptera.

No. 4.

The Comparative Anatomy of the Proboscis in the Blood-Sucking Muscidæ.

IN two previous studies I have described the structure and mechanism of the proboscis in *Philæmatomyia insignis*, Austen, and *Lyperosia minuta*, Bezzi, and in doing so adhered as far as possible to the terms already in use for the various parts of the Muscid proboscis, thereby committing myself to the view that a close homology exists between them. So far as the gross anatomical features, such as the division of the proboscis into the three parts found in *Musca*, and the general shape and relations of the labrum-epipharynx and hypopharynx, are concerned, the homology is evident at a glance, but those structures which are immediately concerned in the act of biting, in accordance with the descriptions of the mechanism given in the papers mentioned above, are modified in remarkable manner, and to so great an extent that the relationship between them and the parts designated by the same name in *Musca* can only be properly understood when the intermediate forms are examined. In the present paper I propose to discuss the changes which have been produced in the Muscid type of proboscis in correlation with the adoption of a blood-sucking habit, and to show that the blood-sucking flies of this group can be arranged in a series, commencing with those flies which are blood-suckers by habit but have no biting mouth parts, and passing on through those flies which, while still retaining the *Musca* facies, are provided with more or less efficient biting organs, to those forms, such as *Stomoxys* and *Glossina*, which are typically blood-suckers, and have entirely lost the characteristic structure on the labella by means of which the non-biting flies absorb nourishment. Arranged in this manner those flies which I have been able to study form a most interesting series, in which the gradual progress of a change in structure along a definite path, correlated to a change in the habit of life, can be traced step by step from its origin to a stage in which the structural modification is extreme. The pointed and rigid proboscis of *Glossina*, typically a piercing organ, bears little or no superficial resemblance to the blunt and retractile organ of *Musca*, and yet there are few structures in the one which cannot be traced in the other, and the mechanism by which food is obtained is closely related in the two cases.

The flies which I have examined are as follows:—Three species of the genus *Philæmatomyia*, viz. *lineata*, Brunetti, *insignis*, Austen, and *gurnei*, Patton and Cragg; *Hæmatobia** *irritans*, Linn. *Stomoxys calcitrans*, Linn., *Lyperosia minuta*, Bezzi, and *exigua* Meij; *Glossina palpalis*, R. D., and *submorsitans*, Newstead. The order in which they are placed in the above list represents approximately the degree of specialisation which is found in their mouth parts, and this corresponds very closely with the positions assigned to the various genera by systematic dipterologists. The genus *Philæmatomyia* closely resembles the genus *Musca*, being distinguished from it mainly by the presence of a ring of biting teeth, the degree of development of which differs considerably in the three species so far known. *Hæmatobia* is remarkable in that, although the general shape and structure of the proboscis shows little difference from that of *Stomoxys*, traces of a pseudotracheal membrane still persist. The genus *Glossina* is placed by Austen in association with *Stomoxys* and *Lyperosia*; the condition of the mouth parts shows that it is more highly specialised than either, and the method of reproduction supports this view. *Stomoxys* and *Lyperosia* closely resemble one another, and the structure of the proboscis indicates that these flies have entirely abandoned food other than blood.

Before going further it will be well to discuss the general aspects of the question and to substantiate the hypothesis indicated in the opening paragraph, that the blood-sucking Muscids are derived from non-biting forms. Special attention is due to this point, for certain workers, notably Minchin and Prowasek, have assumed the contrary to be the case, and the former author has used this assumption as a support for the theory that the Hæmoflagellates are the descendants of organisms which originally inhabited the intestinal tract of vertebrates, and that the flagellates found so commonly in the digestive tract of insects are derived from Hæmoflagellates, those insects in which they occur being either blood-suckers or the descendants of blood-suckers. It would be out of place to discuss the purely parasitological aspect of this question here, but the subject is of sufficient importance to necessitate a consideration of the evidence there is in favour of or against the hypothesis from the entomological point of view.

In the first place, it must be remembered that the Diptera are simply a highly specialised division of the class Insecta, that the Insecta are Arthropods, and that the sucking mouth which is one of the main characteristics of the Diptera is a modification of a biting mouth. The remote ancestors of all Diptera were undoubtedly biting creatures, either animal or vegetable feeders, or predaceous. Even in the Diptera the sucking mouth shows varying degrees of development, and it is most improbable that there are any instances of

* And an undetermined Indian species.

reversion from the advanced condition to the earlier one. As I have shown in a previous paper, the biting flies in the Orthorrapha have a relatively simple form of apparatus, in which the primitive arthropod structures can be easily traced, for piercing the skin of the host. The sucking portion of the mouth is in fact formed by the simple apposition of the epipharynx and hypopharynx, while the true segmental appendages retain a form not at all unlike that found in quite primitive arthropods. *Tabanus*, for example, is a true "biting" insect, in the sense that it makes a wound by means of its mandibles and first maxillæ; the wound having been made, it sucks up the blood by means of a sucking pump in the head, through the canal formed by the apposition of the epipharynx and the hypopharynx, exactly as is done by non-biting flies which feed on vegetable or animal juices. The flies which possess functional mandibles and maxillæ are undoubtedly nearer the primitive arthropod type than those which have neither, and it is reasonable to suppose that, among the Orthorraphic flies, such forms as *Tabanus* are more primitive than the flower feeders, and that in those cases in which the female has a complete biting and sucking mouth and the male only a sucking mouth, the female is the less removed from the immediate ancestor of the species. The loss of the appendages, in this case, is an indication of specialisation. The mandibles and first maxillæ of the biting flies of this group are clearly primitive structures retained, and their existence is good evidence that the flies are more ancient than those which have lost them, due regard being given of course to other characters. In this case and in this limited sense the hypothesis of Minchin is supported by entomological considerations, and it is quite possible that the flagellates present in non-biting Orthorraphic flies have for their immediate ancestors similar parasites which inhabited the intestinal tract of blood-sucking flies.

The case is quite different with regard to the Cyclorraphic flies. In no case do these possess mandibles or first maxillæ, the only recognisable remnant of these being the palpi, which are believed to be remainders of the first maxillæ. The biting apparatus is developed on the labella, which are derived from the second maxillæ, appendages which take no part in the act of biting in the Orthorraphic flies. Not only is the apparatus formed out of different appendages, but it is of a different nature, and consists, as I have shown in the case of *Philæmatomyia* and *Lyperosia*, of an arrangement of teeth which are drawn through the wound by means of muscles situated in the labium. As will be shown in the course of this paper, these teeth are represented in the non-blood-sucking Muscids, and their development is the key to all the modifications found in the different forms.

The labella, at the end of the fused second maxillæ, are modified in most of the Diptera which do not suck blood into an apparatus of the nature of an absorbent pad, for the collection of fluid nourishment, which is sucked up the canal in the proboscis by means of the pharyngeal pump. The commonest form of this is the well known pseudotracheal membrane found in the house fly. This form of apparatus is not peculiar to the Muscid flies, but occurs in the Orthorraphic flies as well, and is absent only in those forms which obtain their nourishment by actually piercing some resistant layer to obtain fluid from underneath, and it is evident that its development is generally coincident with the disappearance of the biting appendages. In some instances, as for example the Tabanidæ, it exists side by side with functional and powerful mandibles and maxillæ, the fly being then able to absorb fluid either from a moist surface or through a resistant dry layer which has to be pierced by the stylets. In no case, however, does one find any form of biting apparatus on the labella existing together with functional mandibles or first maxillæ. The development of labellar teeth is a secondary phenomenon, which takes place when a non-biting fly, the mouth of which is adapted only for sucking fluids from moist surfaces, assumes the blood-sucking habit. How this occurs in nature will be discussed in more detail when dealing with those flies which are blood-suckers but are without biting mouth parts.

We may sum up the evolutionary history of the blood-sucking Diptera as follows. The early insect mouth parts were formed for biting and furnished with simple arthropod jaws: the cockroach represents such a condition. At a remote period the second pair of maxillæ became fused, a condition found in all Diptera. The sucking mouth characteristic of the Diptera is formed by the elongation of the epipharynx and hypopharynx, which together form a tube up which the fluid nourishment is sucked. In the most primitive dipterous types the typical arthropod appendages are retained, co-existent with the sucking tube, and the insect is able to use its appendages to pierce a hole in skin or other substance to obtain fluid food from underneath. Such a condition is found in the Orthorraphic blood-sucking flies. At a later period the appendages of the fourth and the fifth segments of the head, that is, the mandibles and maxillæ, disappear, and the function of obtaining food is carried out by the second maxillæ, the distal ends of which are modified to form a pad suitable for the absorption of fluid from moist surfaces. This condition is found in many families, both in the Orthorrapha and the Cyclorrapha. It reaches its highest degree of development in the complex labella of *Musca*. Still more recently some flies have developed from this stage a most complex arrangement consisting of a ring of teeth on the end of the labium, and have adapted themselves to a blood-sucking habit. Throughout the evolution there is to be noticed a constant diminution in the importance of the anterior appendages, and the gradual transference of the entire function of obtaining food to the second maxillæ. These act in the more primitive forms merely as a sheath for the stylets, in the next stage as an absorbent pad, and in the last stage, that of the blood-sucking muscids, as cutting organs.

To return for a moment to the hypothesis of Minchin. All Diptera, and one may add all Hemiptera also, are descended from biting or mandibulate ancestors, but these ancestors were not necessarily blood-suckers, and consequently flagellates found in non-blood-sucking flies may or may not be descended from ancestors which were at one time hæmoflagellates. It is not to be supposed that there has been any direct line of descent, and it appears to me to be impossible to decide, in the present stage of our knowledge at least, whether those forms, which in the past gave rise to the non-blood-sucking flies we know to-day, were blood-suckers or not. Certainly they were provided with mouth parts which could be adapted for the purpose with comparatively little change, but there is no evidence of any importance one way or the other.

In the case of the Muscid biting flies Minchin's hypothesis can only be accepted in a limited sense. Enough has been said already to show that in this group the evolution has progressed from non-blood-sucker to blood-sucker and that the flies of the *Stomoxys* group are more recent than the simple *Musca* forms. That being the case, if the flagellates found in Muscid flies are descended from hæmoflagellates, then they can only have reached the fly at the remote period when the fly was mandibulate, before the appendages had atrophied from disuse. To be precise, if the ancestral stock of *Herpetomonas muscæ-domesticæ* at any time inhabited the blood of a vertebrate, it must have changed its habitat at that period in the evolution of the house fly when the mandibles and maxillæ were present and functional, and after the outgrowth of the labrum-epipharynx and hypopharynx had taken place; and this change can only have occurred if one of the mandibulate ancestors of *Musca domestica* happened to be also a blood-sucker. Before the formation of the sucking tube the insect was purely a biter, and probably lived on solid or semi-solid food, and after the disappearance of the mandibles and maxillæ it was purely a sucker, and could not make the necessary wound.

The statement made above, that the Muscid biting flies have for their immediate ancestors non-biting flies of the *Musca* type, is entirely in accord with the other features of their structure and life history. A detailed exposition of the reasons for the systematic position of the blood-sucking genera would be out of place here, but two points of importance may be noted in passing. In the first place, the venation of the wing shows characteristic changes. According

NOTE.—I have been unable to consult the paper quoted by Prowasek.—Fr. Brauer, Uber die Verbindungsglieder Zwichen den orthorrhaphen und cyclorrhaphen Dipteren, etc.—Verhandl. der zool-bot Gesellschaft, 1890, s. 273.

to no less an authority than Williston, a concentration of the wing veins towards the anterior margin, and a shortening of the most anterior veins, are evidence of specialisation, and once these changes have taken place they are irreversible; a comparison of the venation of *Musca* and *Glossina* indicates clearly that the latter fly, according to this criterion, is the more recent of the two forms. Secondly, we find that a tendency towards the pupiparous habit, undoubtedly a recent development in the Diptera, and one which indicates a high degree of specialisation, appears along with the blood-sucking habit, though it occurs somewhat irregularly in the group. *Philæmatomyia insignis* is oviparous, but the eggs hatch in a remarkably short time and are larger when laid than one would expect for the size of the fly. *Stomoxys* and *Lyperosia* are normal in their reproduction; *Glossina* approaches very closely to the Pupipara. As the Pupipara are typically blood-sucking and parasitic, there is evidently some relation between the method of obtaining nourishment and the method of reproduction. What this relation may be is not decided, but the modification of the reproductive organs and the divergence from the type found in other Diptera are so extreme that the descent of non-blood-sucking oviparous forms from blood-sucking pupiparous ones is not conceivable. The case is not comparable with the larviparous habit among the *Tachinidæ*, for the larvæ of many Muscid biting flies live in dung or other situations side by side with those of other oviparous Muscids, whereas those of Tachinids are usually deposited in the bodies of other larvæ, and a shortening of the immature stages is almost essential to the continuation of the race.

Without going into any further detail in this matter it will suffice to repeat that the arrangement of the Muscid biting flies in the above order, as more recent and more specialised than those Muscids which have mouth parts adapted only for the absorption of fluid from moist surfaces, is in agreement with the accepted systems of classification, which are for the most part founded on other anatomical or biological features. The theory that the flagellates of insects are descended from hæmoflagellates finds little support from entomological facts; how they originally reached the intestinal tract of the insect it is not the purpose of this paper to discuss.*

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* NOTE.—If I may be permitted to make a suggestion here, the argument of the above paragraphs may be carried further. At that remote geological period when the waters covered the earth, the great majority of insects, and arthropods which were destined to become insects, must have been aquatic or semi-aquatic in their habits; during this phase of their evolution free living flagellates, presumably present in abundance then as now in water rich in organic matter, must have passed into the intestinal tract of the insect either as food or accidentally with the food. In the latter case, presuming that they were able to resist the action of the digestion by encystment in response to an unfavourable environment or otherwise, the conditions for the establishment of parasitism would be present, and the dependence of the flagellate on its insect host for the completion of its life cycle but a short step.

The Proboscis of Musca.

Since all the flies to be discussed in this paper are to be regarded as derived from a Musca-like ancestor, a brief note on the structure of the proboscis of this type must be given. Descriptions of the proboscis of *Musca* and the allied forms are numerous enough, and I have indeed little to add to what has already been said, but it will be necessary, in view of what follows, to define clearly what is meant by certain of the terms employed, and in certain cases to introduce new ones. Any points which I omit, and regarding which the reader may wish to refresh his memory, are dealt with in Kraepelin's complete account. The species which I have specially studied, and to which the description mainly applies, is *Musca nebulo*, the common bazaar fly of Madras. The differences between different species are however so small that the description will apply in all the important points to any species of like habit.

The proboscis of *Musca* consists of three parts, termed from above downwards the *rostrum*, *haustellum*, and the *labella*. Between each two of these, and between the rostrum and the head, there is a joint which permits of movement in a vertical plane. When the proboscis is in use, the three joints are extended so that the three parts are in the same straight line, and the whole proboscis hangs downwards from the under surface of the head of the fly, approximately at a right angle to the long axis of the body. When the proboscis is not in use it is retracted by the flexion of all three joints, in such a way that the three parts are folded on one another and tucked into an orifice on the under surface of the head. This orifice is termed by some systematists the "buccal orifice," an unfortunate name, for it is separated from the true mouth of the fly by the whole length of the pharynx, and is moreover merely an interval in the chitinous integument of the head, and has nothing to do with the buccal cavity. I propose to adopt the term *epistomal orifice* for this aperture. Of the three divisions enumerated above, the rostrum is, strictly speaking, a portion of the head. It contains the pharynx, and the only portion of the true mouth parts in relation to it is the pair of maxillary palps, which are attached to its anterior surface; the haustellum is the proboscis proper, and consists of the surviving head appendages, *viz.*, the second maxillæ, fused to form the labium, and the labrum-epipharynx and hypopharynx. The labella are parts of the second maxillæ which have remained separate at the distal end. The nature of the joints and the range and nature of the movements of the proboscis will be discussed later, but it should be noted here that the extension of the rostrum is of the nature of an evagination of a part of the head capsule. The so-called "buccal orifice" is merely a thickened rim where the rigid chitin of the head capsule gives place to the soft and flexible wall of the rostrum.

The Rostrum.

The rostrum has the shape of a truncated cone, broad end uppermost. Its outer covering consists of a flexible membrane which is continuous at the epistomal orifice with the chitin of the head capsule. At the distal end it is attached to the wall of the haustellum. Within this membrane there is a somewhat complex chitinous structure termed the fulcrum, part of which forms the pharynx or sucking pump of the fly. This structure affords the necessary rigidity to this part of the proboscis, and gives attachments to the various muscles which act on the joint between the rostrum and the haustellum.

The *fulcrum* resembles, to use Kraepelin's admirable simile, a Spanish stirrup iron. It consists of a posterior plate, two lateral plates, and an anterior arch. The posterior plate is oblong, slightly concave forwards anteriorly, and narrower above than below. Its upper and lower borders are incurved, the lateral angles of the former being produced upwards into a pair of stout cornua, which are also intimately connected with the lateral plates. The lateral plates are roughly triangular, and are continuous by their longest sides with the posterior plate, projecting forward at right angles from it; their upper sides are deeply incurved. The anterior side, which is much longer than the upper one, is also incurved, but the contour is abruptly broken at the junction of the middle and lower thirds by the projection forwards of a sharp spur, the border being more concave below than above this point. The anterior arch is situated at about the same level as the cornua on the posterior plate, and passes between the upper anterior angles of the lateral plates; it is a thick ridged bar, which gives attachment to part of the dilator muscles of the pharynx, and is the part which is pressed against the clypeus when the rostrum is rotated in retraction. It lies in, and is continuous with, the membraneous anterior wall of the rostrum.

The *pharynx*, or sucking pump, of *Musca* resembles that of the Orthorraphic flies, consisting of two superimposed chitinous plates, which can be separated by dilator muscles. The posterior of these plates is the one described above as the posterior plate of the fulcrum; the anterior plate, which lies in close contact with it when the organ is not in use, is of similar shape and extent, but is much thinner, and is drawn away from the other by the action of the dilator muscles. It has a thick ridge of chitin running down its middle line, to which the muscle fibres are attached. The anterior plate, however, is not simply pulled away from the other so as to leave a crecentic interval between the two, but is bent forwards on each side as the muscles pull the median ridge forward, so that the resulting cavity tends to be tri-radiate, an arrangement which recalls that of the pharynx of the mosquito. The fulcrum lies in the anterior part of the rostrum; behind it there is a comparatively large space, which in the extended position is occupied by two large cylindrical air sacs, which are of great importance in the mechanism of extension.

In the middle line between these there is the salivary duct, and on either side and behind there are numerous muscles, which act on the joints above and below. These will be dealt with more particularly later.

The fulcrum does not extend quite to the lower end of the rostrum, and communication between the food canal in the haustellum and the pharynx is established by means of the intervention of a small chamber resembling a miniature pharynx. This has been elaborately described by Kraepelin, who, however, did not give it a definite name. Lowne termed the chitin forming its wall the "hyoid sclerite." When describing the corresponding structure in *Lyperosia* I suggested the name *buccal cavity* as having the double advantage of indicating at once the position and the homology. The chamber consists, in *Musca*, of a small triangular piece of thin chitin, arranged with its long axis pointing towards the haustellum, and its broad base between the lower cornua of the fulcrum, so that it occupies the interval between the two divisions of the proboscis. The lateral angles are bent forward, and are connected with one another by means of a thin membrane, which is also attached to the anterior plate of the pharynx. The epipharynx and hypopharynx terminate in the region of this cavity in a manner which will presently be described.

The Haustellum.

The main bulk of the haustellum consists of the *labium*, or fused second maxillæ. The other parts are concealed in a groove on its anterior surface in the normal conditions of the parts.

The labium is roughly cylindrical in shape, thickest in the middle, and tapering a little at each end. Its wall consists of two pieces of chitin united by a loose membrane, which is attached to the lateral edges of each. Of these the posterior, termed the *mentum* (Plate II, figure 3) and homologous with the mentum of other insects, is much the largest; it has the shape of a shallow trough, with the concavity directed forwards, and is contracted at its lower end. It forms the posterior and lateral walls of the labium, and has thickened lateral borders. The arrangement of the parts at its lower end should be particularly noted, as they undergo important modifications in the blood-sucking Muscids. The thickened lateral borders converge towards the distal end, and become somewhat attenuated; the distal border, which is about one-third the length of the lateral sides, has in its middle portion a deep square-shaped incision, on the opposing sides of which there are two longitudinal rod-like thickenings of the chitin, extending the whole length of the sides of the incision. Continuous with these there is on each side a second rod of the same length as the sides of the incision; these two rods pass downwards distal to the lower border of the labium, and diverge from one another. They have an important connection with the chitinous arch which supports the labella behind. If they are examined in thoroughly cleared preparations, it will be seen that although they are continuous with one another, there is a distinct thinning of the chitin at the level of the distal border of the mentum, which suggests that the proximal and distal portions of the rod are moveable on one another.

The other chitinous portion of the labium is very ill defined in *Musca*, and can only be recognised in slightly cleared preparations and in sections. It is a thin sheet of chitin, grooved to form a shallow trough, and situated immediately behind the hypopharynx, the upper part of which is fused with it. On each side of this groove there is a rod-like thickening, which extends from a point a little distal to the base of the hypopharnyx to the labella, to the anterior sclerite of which it is attached. The groove, with its lateral thickenings, may be termed the *labial gutter*. It corresponds to the structure described in *Stomoxys* under that name by Stephens and Newstead.

The membrane which unites the anterior and posterior plates of chitin, and completes the wall of the labium, is in *Musca* very lax and of considerable extent. The two chitinous portions are not continuous with one another at any point.

The chief contents of the labium are the muscles which move the labella; these will be briefly described in connection with the mechanism of the proboscis. In addition there is the labial salivary gland, situated behind the lower end of the labial gutter, and a nerve and trachea on each side. There are no air sacs in the labium and the tracheæ are little larger than the nerves.

The *labrum-epipharynx* (Plate II, figure 5) lies in the groove on the anterior surface of the labium. It is shaped like a lance-head, its greatest breadth being about one-third of its total length. There appears to be some difference of opinion with regard to the composition of this organ, and the terms labrum and labrum-epipharynx are used somewhat loosely in current literature. If one bears in mind that the organ in *Musca* is homologous with the one in the more primitive Orthorraphic flies its dual nature will be evident. The outer part of the organ consists of the labral element. It gives its shape to the structure, and, arching over the anterior and lateral sides, terminates at about the middle third of the posterior surface. The inner portion is the epipharynx, and consists of a gutter having a depth of about half a circle. Between these two chitinous parts there is an interval, which is partly occupied by a fan-shaped muscle passing from the labrum to the epipharynx. The method of termination of the two constituent parts indicates clearly their different origin, for at the proximal end they separate completely. The broad upper end of the labrum becomes continuous with the membrane on the anterior surface of the rostrum, and this of course is directly continuous with the clypeus of the head capsule; the only real difference in the relations of the labrum in the Muscid flies is that it has become separated from the head by the evagination of the rostrum from the head cavity. At the sides of its upper border there are small pits for the articulation of the labral apodemes, stout and heavily pigmented rods which pass upwards and outwards, diverging from one another, into the rostrum. The lower ends of the apodemes are pointed and barbed, the main portion of the rod slightly sinuous, and the upper end expanded for muscle attachment. Some of the muscle fibres attached to these apodemes are probably representatives of the labral muscles found in the Orthorraphic flies, and the apodemes themselves may be derived from the portion of the labrum which in the more primitive group is to be found inside the head capsule, and to which the muscle of the labrum is attached. The upper end of the epipharynx is a considerable distance proximal to that of the labrum, for it projects into the rostrum as far as the upper part of the buccal cavity, to the upper border of which it is connected by means of a soft membrane. In view of the similarity in all essential points between the labrum-epipharynx in *Musca* and that in the Orthorraphic flies, in which the epipharynx is in direct chitinous continuity with the functional buccal cavity, I do not see any grounds for accepting Kraepelin's view, that the organ is a mere evagination from the head cavity.

The *hypopharynx* retains the structure usual in the Diptera, being a simple spatulate slip perforated by the salivary duct. Its proximal third is fused with the labial gutter. At its upper end it projects into the rostrum behind the epipharynx, and is attached by a fine membrane to the pointed end of the triangular plate which forms the main part of the buccal cavity. It will now be evident that the buccal cavity is completed in its distal portion by the attachment to it of the epipharynx and the hypopharynx, which converge together at this point, and are united to the borders of the chitinous plate by membrane. This point, therefore, as correctly stated by Kraepelin, is the true mouth of the fly. It will be shown later that as the blood-sucking proboscis is evolved, the mouth is moved forwards, and the buccal cavity transformed into a tube with complex walls.

I have already noted, in a previous paper, that the hypopharynx, like the labrum-epipharynx, consists of two distinct laminæ, which enclose between them the salivary duct. In *Musca* the labial lamina is only separate in the distal third of the organ. Separation of whole of this lamina with the formation of a free organ is found in the flies to be discussed later. The *salivary duct* emerges from between the two laminæ just above the point of union of the stomadael element with the walls of the buccal cavity.

The Labella.

The labella are oval lobes, separated from one another by a median fissure which extends throughout their anterior surfaces, and is there continuous with the groove on the anterior surface of the labium, but which is incomplete behind. The two labella represent portions of the second maxillæ which have remained distinct while the rest of the appendages have united to form the labium. Each lobe has an outer and an inner wall, the outer being composed of thin plates of chitin with membraneous intervals, the inner of the highly specialised pseudotracheal membrane, by means of which the fly absorbs its food. The structure of this membrane is familiar from many descriptions, and full details of its minute anatomy and mechanism will be found in Graham-Smith's recent paper, so that it will be unnecessary to discuss it here, especially since it is one of the first portions to disappear in the evolution of the blood-sucking proboscis. The outer walls impart the necessary rigidity to the labella, and have the chitin concentrated towards the periphery where the inner and outer walls join one another; at the anterior and posterior parts they bear a large number of pigmented macrochætæ, which project forward as a fringe distal to the organ.

There are two sclerites which support the labellar walls and at the same time unite the labium and labella, forming joints which permit of free movement between the two parts in an antero-posterior direction. The posterior of these is known as the *furca* (Plate II., figure 3). It is shaped like a rather wide horse-shoe, and embraces the posterior half of the labella. The posterior half of the arch fits between the arms of the fork of the mentum, the short transverse part lying opposite the incision between them. The furca is intimately fused with the external labellar wall, and is also attached to the membraneous portion of the wall of the haustellum in the region of the fork of the mentum, so that when it is swung backwards and forwards between the arms of the fork it carries the labellar wall with it; there is in addition a small heart-shaped piece of thin chitin attached to the transverse part of the arch, which passes downwards in the middle line behind, and further assists the furca in its control over the labella. The anterior or *discal sclerite* (Plate II, figure 4, Plate V, figures 27 and 28) lies between the labella, and is attached to the labial gutter. Its shape and position are of great importance from the comparative point of view, as it undergoes important modifications in the blood-sucking forms.

It is a racket-shaped loop of strong and heavily pigmented chitin, the broad distal end of which forms the margin of the oral pit, while the proximal end, corresponding to the handle, gives attachment to an important pair of muscles. The distal end is shaped like an isosceles triangle, forwardly directed and with rounded lateral sides and posterior angles; the base is incomplete in the middle third, the remaining portions projecting inwards as thin flanges. Anticipating subsequent descriptions, this portion of the *discal sclerite* may be called the *axial apophysis*, a term used by Stephens and Newstead in their description of the proboscis of *Stomoxys*. The proximal portion of the sclerite consists of two strong rods, which arise from the thickened posterior angles, and pass backwards, at first parallel to one another, but diverging slightly towards their ends; they are about equal in length to the axial apophysis. When examined in profile it is seen that they are not quite in the same straight line as the distal portion of the sclerite, but are curved a little upwards as they diverge from one another. These portions of the sclerite may be termed the *labellar rods*.

The position of the discal sclerite will be better understood by reverting for a moment to the structure of the labium as a whole. It is essentially a hollow organ, the chitinous and membraneous walls of which are continuous throughout the labium and labella, and enclose a space in which are contained the muscles which move the labella, some tracheæ, and a labial salivary gland, all of which lie in the hæmatocœle, a space continuous with the hæmatocœle of the head and body of the fly. At the distal end, where the labium is divided into the labella, it is invaginated, and so presents a double contour on cross-section, the two opposing inner walls being the pseudotracheal membranes. The discal sclerite is situated in the apex of the invagination, and the converging lateral halves of the membrane are attached to the margins of its expanded distal portion, all the channels terminating around this point. The aperture enclosed by the sclerite is therefore the commencement of the food canal and may be termed the *prestomum*. The mouth, as already pointed out, lies at the distal end of the buccal cavity.

The discal sclerite is attached to the two lateral rods which form the sides of the labial gutter by short tendons, which pass from the attenuated ends of the rods to the thickened posterior angles at the junction of the parallel with the curved portions of the sclerite. Their attachment functions as a joint, and the discal sclerite can be rotated on the fixed point through an angle of ninety degrees or a little more; in the closed position the labellar rods lie distal to and in the same line as the labium; when the labella are expanded for use they are rotated so as to lie perpendicular to the labium, and therefore parallel to the surface on which the fly is feeding.

The *prestomal teeth* (Plate II, figures 6, 7 and 8), though of only secondary importance in the economy of the house fly, have a special significance from the comparative point of view as being the homologues of the powerful cutting teeth of other Muscids. They are situated around the periphery of the prestomum, their proximal ends being attached to the discal sclerite and their distal ends directed outwards. The number and arrangement differ a good deal in nearly allied species, but they always conform to the same general type. Those of *Musca domestica* have been described by Kraepelin, and those of the Blow-Fly by Graham-Smith. The arrangement in *Musca nebulo* resembles the above. In *Musca convexi frons* it is somewhat simpler, as there is only one row of teeth, and only four on each side. Their disposition in this species is represented in figure 8, Plate II, where these are shown in side view, the terminations of the pseudotracheal channels being also indicated. Each tooth is a small petal-like slip of yellow chitin, contracted at its base to a rounded cord and expanded and hollowed distally into a shallow trough. The inner end is articulated to a thin raised flange of the discal sclerite, and the inner half of each tooth is adherent to the membrane between the pseudotrachae; the distal margin is irregularly serrated, but on account of the extreme thinness of this part of the tooth it is difficult to make out the precise outline.

The terminations of the pseudotracheal channels at the prestomum are somewhat peculiar. As the channel approaches the orifice the rings develop a median inward projection, so that when seen in optical section they appear T-shaped instead of straight; in the last complete ring this spur is produced inwards almost to the margin of the orifice, though it does not appear to be actually attached to it. On either side of the end of the channel, and embracing the last ring, there are several curved filaments of chitin which unite to form a thick strand, those of two sides passing inwards in contact with one another, between the teeth, to be inserted into the flange on the discal sclerite.

The Musculature and Mechanism.

It is not necessary to give here a detailed account of all the muscles and other structures which are concerned in the mechanism of the proboscis, but rather to indicate the main features of the movements and the musculature, so that the modifications found in the blood-sucking members of the group may be compared with the *Musca* type. The muscles are extremely difficult to study, and the chances of making an error with regard to their exact points of attachment are so great that it would not be worth while to attempt to describe minor differences. A full account of the different muscles and their actions will be found in Kraepelin's paper.

The first movements to be considered are those which result in the extension and retraction of the proboscis; as already stated, the whole organ is drawn up underneath the head when not in use, and can be extended into a straight line perpendicular to the long axis of the body when required. The labella also can be folded and expanded. The movement has to be considered joint by joint, though it must be remembered that in life all the joints are moved at the same time, the extension and retraction taking place rapidly. The extension of the rostrum on the head is brought about by a rotation of the fulcrum on the anterior border of the epistomal orifice, in such a way that its lower end passes forwards and downwards. The motive power for this is to be found in the distension of the large air sacs which lie on either side of the fulcrum, the air being expressed from the body of the fly into the head by means of the respiratory movements of the fly, as described by Kraepelin. The rostrum is extended, in fact, much as one would straighten the finger of a glove by blowing into it. The extent of possible movement is approximately rotation through a right angle, from the horizontal to the vertical position. Extension of the haustellum on the rostrum is accomplished mainly by the contraction of the muscles which are attached to the apodemes of the labrum, passing between the expanded upper ends of the apodemes and the lower end of the fulcrum; they pull in a downward and inward direction, and so force the labrum, and with it the labium, into line with the rostrum, by straightening the two at the loose joint in the region of the buccal cavity. The actual point on which the rotation occurs appears to be the membraneous union between the epipharynx and hypopharynx and the small chitinous plate which forms the walls of the buccal cavity.

The movements in these two joints by which the proboscis is retracted are both produced by muscular action. The fulcrum is rotated upwards and backwards by means of two pairs of muscles. The anterior pair of these is short, and passes between the internal surface of the head capsule, at a point just below the antennae, and the prominent posterior horns of the fulcrum; its action causes the fulcrum to rotate on the fixed point provided by the pressure of the anterior arch against the anterior edge of the epistomal orifice. The posterior muscle is very long, and passes between the internal surface of the head capsule in the region of the occipital foramen and the upper border of the mentum. The two act together, and the fulcrum, and with it the rest of the rostrum, is drawn upwards as it is rotated. The folding of the haustellum on the rostrum is accomplished by means of certain groups of muscles lying on the anterior surface of the rostrum; these are somewhat ill-defined, and many separate muscles which may fulfil this function have been described. The most important ones appear to be a pair which pass between the distal ends of the labral apodemes and the anterior arch of the fulcrum, and act in the reverse direction to those which are inserted into the expanded ends of the apodemes.

These two joints provide a very wide range of movement, and the distal end of the labium may be moved to any point within a segment of a circle the centre of which is situated at the point of attachment of the rostrum to the head, and the radius the length of the organ in the extended position. The upper limit of this segment is in the horizontal plane, a little below the line of the long axis of the body; the posterior limit is the vertical line between the epistomal orifice and the surface on which the fly is feeding. The joints do not permit of any lateral or rotatory movement.

The movements of the labella are somewhat complex, but as these organs become fixed and greatly altered in the blood-sucking flies, a brief note will suffice here. The movement is of two kinds, produced by different forces, and brings about very marked changes in the form and position of these organs. In the normal resting position the labella are compressed, and their two walls are separated from one another by only a small amount of cellular tissue. The two lobes are folded backwards on the end of the haustellum, rotation taking place at the joint between the end of the labial gutter and the discal sclerite, and between the fork of the mentum and the furca. The distal margins of the outer walls of the two labella are in contact with one another, and the oral surface is completely concealed. When they are required for use they are distended with blood from the hæmatocœle of the labium, which is of course in direct communication with the rest of the body cavity, in such a way that their internal surfaces are forced apart, and the outer walls rotated outwards and upwards as the space between the internal and the external wall of each labellum is increased. At the same time the discal sclerite and the furca are rotated by muscular action, so as to bring the expanded surface, which has now been formed by the two internal walls, into a position at right angles to the rest of the proboscis in its extended position.

The muscles which produce these actions are found in the blood-sucking flies in very much the same arrangement as in *Musca*. There are three main groups, two longitudinal and one transverse. The transverse muscle is comparatively small, and is found only in the lower part of the labium; it runs on each side between the internal surface of the mentum and the labial gutter, and by reducing the transverse diameter of the labium tends to drive the blood into the labella when they are to be distended. The anterior and median of the two groups of longitudinal muscles, arising from the mentum in its upper part, is inserted into the labellar rods of the discal sclerite, and on contraction rotates them backwards at the joint formed by its attachment to the ends of the labial gutter. The posterior and lateral group of muscles becomes of very great importance in the more highly specialised flies. It arises together with the retractors of the discal sclerite, and is inserted into the arms of the furca. As one pair of these muscles is inserted into the anterior and the other into the posterior of the two sclerites which connect the labella with the labium, the two are antagonistic; when they act together they will spread out and stretch the labellar walls, and when they act independently one will erect the labella and the other, the one attached posteriorly, will bring the labella to the position of rest. Both acting at the same time will retract the labella, and will therefore antagonise the transverse muscle, which by driving the blood distally will tend to distend them. The distension of the labella is not, however, due entirely to the action of the transverse muscles, but is helped by the muscles of the abdomen acting as in respiration; the longitudinal muscles of the labium have to antagonise the transverse muscles to the extent of driving the blood from the oral lobes, when the proboscis is to be retracted.

The evagination and invagination of the labella in *Musca* should be particularly noted, for it furnishes the clue to the mechanism of the biting apparatus of the blood-sucking flies of this group, in which the undoing of the evagination between the walls of the labella, by which the internal surfaces become external, constitutes the act of biting.

The prestomal teeth of the house fly are probably used to scrape food surfaces, and are moved by the alternate contractions of the anterior and lateral muscles, which cause the discal sclerite to rotate in an anterior and posterior direction on the pivot formed by its attachment to the labial gutter. When they are in use the posterior portion of the wall is drawn backwards out of the way by the muscle attached to the furca; as only the distal half of each tooth is free from the membrane, they cannot be very efficient weapons, but in view of the homology existing between them and the powerful teeth of other flies their method of action is interesting.

The Development of the Blood-Sucking Habit.

While the domestic species of *Musca* are mostly omnivarous, it is a matter of common knowledge that they are especially attracted by animal juices, either excrementa or exudations from the living body. Any slight cut or abrasion of the skin is certain to be sought out, and in the case of sick animals, too weak to protect themselves with their tails, flies collect in enormous numbers, especially in tropical countries, to feed on the exuded fluids. The prestomal teeth are probably sufficiently powerful to scrape away coagulated serum so as to enable the fly to reach the moisture beneath, though not to cut through living tissue. It is not unreasonable to infer that, in the ordinary course of evolution and differentiation of species, certain forms arose which had a special taste for blood and at the same time specially strong prestomal teeth, by means of which they were able to scrape an abraded surface more effectively, and, in a further stage, to make a wound on unbroken skin. Once such a habit was started it would be only a matter of time until the fly became confirmed in this manner of obtaining food, and in succeeding generations the whole structure of the proboscis would become adapted for this specialised function, the separate stages of the process remaining as distinct forms, more or less predominant and widespread according to the degree of perfection of their adaptation to their environment.

It so happens that these theoretical considerations receive confirmation from the study of the habits of some members of the genus. There are at least three flies, and probably many more, which, although their teeth are no more powerful than those of *Musca nebulo*, are nevertheless confirmed blood-suckers, and probably have no other food. These are *Musca corvina*, Portchinski, *Musca pattoni*, Austen, and *Musca convexi frons*, Thompson. The two latter are both common cattle flies in Madras, and have the peculiar habit, first pointed out by Captain Patton, of feeding on the blood which exudes from the wounds made by true biting flies, most frequently associating for this purpose with *Philæmatomyia insignis*, the commonest biting fly in this district. Both these flies are much larger than *Philæmatomyia*, and it is very remarkable to watch them, often half a dozen at a time, collect round the smaller fly as it is in the act of feeding, and endeavour to thrust their proboscides near the wound. As soon as the biting fly has finished its meal and flown off, one of the others takes its place and at once settles down to feed, only leaving the wound when it is as fully gorged as possible; both these flies resemble true biting flies in taking at one meal the maximum quantity of blood that they can contain.

These three flies, then, are examples of an early stage of the development of the blood-sucking habit; closer observation of the habits of other species in other parts of the world will probably reveal many instances of this peculiar form of parasitism. The matter is one of considerable economic importance, for such flies are as capable of transmitting blood parasites as those on which they rely for food.

The presence of even minute prestomal teeth is worthy of consideration when dealing with the question of trypanosome transmission, for it has been repeatedly shown that the discharge from ulcers, which are so constant a

N. B.—Since writing the above, another species which has the same habit has come to light. This fly, which has the additional peculiarity of being larviparous, has been described by Captain Patton and myself under the name of *Musca bezzi*, in a paper in the Indian Journal of Medical Research, Vol. I, No. I.

feature of many trypanosome diseases, contain large numbers of trypanosomes. Any such delicate organism would die after a very short exposure to the air and to the tropical sun, but flies with teeth sufficiently strong to scrape away the protective clot so as to reach the moisture underneath would be quite capable of transmitting live trypanosomes from one animal to another.

The Structural Changes in the Proboscis.

Before considering the different forms in detail it will be of advantage to indicate briefly the directions in which the structural changes, which are the response to the change in the habit of life, are to be looked for. All the modifications can be traced to the development of the prestomal teeth, the increase in the size and importance of which has rendered necessary a corresponding increase in the stability of the structures which support them, and in the strength of the muscles which bring them into play. At the same time the proboscis is altered in shape in such a way that it has actually become a piercing organ, pointed at the distal end and able to enter the skin of the host, in some cases to a considerable depth; and as the piercing parts are limited to the haustellum, this part of proboscis has become elongated, until it may be, as in *Glossina*, more than three times the length of the rostrum. The muscles which actuate the biting apparatus, greatly increased in size, are collected towards the posterior end of the labium, and connected with their insertions by tendons. At the same time the pseudotracheal membrane, no longer of use to the fly, has disappeared. The anterior of the two joints by which the labella in *Musca* are articulated to the labium is fixed more or less firmly in that position in which the labella are in a line with the labium. The discal sclerite is separated into two parts, the axial apophysis and the labellar rods, to the latter of which the teeth are attached by means of a projecting flange. The rods themselves are expanded into plates forming an incomplete collar round the prestomal orifice. The furca, to which the powerful muscles which move the teeth are attached, is greatly thickened, and takes part in a much more definite articulation. The fork of the mentum is resolved into its two parts, the distal one of which is moved forwards and outwards and takes little or no part in the articulation. The most obvious change is in the position of the proboscis in the resting attitude. On account of its increased length the haustellum can no longer be concealed when it is retracted, and projects conspicuously in front of the head.

The pseudotracheal membrane of *Musca*, as pointed out by Graham-Smith, fulfils a special function in filtering the food of the fly so as to prevent the ingress into the food canal of particles too large for its lumen. In the biting flies the membrane no longer exists as such, but some sort of filter is as necessary in these flies as in the non-biting ones, for on account of the method by which the wound is made there must be many particles, torn off by the teeth, sufficiently large to block the canal between the epipharynx and the hypopharynx if they gained access to it. This is prevented by the development, from the remains of the rings of the pseudotracheæ, of a series of processes, which are attached between the teeth and are swept through the wound in advance of them to keep clear the surface to which they are applied.

The Genus Philæmatomyia.

The genus *Philæmatomyia* was created by Austen in 1909, for one species, *insignis*. The characteristic feature of the genus is the presence of a circlet of teeth at the apex of the proboscis, between the labella. In other respects it closely resembles *Musca*, and unless the teeth are noticed there is nothing about the general appearance of the proboscis to suggest that the fly is a blood-sucker; it is probable that the above species, which appears to be widely distributed and common where it occurs, had previously failed to attract notice on account of its innocent and inconspicuous appearance.

Since the description of the above species two others have been found, *viz.*, *Philæmatomyia lineata*, Brunetti, and *gurnei*, Patton and Cragg. Both these, and especially the latter, appear to be rare flies, at least in Madras, where *insignis* is extremely common. All three are of exceptional interest, as they represent separate and early stages in the evolution of the blood-sucking proboscis. In all the proboscis is of the simple *Musca* type, is completely retractile within the head, and possesses a pseudotracheal membrane: the relative proportions of the rostrum and haustellum are the same as in *Musca*, the labella are only a little reduced in size, and the hairs and macrochætæ are similarly distributed and fairly abundant. It is obvious that such a proboscis cannot be simply thrust into the skin of the host, and, as will be seen when the mechanism is discussed, the wound made is a scarification rather than a puncture. The teeth are used, in fact, very much in the same way as those of a non-biting *Musca*.

The structure of the proboscis being for the most part identical with that of *Musca*, it need not be described in detail, and we may proceed at once to consider the modifications which are found. They are all in connection with the teeth, the discal sclerite, and the labial gutter; it will be convenient to deal with each fly separately.

Philæmatomyia lineata.

The evidence with regard to the blood-sucking habit of this species requires confirmation. In Brunetti's original description it is stated that Dr. Annandale has seen it gorged with blood, but this is not absolute proof that it can itself make an effective wound, for it may have the same habit as *Musca pattoni* and *convexi frons*. It is not common in Madras, and neither Captain Patton nor myself has been able to confirm Dr. Annandale's observation, or to ascertain if it can make a wound for itself, though we have frequently seen it on cattle.

The *teeth* (Plate IV, fig. 24) are shaped like rose thorns, and are attached to the membraneous inner wall of the labella by expanded bases, as thorns are attached to a stem. When seen in profile it is evident that only the distal half of each tooth is free from the membrane; the middle portion is composed of a slightly expanded base; the proximal portion of the tooth is flattened, adherent to the membrane, and distinctly divided in its long axis, so that it consists of two lateral ribs with a thinly chitinised interval between them; these are articulated to a flange of the discal sclerite.

There are four of these teeth, similar to one another in size and shape, situated at the prestomal orifice, and alternating there with the terminations of those pseudotracheal channels which open directly into the prestomum. The pseudotracheæ do not extend quite so far inward as do the corresponding ones in *Musca*, but terminate at the level of the distal portion of the attached bases of the teeth. On each side of each channel there is a pair of narrow flattened chitinous strands, which unite with those of the opposite sides to form a thicker strand at the level of the separation of the tooth from the membrane. This strand is continued between the teeth to near the attachment of the inner wall of the labellum to the discal sclerite, there being one such strand between each two teeth and one on the proximal side of the proximal tooth. At the distal side of the four large teeth there is a smaller thin slip of chitin, which appears to represent a rudimentary tooth. It is situated at the point where the anterior collecting channels terminate, and is contiguous with the irregularly shaped plates of chitin which replace the rings of the collecting channel in this region.

The *discal sclerite*, though retaining the general shape and appearance of that of *Musca*, shows evidence of the commencement of important changes. In the first place, it is much stouter and more heavily pigmented than in the non-biting species, to correspond with the increased size of the teeth and the necessity for more powerful muscles. The racket shape is modified by the wide separation of the labellar rods, with the result that the sclerite is V-shaped, the point corresponding to the junction of the parallel rods with the loop in *Musca* being marked by a prominence on the external surface.

The separation of the discal sclerite into two portions is evident even at this early stage. If a well cleared preparation (Plate V, fig. 31), carefully decolourised with chlorine, be examined under a high power, it will be seen that there is a definite fissure separating the anterior fourth from the posterior three-fourths, commencing on the external surface a little below the pointed apex and running backwards and slightly outwards towards the inner surface. The portion anterior to this fissure is the axial apophysis, and that posterior to it the labellar rod; the importance of this distinction will be seen later.

The *axial apophysis* is Y-shaped, the long arm of the Y, free and forwardly directed, being the most distal part of the sclerite; the lateral arms are only separated from the labellar rods by the fissure described above. The distal part is not straight, but is bent forwards at a right angle, so that its extremity lies in approximately the same plane as the teeth when extended for use; it is interesting to note that in decolourised preparations a median fissure separating the axial apophysis into two lateral halves can be made out.

The *labellar rods* consist of three parts, a posterior part in which the muscles are inserted, an anterior part which unites with the axial apophysis, and a tooth plate. The posterior portions, composing about half the length of the sclerite, are wedge-shaped and have their pointed ends directed outwards and backwards; their broad ends form prominent tuberosities on the outer sides of the sclerite. The anterior part is thinner and somewhat flattened from side to side. The tooth plate is a narrow flange of thin chitin, arising from the whole length of the outer edge of the anterior portion of the sclerite and following its curve; it is continued in front of the fissure separating the axial apophysis from the labellar rod, but at the fissure it turns directly forwards as an isolated spur, which reaches to about the level of the tip of the apophysis. It is from this spur that the rudimentary tooth arises. Posteriorly the flange is continued inwards and upwards across the tuberosity, the most posterior portion projecting inwards towards that of the other side. When seen in profile the tooth plate presents a sickle-shaped free border, the anterior and posterior extremities of which are placed at the terminations of the two longitudinal collecting channels of the pseudotracheæ. The bases of all the teeth and the terminations of the central pseudotracheæ fit into the concavity, and the proximal ends of the teeth and the supporting strands of the pseudotracheæ are attached around its margin. In this way the tooth plates of the two sides form a sort of cup into which the bases of the teeth fit.

The *labial gutter* of this species differs from that of *Musca* in the greater thickness and pigmentation of its chitin. The lateral rods are definitely demarcated, and articulate with the labellar rods at the junction of the anterior and posterior portions. They can be traced almost to the proximal end of the mentum, lying on either side of the labrum-epipharynx. *The hypopharynx is free from the gutter except at the extreme upper end.*

The *pseudotracheal membrane* does not differ from that of *Musca*. There are, however, only eighteen channels, whereas twenty six seems to be the average number in non-blood-sucking forms.

The mechanism of the proboscis appears to be identical with that described for *Musca nebulo*. The teeth are brought into play by the contraction of the muscles inserted into the furca, the requisite resistance and adaptation being obtained by the muscles inserted into the labellar rods. When in use the labellar rods are placed more or less perpendicular to the labium, and the teeth, turned outwards by the tightening of the membrane to which their bases are attached, are arranged in a half moon with the axial apophysis in the centre, not in a circle as stated by Brunetti. They may either be drawn across the surface in an antero-posterior plane by the movement of the labellar rods on their attachment to the labial gutter, or they may cut by the simple eversion of the labellar walls, which turns them outwards and at the same time draws their points across the skin.

Philæmatomyia gurnei.

In a recent paper written in conjunction with Captain Patton of this Institute the discovery of this species was briefly chronicled, a detailed description being deferred in the hope of obtaining more material. Unfortunately this hope has not been realised, and up to the present time the only specimen in our possession is the one from which the original description was given.* It happened, however, that this specimen was caught in the act of sucking blood from a cow, and had its abdomen distended with blood, so that there is no doubt regarding its habits. The proboscis was removed from the head, cleared in potash, and partially dissected so as to display the teeth and connected structures. The discal sclerite, separated from the labium by the rupture of its tendinous attachment to the end of the labial gutter, was flattened out and compressed, in order to display the teeth of both sides, and in doing so the attachments of the axial apophysis to the labellar rods were fractured and the pseudotracheal membrane and part of the outer wall of the labella, torn. The microphotograph (Plate V, fig. 32) represents the appearance after this dissection.

The *teeth* are much stouter and shorter than those of *lineata*, though they resemble them in general configuration; their greatest breadth is about one-fourth the length. There are five principal and three rudimentary teeth on each side, arranged in a similar manner to those of *lineata*; the large teeth are

* A series of this species has been obtained while this Memoir was in the press. A detailed description appears in the Indian Journal of Medical Research, Vol. I, No. 1. Examination of further specimens has confirmed the above account.

in the middle, and on each side there is another similar in shape but only about one-fourth the size, and on the inner side, internal to this, there is a small slip which may be taken as a rudimentary tooth. As in *lineata*, only the distal half of each tooth is free from the membrane; at the extreme tip there is a series of rather coarse serrations. The serrated edge must be directed upwards when the teeth are everted. The proximal ends of the teeth are distinctly bifid. They are not directly attached to the tooth plate.

Between the teeth there are certain structures (Plate II, fig. 9) simple in this species, but assuming an extraordinary complexity in the more differentiated forms, which may be termed generally the *interdental armature*. They occupy the position of the Y-shaped strands of chitin which support the terminations of the pseudotracheæ in *lineata*, though they, like the teeth, are not attached to the tooth plate directly. They consist in this species of small leaf-like plates of chitin, arranged in pairs, one pair between each two adjacent teeth. The two blades of each pair are turned slightly inwards towards one another, so as to enclose between them the end of the pseudotracheal channel. The blades are about the same length as the teeth, and arise from the membrane by short stalks; the extreme tip and the edge most distant from the pseudotracheæ are thicker than the rest of the blade.

There are twelve pseudotracheal channels, arranged in the usual manner, except that the anterior and posterior collecting channels are each only continuous with two pseudotracheæ, the remainder terminating directly at the prestomum. There is a slight difference in the method of termination; the rings, instead of having inwardly directed projections, are split into two halves, and each half is turned inwards towards the tooth plate, one being in advance of the other so that they appear to alternate.

The *discal sclerite* shows a further advance in specialisation both in the degree of separation of the two constituent parts and in the thickness of the chitin. The *axial apophysis* is a stout conical piece of very deeply pigmented chitin, about twice as long as broad, and produced distally to a sharp point; it lies between the anterior ends of the labellar rods, and is fused with them in the posterior third of its extent. The apex of the apophysis is situated on a level with the bases of the pair of teeth nearest the middle line, so that when the teeth are turned outwards its point must project beyond them. The *labellar rods* consist of two portions differing greatly in the thickness of the chitin; the posterior portions are stout wedge-shaped rods bent slightly outwards from one another and terminating in blunt and rather thinner ends; they therefore closely resemble the corresponding parts of the sclerite in the last species. The expanded distal ends of these rods extend much further on the outer than on the inner side, so that the rods are triangular, with two nearly equal sides and one long one externally. The distal side of this triangle is produced forwards and inwards into a thinner sheet of chitin, roughly quadrilateral in shape, which is fused internally with the axial apophysis, and to the distal margin of which the tooth plate is attached; this flattened sheet corresponds to the distal curved portion of the sclerite in *lineata* and to the horse-shoe shaped arch in *Musca* (the extreme tip excepted).

The *tooth plate*, as seen in the flattened preparation, is a thin sickle-shaped slip of yellow chitin arising from the distal margin of the labellar rod on each side. The anterior portion, corresponding to the handle of the sickle, occupies about one-third of the length, and is directed straight forwards, those of the two sides being approximately parallel to one another, and situated on either side of the axial apophysis. They are attached to the labellar rods at their proximal ends, the rest of their periphery being connected only with the membrane forming the inner wall of the labella. The middle third of the plate is not distinguishable from the margin of the rod, but the posterior third extends forward and outward to about the level of the tip of the axial apophysis. In this way the tooth plate of each side forms a hollow cup into which the bases of the teeth fit, though *in this case without any chitinous attachment*.

The *labial gutter* in this species appears for the first time as a definite isolated structure, very different from its inconspicuous homologue in *Musca*. It is a thick and heavily pigmented rod, running the whole length of the labium, and composed for the anterior two-thirds of its length of much thicker chitin than any other part. The lateral margins of the gutter are separated from the middle portion by a narrow area of thin chitin; they do not reach quite to the upper end of the labium, but merge with the base of the hypopharynx and the adjacent membrane, which connects them with the mentum. The median groove, so far as can be judged from a specimen mounted on its side, is of considerable depth; like the lateral portions, it is thinnest at the upper end.

On the posterior surface of the gutter there is a median backwardly projecting ridge, commencing about the middle of the gutter and increasing in width as it passes upwards, but at the same time becoming thinner, until it is lost in the neighbourhood of the base of the hypopharynx. This is the "keel", corresponding to the structure in *Stomoxys* described by Stephens and Newstead. It projects backwards into the cavity of the labium, dividing it into two lateral halves, and is developed to provide additional attachment for an important group of muscles. Its significance will be shown in connection with the next species, in which it has been more closely studied, and it will be sufficient to note here its occurrence and extent.

The distal end of the gutter, where it articulates with the discal sclerite, is apparently moulded to form a joint. On the posterior surface there is a deep notch, caused by the extension of the lateral rods beyond the median portion of the gutter; the extremities of the sides of this notch are indented, and project forwards in their most anterior parts. There is no continuous chitinous union between the end of the gutter and the discal sclerite, and it looks as if the two were articulated by this simple joint to permit of free movement; under a high power the slightly projecting internal angles of the posterior portions of the labellar rods can be seen to be distinctly moulded so as to fit into the notch on the end of the labial gutter. The wide separation between them as shown in the drawing is of course an artifact due to the splitting of the sclerite by pressure.

The *mentum* shows some modification in this species as compared with the preceding. It is deeper, narrower, more capacious at its proximal end, and more pointed distally. The arms of the fork of the *mentum* are not so long, and the distinction between the two joints of the fork cannot be made out in my specimen. The *furca* is somewhat rounder and stouter, and is distinctly thickened in its middle portion, where it lies between the arms of the fork.

Philæmatomyia insignis.

The structure of the proboscis of this fly has already been fully described in a previous memoir, and it will only be necessary to recapitulate such points as have an importance from the present point of view. It is the most highly specialised of the genus, and we may note in passing that it is, so far as is known at present, also much the most common and widely distributed one. In Madras it is quite the most common biting fly found on cattle, and an idea of its prevalence may be gathered from the fact that one can frequently count twenty or thirty specimens on a single cow. It would be almost justifiable to infer that whereas the two previously considered members of the genus have not advanced sufficiently far to adapt themselves with success to an exclusively blood-sucking habit, and have at the same time become less fitted to obtain food in the manner usual in Muscids, this species has succeeded in establishing itself, and has become predominant.

In external appearance this fly differs no more from *Musca* than do the other species. Its proboscis is as completely retractile and is blunted at the tip, and the only suggestive thing to be noticed about it is its attitude when feeding. Instead of moving about the skin of its host, it settles down in a crouching attitude and remains on the same spot till obviously gorged with blood, all its legs bent and its head depressed, in an attitude very like that assumed by *Stomoxys*. This species appears to take no food other than blood, and it is somewhat remarkable that the pseudotrachael membrane should be retained in an apparently functional condition, co-existing with a biting apparatus which, as the anatomy of the parts and the observed habits of the insect both go to show, is an extremely efficient one. It is possible that the membrane is used in the same way as that of *Musca*, when the fly sucks up the blood from the wound.

The changes from the Muscid type are all found in the labium and the labella. In the rostrum all that can be distinguished is the relatively rather shorter length, and some elongation of the buccal cavity, the sclerite composing the walls of which is more pointed than in *Musca*, and curves over a little more laterally. The teeth are reduced in number and increased in size and strength, and are fitted more closely to the end of the discal sclerite. The discal sclerite itself shows complete differentiation into its two parts, and a definite change of form, the object of which is to render the joint between it and the end of the labial gutter more compact, and to fix the bases of the teeth more firmly. The method of attachment of the teeth should be particularly noted. Their bases are not attached to the sclerite, but lie in a cup formed by the projecting flange termed the tooth plate, the bases of the two smaller teeth at either end of the set on each side being a little in advance of those of the larger teeth, so that although the teeth are unequal in size their apices are in approximately the same line, while their bases form a concave line corresponding to the shape of the cup in which they fit. Owing to the alteration in the shape of the sclerite the teeth are attached to its distal end, and are directed downwards when the labellar rods are in the same line as the labium, whereas in *Musca* the teeth are directed downwards when the discal sclerite is perpendicular to the labium. As a consequence of this the axial apophysis now points in the same direction as the teeth when they are not everted; when they are spread out it forms the most distal part of the proboscis, and it is possible that it is used as an accessory tooth, or perhaps as a fixing point when the teeth cut by eversion. The interdental armature, inconspicuous in the other two species, reaches a high stage of development in the serrated blades, while the pseudotracheal membrane is distinctly smaller than one would expect from the size of the fly; the rod-like hairs make their first appearance in this species. The labium shows a high development of the labial gutter, and changes, such as the narrowing at the lower end of the mentum, the consolidation of the joint between it and the furca, and the thickening of the latter, which indicate an approach to the *Stomoxys* type of piercing proboscis.

Summary of the Genus Philæmatomyia and its relations to Musca.

We have in the genus *Philæmatomyia* a series of three flies which mark different stages in the adaptation of the Muscid type of proboscis to a blood-sucking habit. Notwithstanding the fact that the last member of the group is a voracious blood-sucker, and has, so far as I have been able to ascertain by a close observation of its habits and by repeated examinations of its intestinal contents, no other food than blood, there is no change in the external appearance of the proboscis, and the existence of biting parts may be unsuspected until they are revealed by dissection ; the proboscis retains its retractility, and is withdrawn in a typical Musca-like manner when not in use.

The changes from the *Musca* type fall into three groups ; those dependent on the increase in the size and in the functional importance of the teeth, those in the pseudotracheal membrane, and certain modifications in the general form of the proboscis. These latter are inconspicuous and will be referred to later in connection with the more marked changes of a similar nature found in the *Stomoxydinæ* and in *Glossina.*

In addition to the increase in size, the teeth show a tendency to an approximation of their bases. As this occurs, the flange of the discal sclerite which supports them develops into a cup, formed by the flanges on the two sides and situated at the distal end of the sclerite, into which their bases fit. In *Musca* the proximal ends of the teeth are attached directly to the chitinous margin of the prestomum, but in the last two species they are quite free from it, being attached only to the membrane on the inner wall of the labellum, and held in position by the flange; this facilitates eversion.

The discal sclerite is separated into its two parts, the axial apophysis and the labellar rods, to an increasing degree in the three species; at the same time the parts change their shape and their relations. Comparing the two extremes, as seen in *Musca* and in *insignis*, we find that there has been a backward displacement of the axial apophysis, or, what is the same thing, an elongation of the labellar rods, and that at the same time the attachment of the teeth to the discal sclerite has passed from the sides of the sclerite to the distal end. In *Musca* the teeth are attached to that side of the sclerite which is distal when the oral lobes are distended for use and the sclerite perpendicular to the labium, but in *insignis* they are situated at the end of the sclerite, which can only be distal in position when the labellar rods are in the same line as the labium. In each case the teeth are arranged around the incomplete chitinous ring which is formed by the discal sclerite at the prestomum, but in *Musca* this is only directed downwards, in which position it must lie when the fly feeds, when the labellar rods are parallel to the food surface and therefore perpendicular to the labium, while in *insignis* the orifice is only open in a position at a right angle to this. There is therefore an alteration in the position of the discal sclerite, when the teeth are in use, which amounts to a right angle, and we have to consider the causes which have brought this about.

It was stated in the account of the mechanism of the proboscis of *Philæmatomyia insignis* that the teeth cut by eversion, this being effected by the muscles inserted into the furca and acting on the teeth through traction on the inner wall of the labella. Now the relation of the size of the teeth to the extent of the inner wall is very different in *Musca* and in *insignis*, for in the former the pseudotracheæ are functional and the teeth rudimentary, while in *insignis* the membrane is reduced in size and complexity, and the teeth very large. It follows that cutting by eversion will be much more effective in *insignis* than it could be in *Musca*, though it probably does occur in the latter form. But the teeth of *Musca* can also be brought into action by alternating contractions of the anterior and posterior muscles, which rotate the discal sclerite in opposite directions on its point of attachment to the labial gutter, and such a movement will evidently be more effective than simple eversion on account of the greater range of movement of the teeth. Probably in *Musca* the two go on together. The teeth are first everted, the membrane drawn away, and the sclerite moved on its fixed point so that the everted teeth scrape the surface. As in succeeding generations new forms were evolved, the larger size of the teeth would make the act of eversion a more effective one in the scraping operation. But at the same time displacement of the teeth towards the distal end of the sclerite would be most advantageous to the fly, for it would shorten the arm of the lever to which the muscle is attached, and lengthen the one which bears the teeth, in this way giving to the cutting apparatus an increased facility for rapid action. We find then that in the three species of *Philæmatomyia*, contrasted with *Musca*, the teeth show a progressive increase in size, closer approximation of their bases, and displacement towards the distal end of the sclerite. This is associated with a difference in the relation of the labellar rod to the labial gutter in the position of action, for in *Musca* the discal sclerite can only be rotated on its fixed point until it comes to a perpendicular position, whereas the sclerite of *insignis* can pass back until the labellar rods are in line with the labium, a position which would be of no advantage to *Musca*, but which gives a much longer range of excursion to the teeth in *lineata* and in *gurnei*, in the former of which the sclerite can certainly be brought more into line with the labium than it can in *Musca*. At the same time the joint between the sclerite and the end of the labial gutter has become consolidated, until in *insignis* we find the two parts definitely moulded to one another as a regular articulation. But in the latter species, the sclerite being in the same line as the labium, the teeth in their final terminal position, and the pseudotracheal membrane considerably reduced in extent, the action of eversion of the teeth, brought about in the manner described, will be a most effective one. It is obvious that excursion through a short arc is more suitable for piercing, while a comparatively wide sweep of the teeth, such as would be obtained by rotation of the sclerite on its fixed point with the teeth in the everted position, is the better for scraping a surface. It is probable that scraping by rotation of the sclerite as a whole in an antero-posterior plane, through an angle of half a right angle or thereabout, with the teeth in the everted position, is the predominant factor in *Musca* and perhaps in *Philæmatomyia lineata*, while in the higher form which is exemplified in *insignis* the labellar rods are erected once for all at the commencement of the act of feeding, and the wound actually made by rapidly repeated eversions of the teeth.

In spite of the changes in the form and position of the sclerite the relations between it and the labella remain unaltered. The inner wall is attached to the borders of the sclerite as in *Musca*, and the interval between the two labellar rods corresponds to the median fissure on the anterior surface, between the two lobes. In order that the prestomal orifice may be directed distally, however, the labellar rods must be in line with the labium, not perpendicular to it. It should be remembered that the prestomum is not a closed ring, but is simply the point where the labellar walls converge to each other, and that it is defined by the discal sclerite. In *Musca* the opening through which food passes is at a right angle to the long axis of the sclerite, and *insignis* in its long axis, but in each case the interval between the labella is only closed in by the apposition of the two inner labellar walls.

The modifications of the labial gutter and the posterior joint are an obvious result of the method of action. The teeth and the discal sclerite are increased in size, and therefore require greater strength in the gutter which supports them; the increased weight and the more forcible movement demand greater consolidation of the joint and increased muscle, and this latter factor necessitates an increase in the area of muscle attachment, a demand fulfilled by the development of the keel. The posterior joint and its muscles also show an increase in strength and stability, in accordance with the greater importance of the muscles which evert the teeth.

Considerable interest attaches to the origin of the interdental armature, which, from its persistence in all the Muscid biting flies, is evidently an essential part of the biting apparatus. The key to its homology is to be found in a comparison of the two early forms with one another and with *Musca*, and in the relation between the degree of development which it exhibits and the extent of the pseudotracheal membrane. It was stated in the description of *Musca* that the method of termination of the channels of the pseudotracheæ was variable, and the large amount of variation there is in even closely allied species is indeed remarkable. The variations are slight and difficult to make out, it is true, but it is just in such a labile structure that one would expect to find new developments. The usual method has already been described; the rings adjacent to the sclerite become more open, and develop a median T-shaped projection which is turned towards the prestomum. It is not actually attached to the chitinous margin, and on either side of it there are thin slips of chitin, sometimes simple, sometimes branched in an irregular manner, which pass from the sides of the open gutter at the termination of the channel towards the prestomum, and terminate either in very close proximity to it or by actually fusing with it. In some cases there appears to be a sort of loose joint between the two. These strands of chitin lie between the teeth and on either side of the gutter at their terminations; they are evidently of the same nature and origin as the rings of the pseudotracheæ, and are almost certainly formed by the splitting in the middle line of the terminal T-shaped rings. Now in *Philæmatomyia lineata* we find similar but much more conspicuous strands, arising from a common stalk between each pair of teeth, and dividing into four filaments terminally, two of these passing to each side of the end of the gutter. In *gurnei*, some of the last rings are divided into two, and pass towards the sclerite; outside these, and attached near the chitinous margin, there are two definite leaf-like blades, distinguished from the strands by their flatness, but otherwise disposed in precisely the same way. These are turned slightly outwards from one another at the distal end, where they lie on the sides of the terminal gutter of the pseudotrachea. In *insignis* the serrated blades, although elaborate, are essentially of the same nature as those seen in *gurnei*, and like them are derived from the proximal rings at the terminations of the pseudotracheal channels; each of the blades in each bunch represents a modified strand of chitin such as those in *gurnei*, attached to a common stalk, and the complexity of structure is more apparent than real. A comparison of the serrated blades of *insignis* with the chitinous strands which occur in the prestomal region of the blow-fly, as figured by Graham-Smith (his figure 8, *e.g.*) shows at a glance how the transformation has occurred.

The origin of the interdental armature from the pseudotracheal channels is all the more interesting when one considers the function which they fulfil in the two forms. As pointed out by Graham-Smith, the pseudotracheal channels of the blow-fly act as a filter to prevent the ingress into the mouth of particles too large for the food canal, and as I have shown in the case of *Lyperosia*, which is provided with an arrangement similar to that of *insignis*, the blades are swept across the wound in advance of the teeth at each eversion, and will thus keep the surface clear while the wound is being made. When it is sufficiently large for the blood to flow, all the fluid which enters the prestomum must first have found its way through the network formed by the blades, which form a sort of brush at the extremity of the proboscis, an arrangement which must act as a most efficient filter. Thus, though the rings of the pseudotracheal channels have undergone a great change of form, the function is retained.

The affinities of the three species, so far as can be judged from the structure of their mouth parts, are as follows:—*lineata* is closely allied to *Musca*, while *gurnei* represents a much greater advance, and is probably the first stage at which the fly can make a wound for itself. *Insignis* is much further removed from *gurnei* than that fly is from *lineata*, as shown by the definitely erect position of the labellar rods in the position of action and the high degree of development of interdental armature. So far these are the only three species known, but it is highly probable that more will be found, as the first species described, *insignis*, has proved to be so common and so widely distributed since it was first differentiated from *Musca*. New species will be awaited with great interest, for among them one may expect to find forms showing intermediate stages, in which the teeth will not be quite terminal in position, and the discal sclerite not so much thickened nor quite in line with the labial gutter in the position of action. Such forms may also be expected to show stages in the evolution of the interdental armature midway between *gurnei* and *insignis*.

The Stomoxys Group.

The next three flies, *Hæmatobia*, *Stomoxys* and *Lyperosia*, are included in the *Stomoxydinæ*. The proboscis of *Lyperosia*, perhaps the most specialised of the group, has been described at length in a previous memoir, and in their main features the other two are so similar that no general description of them is necessary. The three flies studied in the present research do not present a connected series comparable with that formed by *Musca* and the genus *Philæmatomyia*, but there are certain points which appear to indicate that the order in which they are placed above is that representing their respective degrees of specialisation. There is a wide gap between these flies and those of the genus *Philæmatomyia*, but doubtless future research will reveal the existence of intermediate forms which will show the course of the evolution more precisely than it can be seen at present.

In view of the close similarity of these genera with regard to the structure of their mouth parts, a general account of the form of the proboscis in its relation to the Muscid type will be given first; the details in which they differ from one another, so far as they are cognate to the subject, will be given later.

All the changes from the *Musca* type are directed to one end the production of a piercing organ, to enable the fly to pierce the skin of vertebrate animals in order to suck their blood. The fundamental difference between the flies in this group and those of the genus *Philœmatomyia* is that they actually do pierce the skin, whereas *Philœmatomyia* only scarifies it.* The two essential features in such a piercing organ are that it should be rigid and that it should terminate in a point. It is in these directions that the proboscis in the *Stomoxydinæ* is altered from that of *Musca*.

Rigidity is obtained by the consolidation of the rostrum and the haustellum, the reduction in size of the former, and the closer linking of the two by means of the buccal cavity. The haustellum is greatly strengthened by the increase in the extent to which its wall is formed by the mentum, which curves forward so as almost to meet in the middle line in front, leaving only a narrow membraneous interval between it and the labial gutter. The teeth are also more closely united to one another, though still equally free to move in the socket formed by the tooth plate. The alteration in the attitude of the proboscis, which is the most striking feature, is merely due to the increased length of the haustellum, which can no longer be folded on the lower surface of the head, but projects horizontally forward when in the position of rest.

The movements of proboscis, though not so conspicuous as those of the house fly, are essentially the same, and have practically the same range. They are used to bring the proboscis from its horizontal position of rest into a more or less perpendicular position when the fly is feeding. On account of the alteration in the relative size of the haustellum and the rostrum, however, the latter is more or less fixed in the position of extension, and when the fly is at rest the two parts of the proboscis are at a right angle to one another; the rostrum is apparently capable of being moved in a forward direction to a greater extent than in *Musca*, and one can at times see the whole organ extended and pointing in a direction anterior to the perpendicular. One may note in passing that the arrangement of these joints is quite the least advantageous possible for the propagation of any force from behind, and that it is anatomically impossible that the piercing parts should be inserted by means of the muscular power of the body of the fly; the proboscis is merely lowered into the wound as it is made.

Rigidity is also produced by the consolidation of the anterior joint between the discal sclerite and the labial gutter, by the partial fixation of the labella in a position which corresponds to that of extension in *Musca*, and by the con-

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* This does not mean that the proboscis of *Philœmatomyia* is necessarily a less efficient organ than that of *Stomoxys* and its allies. One may express the difference by saying that the one scrapes a hole in the skin, the other bores a hole.

solidation and modification of the posterior joint between the furca and the mentum.

The alteration in the shape of the proboscis is practically confined to the haustellum. This is always much broader in the upper than in the lower part, and tapers to a point anteriorly. The labella are so much reduced in diameter that they are little if at all wider than the narrowest part of the haustellum, and thus offer no obstacle when the proboscis enters the skin. The macrochætæ which are so conspicuous in *Musca* are reduced in number and in size, both at the distal margin of the labella and on the sides of the mentum.

The alteration in the appearance of the proboscis depends mainly on the progressive enlargement of the haustellum and diminution in size of the rostrum. This change in the relative proportions of the parts of the proboscis is a fundamental one, and can be traced through the whole group from *Musca* to *Glossina*. It forms a reliable index of the correct position of the several members of the group. The following are the proportionate lengths of the rostrum and haustellum in all the flies considered in this paper. In the case of the *Stomoxydinæ* the measurements were made along the posterior plate of the fulcrum from the upper to the lower cornua, and from the upper limit of the mentum to the tip of the labella, following the curve of the organ. In *Musca* and *Philæmatomyia*, an equivalent measurement of the haustellum was obtained by adding together the length of the labial gutter and of that portion of the discal sclerite which is distal to the articulation, including the teeth. The figures represent an average of several observations on different specimens; on account of the impossibility of obtaining a series of preparations mounted in exactly the same way they are to be regarded as roughly approximate only.

	Rostrum.		*Haustellum.*
Musca nebulo	1	to	·712
Philæmatomyia gurnei	1	to	·733
Philæmatomyia lineata	1	to	·777
Philæmatomyia insignis	1	to	1·411
Hæmatobia irritans	1	to	1·86
Stomoxys calcitrans	1	to	1·91
Lyperosia minuta	1	to	2·53
Glossina submorsitans	1	to	3·70

As will appear later, the progressive increase in the length of the haustellum is directly proportionate to the degree of fixation of the joint between the discal sclerite and the labial gutter, and to the degree to which the haustellum is drawn out to a point.

The *rostrum*, in addition to the reduction in size and the limitation of movement, is a much more firm and rigid structure than that of *Musca*; the investment of the fulcrum in the membraneous wall is closer and the air sacs posterior to the fulcrum, by the distention of which the rostrum is pushed forward, are not nearly so conspicuous. The lateral plates of the fulcrum extend further forward, and the membrane uniting them on the anterior surface is thicker and merges indefinitely into the chitin at the sides. On the other hand, the anterior arch is not thickened into a stout bar for muscle attachment, and the whole structure is more closely fixed to the head than in the species previously considered.

The buccal cavity has undergone a remarkable transformation. Elongation is foreshadowed in the case of *Philæmatomyia insignis*; in the *Stomoxys* group we find that it has gone on to such an extent that the cavity has entirely lost its original shape and structure, and is converted into a duct with specialised walls, connecting the food canal in the haustellum with the pharynx. It is essential that this duct should be capable of flexion without occlusion of the lumen, for these flies feed with the joint between the haustellum and the rostrum a little flexed, and not with the whole proboscis fully extended as in *Musca*. When the organ is in the resting position the buccal cavity forms a tube at the lower end of the rostrum, the upper end of the tube being in line with the pharynx and the lower end with the haustellum, so that there is a point about its middle portion where it is flexed at a right angle. To ensure that flexion will not result in the occlusion of the lumen the wall of the tube is composed of two parts, an inner and outer; of these the inner consists of a simple tube of thin but rigid chitin in the upper half, where it is in line with the pharynx, and below this of a softer membrane. Outside this there is a series of transverse rings, thicker behind than in front, and approaching one another in the middle line behind so closely as to appear to be fused with one another. These rings will thus keep open the lumen of the tube should it be flexed during the act of feeding,* whereas the food channel of *Musca* is probably blocked in the flexed position by the approximation of its walls at the buccal cavity. In all the Muscid biting flies the buccal cavity is merely a channel, dilated in the early forms and tubular in the higher, which connects the food canal in the *haustellum* with the pharynx. It takes no part whatever in the sucking action.

The *haustellum*, instead of the loose cylindrical arrangement of chitin and membrane seen in *Musca*, is here a compact and almost entirely chitinous spindle, tapering gently from the expanded upper portion, known as the "bulb", to a point. The entire surface as seen externally is composed of the mentum

* This arrangement of chitinous rings has another and more important object, *viz.*, to prevent occlusion of the channel when a negative pressure is brought about in the pharynx, into which it opens, during the act of sucking.
The negative pressure in such a fly as *Stomoxys*, which fills itself to repletion within a few minutes, must be much greater than in the pharynx of intermittent feeders such as *Musca*.

of the labium, the lateral portions of which curve inwards and forwards so as to almost meet in front. The labial gutter lies out of sight between the edges of the mentum, and the membrane uniting the two is of very small extent. There are no large pigmented macrochætæ on the mentum, and the few hairs which are present are short and inconspicuous.

The *labella* have undergone a complete transformation from the type seen in *Musca*, and have become converted into a pair of small compact and partially fixed organs, the sole function of which is to pierce a hole in the skin of the host. In consequence of the loss of function the pseudo-tracheal membrane has disappeared, and it is only in *Hæmatobia*, the first member of the group, that traces of it can be recognised. The hæmatocœle, or space between the inner and outer walls of the labella, being no longer required to contain enough blood to distend the large oval lobes, has become very much reduced in size, and all that remains of the walls is sufficient to cover the teeth and the interdental armature in the position of rest. Both joints of the labella are consolidated; the anterior joint is limited in movement, but the posterior one permits of an even greater range of movement than in *Musca*.

The teeth are not, as one might expect, larger than those of *Philæmatomyia*, but the mechanism by which they are brought into play is a much more efficient one. All the teeth of one side are attached to one another by their bases, and the ridge of chitin so formed lies parallel with the edge of the discal sclerite, though it is not continuous with it. The interdental armature persists; it varies with the species in matters of detail, but is always attached to the prestomum in a manner similar to that in which the Y-shaped strands of chitin terminate in this region in *Musca*. Certain accessory structures, probably sensory, also become prominent.

The discal sclerite appears in a new form, which is not, at first sight, at all comparable with that of either *Musca* or *Philæmatomyia insignis*. Closer examination, however, reveals their essential similarity and homology. In all three flies it has the form of a funnel-shaped collar of chitin, surrounding the prestomum, and articulated with the ridge of chitin formed by the united bases of the teeth in front and with the labial gutter behind. The funnel is composed of two flattened plates, roughly oblong in shape, with the vertical diameter greater than the antero-posterior, and the distal border concave. They are continuous on the anterior borders with the median fissure between the labella, and are united ventrally. The space between them, which appears empty in sections, is oval in shape, and broader in the middle than at the upper and the lower angles. These flattened lateral portions represent the labellar rods. On the ventral side there is a third piece, always more conspicuous in sections than in cleared preparations, which binds the two lateral plates together and forms the floor of the funnel. This represents the axial apophysis, a term which was first applied by Stephens and Newstead to this piece in *Stomoxys*, and subsequently used by me to indicate its homologue in *Philæmatomyia insignis.* The ridge of chitin at the bases of the teeth is closely apposed to the concave distal border of the sclerite, and is firmly bound down to it by a narrow band of fibrous tissue. The ridge is also attached by a fibrous band at the point where the lateral walls and the axial apophysis fuse together at the anterior ventral angle. The posterior end of the sclerite is irregular in shape, and articulates with the end of the labial gutter in a manner which differs slightly in the three forms, but in all cases is such as to indicate that the range of movement at this joint is a very small one, not in the least comparable to that in either *Musca* or *Philæmatomyia,* but more marked in *Hæmatobia* than in *Stomoxys.* The sclerite has, in fact, become fixed in the position of extension, as seen in *Philæmatomyia* when the labellar rods are in line with the labial gutter and the axial apophysis directed straight downwards. Normally the labella are directed a little backwards from the long axis of the labium, and are brought into line with it when the parts are in use, in the same way that the discal sclerite is erected in *Musca.*

As a consequence of this fixation of the anterior joint, the muscles which act upon it are reduced, together with the extent of their surface of origin. The anterior and median set of muscles is reduced to a very much smaller size than is found in *Philæmatomyia*, and the keel of the labial gutter from which it arises is diminished to a commensurate amount progressively in the three flies of the series. It is interesting to note that with the shortening of the arm of the lever to which this muscle is attached there is a corresponding decrease in the distance between its origin and insertion, for we find that the keel of the gutter, which in *Philæmatomyia* is attached to the upper portion only, is in these flies situated at the lower end, and that it becomes less extensive and more distal in position progressively with the other changes. The labial gutter itself, having no longer to bear the strain of a powerful pair of muscles, and since it is to a large extent replaced as a supporting structure by the mentum, reverts to its original function of protecting the labrum-epipharynx and hypopharnyx, and is composed of chitin little thicker than that of the mentum; the thickness, however, varies according to the amount of muscle attached to it, and is much greater in the region of the keel and at the extreme lower end, around the articulation, than further up. At the same time the distinction between the lateral and the median portions of the gutter remains well marked at the distal end, and they are here moulded so as to form a more or less complex joint with the discal sclerite.

The posterior articulation, between the fork of the mentum and the furca, now becomes the most important joint in the proboscis, and is specialised to a high degree. In the case of *Philæmatomyia* both the joints probably come into play; the anterior one allows a backward rotation of the labellar rods on the end of the labial gutter, so that the teeth can sweep backwards across the skin, while the posterior one allows the teeth to be pulled outwards, traction being exercised on the inner walls of the labella by means of the intimate attachment of the furca to the outer wall. In this series of flies the first action is restricted to the straightening of the labella on the labium, and all the cutting is performed through the last joint, the various parts of which are modified and strengthened in accordance with their increased functional importance. The actual line of the joint has become displaced backwards, so as to lie between the furca and the proximal portion of the arm of the fork.

The posterior margin of the lower end of the mentum is not notched as in *Philæmatomyia*, but shows at most a shallow groove. On either side of this there is a thick rod of chitin, having the shape of an elongated wedge with its base directed distally and its most prominent angle turned outwards; this corresponds to the proximal division of the arm of the fork. The *furca* is reduced in size in accordance with the greatly reduced diameter of the labella; it is a wide and thick arch, the middle portion of which articulates with the thickened ends of the arms of the mental fork. On each side of it there is a short thick rod of chitin, closely pressed against the furca laterally, and having its proximal end only slightly separated from the fork of the mentum; this is the distal joint of the fork, which in *Philæmatomyia* lies parallel with the furca when the labellar rods are rotated into a position corresponding to that in which they have become fixed in the *Stomoxydinæ*.

The outer wall of the labella is almost entirely composed of a sheet of rather thin chitin, which is intimately connected with the extremity of the furca on each side. It reaches to the distal edge of the labella, and there bears a fringe of more or less conspicuous hairs, those of the two sides intermingling when the labella are closed. At the margin it gives place to a softer and more flexible membrane, which occupies the inner surface and bears the teeth and connected structures, and is continuous with the thicker fibrous tissue which unites the teeth to the discal sclerite. In this way the teeth are connected much more directly with the furca than in any of the flies previously considered.

The great increase in the strength and importance of this joint has brought about other changes in the structure and relations of the parts. Most important of these is the great increase in the size of the muscles which act on the posterior joint, and which are homologous with the posterior and lateral muscles, or retractors of the furca, in *Musca*. As the mentum is now narrowed to a point, the muscles are displaced to the upper end, which is dilated into the "bulb" to accommodate them, and they are connected with their insertions by long tendons. The tendon of insertion is spread out after the manner of an aponeurosis. In addition to its main insertion into the lateral arm of the furca, it sends numerous fibres to the external wall of the labellum, and to the distal portion of the fork of the mentum, which is displaced forwards and fused with the labellar wall as stated above.

The mechanism of the proboscis has been dealt with in the description of *Lyperosia*, and the other species show no divergence from that fly except in very minor details. It will be evident from that account, bearing in mind what occurs in *Musca* and in *Philæmatomyia*, that the efficiency of the cutting action depends entirely on the great increase in the strength of the posterior articulation between the labium and the labella, and in the muscles which act upon it. The anterior joint is on the contrary limited to such movement as will place the teeth in the position for the next cut, and the muscles which act upon it, not having to work against the same resistance, are of much smaller size. A further point which is of some importance in considering the mechanism both of these flies and of *Glossina* is that there is a membraneous interval on the lateral aspect of the haustellum in the neighbourhood of the joints, which, while it permits of free backward rotation of the furca, would also detract from the rigidity of the proboscis as a whole, were it not for the fact that the labial gutter reaches its greatest thickness at this point.

The labrum-epipharynx and the hypopharynx are remarkably little altered from the *Musca* type. As a consequence of the narrowness of the groove in which they lie, they are narrower than those of the non-biting flies, and as from the same circumstance they are much better protected, they are more slender and less rigid. The labral apodemes are also somewhat shorter, corresponding with the reduction in size of the rostrum as a whole, and are not quite so thick. The most important feature of the food canal is that the fusion of the two lips of the groove in the epipharynx takes place at a higher level in these flies than in *Philæmatomyia*, which shows that there is a tendency for it to become converted into a closed tube, a continuation into the proboscis of the stomadeaum as a closed canal, instead of as dorsal and ventral outgrowths. On the other hand, the separation of the lower lamina of the hypopharynx from the labial gutter is maintained as in other blood-sucking flies.

Hæmatobia (Plate III).

The proboscis of *Hæmatobia* presents a most interesting feature in the possession of the remains of a pseudotracheal membrane, and certain other peculiarities which indicate that it represents a relatively early stage in the evolution of the blood-sucking proboscis. I am indebted to Captain Patton of this Institute for named specimens of *Hæmatobia irritans* and to Mr. Howlett for specimens sent from Pusa. Unfortunately the genus does not appear to occur in this neighbourhood and lack of fresh material renders my description somewhat more meagre than it would otherwise have been.

The relative lengths of the rostrum and the haustellum are practically the same as those in *Stomoxys*, but the difference in shape is greater than the measurements indicate, for the thickest part of the labium is at the junction of the upper and adjacent fourth, from which the proboscis narrows evenly to the furca, while in *Stomoxys* the greatest thickness is well above this line, and distal fourth of the labium is practically of a uniform diameter.

In the position of rest the labella are bent distinctly downwards on the end of the labium, much more so than is the case in *Lyperosia* or *Stomoxys*, and are distinctly wider than the adjacent part of the labium; they also bear a fringe of moderately large macrochætæ along the distal margin. All these points indicate a closer relationship with the *Musca* type. The keel of the labial gutter, though not so thickly chitinised as that of *Philæmatomyia*, is almost of equal extent, and is present in the upper two-thirds of the labium, reaching in the upper part almost to the mentum; it thus provides a considerable area for the attachment of the anterior set of muscles. The gutter itself is strong and deeply pigmented, and at its lower end (Plate V, figure 25) the separation between the lateral and the median portion is well marked. The articulation between it and the discal sclerite is obviously one which allows of a greater range of movement than can take place in *Lyperosia*. The lateral portions of the labial gutter are produced into rounded processes, which are inclined slightly backwards (downwards in the position of rest, the labium being horizontal) and extend beyond the median portion of the gutter. They lie in an L-shaped depression at the upper and anterior angle of the sclerite, and are in contact with it when the labella are straightened on the labium, but separated from it when the labella are in the position of rest. The bottom of the median groove in the gutter is produced beyond the rest of the median portion and fits into the space between the lateral walls of the sclerite, through which it can be seen in well cleared preparations. The labella, through the discal sclerite, can therefore be straightened on the labium, and maintained in the extended position by the pressure of the upper border of the lateral wall of the sclerite against the lateral portion of the labial gutter. When in this position the median portion of the gutter projects between the two walls of the discal sclerite, and will afford additional support. The discal sclerite itself presents no differences from that of *Stomoxys*, except that the axial apophysis is more pear-shaped, and that its pointed end projects further forward.

The outer wall of the labellum is partly membraneous and partly chitinous. The chitinous portion is in the form of a plate shaped like a cockle-shell; the rounded edge of this forms the lower border of the labellum, and bears some of the hairs forming the terminal fringe; the upper end, which corresponds to the hinge of the shell, is thickened and drawn out, and is closely fused with the extremity of the furca. The upper portion of the posterior side of this plate is also attached to the lower border of the furca by a thin chitinous prolongation, so that the whole outer wall of the labellum is firmly bound down to it, and must follow it when it is drawn upwards. This plate corresponds in position to the space on the inner wall occupied by the teeth, which can be seen by focussing through it in a cleared preparation.

The rest of the outer wall is membraneous, and is continuous with a membraneous area, on the anterior and lateral aspects of the end of the labium, which extends upwards above the furca for a distance equal to the length of the labella. The membrane is quite different in appearance to any that is met with in the flies already described; it consists of a transparent, homogeneous, and structureless groundwork, in which there are placed small plates of thin chitin, irregularly oval in shape and set close together, though not actually touching one another. At its boundaries it merges indefinitely with the attenuated edges of the chitinous plates, and at the border of the labella it is continuous with the inner wall.

At the distal border of the labella there is on each side a row of five finger-like flaps, passing distally beyond the margin, and continuous with its outer wall. They are processes of the labella, and it is on their inner surfaces that the channels of the pseudotracheal membrane are to be found; they will be dealt with in connection with the structures found on the inner wall of the labella.

The teeth are five in number on each side. Counting from the dorsal or anterior side, the second is the largest, the first and third equal in size and slightly less than the first, and the third and fifth distinctly smaller, the fifth being the smallest of the set. The largest tooth is about one-fourth the length of the labellum. Each tooth is conical in shape and about twice as long as it is broad; the distal end is produced to a blunt and slightly curved point, just below which there is a notch in the margin of the tooth, the edge proximal to the notch forming a second cutting point. The notch is situated on the dorsal borders of the first and the second teeth, on the internal border of the third, and on the posterior or ventral borders of the fourth and fifth. On the internal surface of each tooth, that is to say, on that surface which is turned outwards when the teeth are everted, there are a number of peculiar secondary teeth (Plate III, figures 18 and 19). These are situated about the middle of the surface, and are arranged in rows across the tooth. Each is a small oblong or oval eminence, the distal end of which is free from the surface of the large tooth and forms a cutting point. All the teeth are united at their bases by chitinous prolongations, the union of the first two and the last three to one another being the most firm. When flattened out by the pressure of the coverslip, as in the preparation drawn (Plate IV, figure 22), the bases of the teeth are in the same straight line, but when the proboscis is mounted whole it is seen that in the position of rest they are arranged in a curve which corresponds with the line of the distal margin of the discal sclerite.

The interdental armature consists of a series of lanceolate leaf-like blades closely resembling the "petiolated blades" described by Stephens and Newstead. Like those of *Stomoxys*, they are extremely delicate objects, containing little or no pigment. Their surface is finely granular, and the stalks from which they arise are thicker and flatter than those of *Stomoxys*. They are arranged as follows:—There are three sets, similar to one another, between the first and second, second and third, and third and fourth teeth. Each of these consists of a central stalk, from each side of which three blades arise and pass forwards, those of the two sides diverging from one another. The terminal pair of blades lie on either side of the pseudotracheal channel. External to the first tooth there is a set of smaller and narrower blades, five pairs on a common stalk, the terminal blades also surrounding the termination of a channel. External to these there are two stouter elongate filaments of chitin arising at the base of the first tooth. Between the fourth and fifth teeth there is a common stalk bearing only two pairs of smaller blades, the diameter of which is little greater than that of the stalk. External to the fifth tooth there is another stout stalk which bears two pairs of blades, and arises from the ridge of chitin at the base of the tooth. On account of the extremely heavy pigmentation of the teeth and their close approximation I have not been able to ascertain whether the middle sets of blades arise from the teeth or from the membrane of the inner wall of the labellum.

Between the petiolated blades, and situated opposite the apices of the teeth, there are certain prominent hairs, the position of which should be noted. These correspond to those termed by Stephens and Newstead the "rod-like" hairs; they are short and stout, arise from prominent raised and expanded bases, and terminate in truncated ends. They are darkly pigmented and conspicuous, slightly curved, and about five or six times as long as thick. The appearance of a groove is probably due to the presence of a central canal and not to an actual groove. They are arranged as follows:—One opposite the first tooth, two opposite each of the second, third, and fourth teeth, and one opposite the fifth tooth; in addition, there are two smaller ones placed between the small petiolated blades external to the first tooth and the extreme anterior strand of chitin. These rod-like hairs occur in all the biting flies dealt with in this paper, except the first two species of *Philæmatomyia*, and presumably have some special sensory function connected with the biting habit.

The membrane forming the inner wall of the labellum, as far forward as the attachment of the two distal petiolated blades to the common stalk, is transparent, homogeneous, and apparently structureless; its existence is only shown, in cleared preparations, by the way it holds the parts together. But distal to this it consists of a membrane of the same nature as that which forms the non-chitinised parts of the external wall, and is produced beyond the distal border of the labella as the inner wall of the finger-like flaps already referred to. The structure of these flaps is as follows :—

Each flap is roughly triangular in shape, and consists of two walls, an inner and an outer. The outer wall is continuous with, and of the same structure as, the membrane which forms part of the external wall of the labellum, and which dips in between the two lobes at the anterior median fissure. The squamæ in this region are thinner and less sharply defined than elsewhere, and are all more or less pointed and distally directed. Those at the extreme tip of the flap are turned inwards towards those of the opposite side. In the middle line of each flap there is an area over which they are deficient, corresponding in position and extent to the pseudotracheal channel on the inner wall. The inner wall of each flap is continuous with the homogeneous and structureless layer of tissue which lies subjacent to the teeth, the line of junction between the two being situated at the level of the distal border of the chitinous plate in the external wall of the labellum. The distal portion, that is to say, that which is opposite to the outer wall of the flap, is composed of a membrane similar to that of the outer wall, but the squamæ are here so disposed as to form a shallow channel, the representative of the pseudotrachea. The plates are only found in the area which corresponds to that on the outer wall in which they are absent, so that the distinction between the two layers of the flap can only be made out by careful focussing in a preparation which has not been compressed by the coverslip, and by using a high magnification. The channel is formed by a series of thin transversely elongated plates, set side by side and fitted loosely to one another; each plate is curved to such an extent that the channel, in cross-section, would be approximately semi-circular, and the lateral extremities of the plates are alternately bifid and narrowed. At the distal end the channel is turned upon itself in such a way that the last three or four of the plates are in the same line as those proximal to them, or nearly so. Opposite to the termination, which is not at the distal end of the flap, but some distance away from it on account of the bend at the end of the channel, there is a minute, short and stout hair set on a thicker base.

At the proximal end of the flap the flat plates which form the groove are replaced by rounder rods very similar in appearance to those of ordinary pseudotracheal channels. The transformation takes place gradually and regularly, and there is no doubt that the plates in the region of the flap and the rings between the petiolated blades are the same structure in different forms. The termination of the pseudotracheal channels in the region of the teeth is abrupt and simple, and there are no T-shaped rings, or rings split in half, such as have been described in the previous forms. The terminal rings differ from the rest only in being produced into U-shaped loops.

There is no doubt that this structure represents a pseudotracheal membrane, and is homologous with that found in *Musca*. In order to ascertain definitely to what degree the function is retained it would be necessary to examine fresh specimens, but it appears likely that the channels do actually act in conveying the fluid to the prestomum. The space between the two walls of the flap is evidently a part of the hæmatocœle, and will therefore be distended by the blood of the fly as in *Musca*. It was shown in the case of *Lyperosia* that the teeth are returned into position for cutting by the distension of the hæmatocœle. In the case of *Hæmatobia* this distension will also result in the approximation of the two ends of the elongated transverse plates, in the same manner as that in which the pseudotracheal channels are closed in *Musca*. Possibly the two ends interlock, leaving only the interbifid spaces open as in the non-biting Muscids.

The occurrence of this structure in a fly with a piercing proboscis is very remarkable, and has an especial interest as indicating the source of the pseudotracheal channels. Evidently these, in *Musca* and its allies, are mere thickenings of the wall of the labella, and are similar in origin to the squamæ in *Stomoxys* and *Hæmatobia*.

Stomoxys.

The anatomy of the proboscis of *Stomoxys* has been described in great detail by Stephens and Newstead, and I may say at once that as regards the details of structure and armature there is little to add to their account, my dissections having in the main confirmed their results. Their work on *Stomoxys*, however, was done after an examination of *Glossina*, the most complex and highly specialised of the series, and the true homology of the parts, which can only be understood by proceeding from the simplest forms to the more complex, is not brought out in their paper. The terms used by them are descriptive and provisional only, the establishment of a definite nomenclature having been postponed pending further research. The account therefore lacks cohesion, and is difficult to follow unless one has the actual preparations before one. It will therefore be necessary to explain the relation of the terms used by them to those used in this paper. In so far as they are applicable to structures not already named in *Musca*, their terminology has been retained and used in the previous papers of this series.

To commence with the labium: the whole of the chitinous wall as seen externally, including the bulb, I regard as the mentum, homologous with that of *Musca*; the two joints of the fork at the lower end are separated from one another, the proximal one being the support of the furca on each side, and the distal one pressed forward against the furca. The former of these is called the "ventral sclerite," the latter the "lateral sclerite of the fork." For the labial gutter and the keel I have used their terms, which are equally applicable to the corresponding parts in other flies. In the labial gutter they distinguish the lateral borders of the terminal portion concerned in the articulation as the "dorsal hooked sclerite" and the base as a separate sclerite, which unites with the lateral ones proximal to the articulation. In their description of the labella there is a good deal of confusion, owing partly to their having placed too much reliance on the appearances seen in sections, and to their not having recognised the nature of the joint. Their figures are so accurate and clear that the confusion of the text is to a large extent removed when one compares them with dissections. Their tooth plate (k) corresponds to that part of the sclerite which I have termed the labellar rod; the axial apophysis, as before, represents the tip of the discal sclerite which has become displaced upwards. The petiolated blades constitute the interdental armature; the "fork" is the furca, and should not be confused with the fork of the lower end of the labium. The tendon which is shown in their sections is the tendon of the muscle of the bulb, which pulls the teeth outwards and actuates the cutting mechanism.

With regard to the mechanism of the cutting apparatus my view, as explained in connection with *Lyperosia*, differs from theirs. I can find no joint in the whole of the proboscis which could permit of a lateral rotatory movement of the teeth, and the transverse muscles at the lower end of the labium fulfil a function entirely different to the one suggested by them. So far as one can gather from their paper these authors do not appear to have had access to fresh material for dissection, a most serious handicap, for without that, and a considerable quantity of it, it is extremely difficult to make sure of points such as these. The action of the muscles of the bulb can only be fully realised by dissecting out the bulk of the muscle and making traction on it while holding the labium firm at a lower point on the other side, thus imitating the natural contraction of the muscle. This is a difficult manœuvre, and one requires a large number of fresh specimens to demonstrate the effect beyond doubt.

The proboscis of *Stomoxys* conforms to the general description already given; all the points which indicate an advance in specialisation are more marked in this fly than in *Hæmatobia*. The labium is more pointed, the bulb confined more to the upper part, and there are fewer and smaller hairs at the discal fringe and at the sides of the mentum, points which indicate that the organ is more adapted for piercing. As showing the greater fixation of the anterior joint, the labial gutter is not so well marked and its keel is confined to the distal part of the labium; the labella are not so large as those of *Hæmatobia* and are placed more nearly in the same long axis as the labium in the position of rest. The joint between the end of the labial gutter and the distal sclerite is a closer one, and the two parts are united by a strand of chitin which passes between the distal ends of the lateral portions of the gutter and the dorsal part of the sclerite, thus limiting still further the amount of movement between the two, already small by reason of the nature of the joint. The teeth and the other structures on the inner wall of the labella, which have been described in great detail by Stephens and Newstead, resemble generally the arrangement in *Hæmatobia*, but some structures described by these authors have not been recognised either in *Hæmatobia* or in *Lyperosia*. The external wall of the labella is much less chitinised, and the membraneous portion between the truncated end of the mentum and the furca is more extensive, and is marked by folds indicating its disposition when the furca is drawn upwards.

Lyperosia.

While one can readily believe that *Stomoxys* has had for its immediate ancestor a *Hæmatobia*-like form, it is clear that *Lyperosia* is not descended from the *Stomoxys* stem, but from a common ancestor of the two, although the relation between the three flies is a very close one. Perhaps when the opportunity occurs to examine some of the other genera of Muscid biting flies forms will be found which will explain more clearly the positions which these flies ought to occupy in the group.

In the greater length of the haustellum in proportion to that of the rostrum, and in the much more typical spindle shape of the labium, we have clear indications that this fly is more perfectly adapted for piercing the skin than is *Stomoxys*. But in other details, small in themselves but significant when taken together, the adaptation appears less perfect. The palps approximate more to those of *Hæmatobia* than to those of *Stomoxys*, a point on which systematists lay some stress. The distal border of the labella has a fringe of macrochætæ which are distinctly more prominent than those of *Stomoxys*, though not so conspicuous as those of *Hæmatobia*. The external walls of the labella are far more chitinised than those of *Stomoxys*, though the chitin is thin and the plate which it forms is interrupted by the presence of longitudinal fissures, which will to a certain extent compensate for the rigidity. The form of the discal sclerite, however, shows clearly that *Lyperosia* is not directly related to either *Hæmatobia* or *Stomoxys*, and at the same time suggests that it is more specialised than either. In its general shape and relations it conforms to the type already described, but, when seen in section, it is found to be a much more complex structure, the relation of which to the mechanism of the joint it is by no means easy to determine. The change is limited to the axial apophysis, which has lost the solidity of the corresponding part in the other flies, and consists of a shell of chitin with cellular tissue inside. The proximal end is turned upwards behind the end of the labial gutter in a curious manner, and appears to take some part in the mechanism of the joint, though neither muscle nor tendon can be found attached to it. The joint between the labial gutter and the discal sclerite is of the most complex description, and can obviously permit of only a slight degree of movement.

Glossina.

Glossina is as widely separated from the flies previously considered as regards the structure of the mouth parts as it is in its other anatomical features and in its life history, and there is at least as wide a difference between its proboscis and that of *Lyperosia* as there is between *Lyperosia* and *Musca* in this respect. Nevertheless we find that the great changes in the anatomy of the parts are but an extreme instance of the adaptation of the Muscid proboscis to a blood-sucking habit, and there is little doubt that the proboscis of this fly is but a modification evolved from the *Musca* type.

The anatomy of the proboscis has been minutely described by Stephens and Newstead, but these authors have not touched on the subject from the point of view of this paper, and have simply described the appearances as seen, with a suggestion regarding the mechanism. My remarks on this fly will resolve themselves into an interpretation of the homology of the parts as described by them, and to a consideration of the mechanism of the proboscis as a whole, dealing in more detail, however, with the structure of the rostrum, which is not touched on in their work. My material has been limited to some dried specimens of *Glossina sub-morsitans*, for which I am indebted to Professor Newstead, and one specimen of *Glossina palpalis*, placed at my disposal by

Captain Patton. To make the most of such limited material the specimens, after clearing in potash, each for a different period, were mounted whole in different positions, and after examination replaced in clove oil, dissected, and remounted in balsaam. I have found no differences from the description or figures in either *palpalis* or *sub-morsitans*.

The proportionate lengths of the rostrum and the haustellum as given on page 45 are somewhat misleading, as the position in which the proboscis is held is a much more definitely fixed one than in the other flies, and it is not possible in cleared preparations to stretch the two divisions out into the same straight line. In the figures given by Stephens and Newstead and by Hansen, the haustellum is shown to be about three and a half times as long as the rostrum. The rostrum is short and compact, and is almost entirely occupied by the fulcrum, the space available for air sacs between its posterior plate and the limiting membrane being very small. The fulcrum is much more regular in shape and more evenly chitinised than in any of the previous flies. Seen in profile it has the shape of a triangle with three approximately equal sides; the posterior side is gently convex backwards, the anterior convex forwards in the upper part, where it is produced into a sharp angle, and concave below; the upper side is concave, but is not produced in the definite cornua at the posterior angle as in *Stomoxys*. The walls of the fulcrum are equally chitinised throughout, and from this fact and from the absence of ridges for muscle attachment, and from the lack of cornua at the upper aud posterior angle, one would infer that the movements of the rostrum on the head, though of the same nature as those of the other flies, are reduced to a minimum; and that the adaptation of the position of the proboscis for feeding is carried out by movements of the body of the fly and by the joint between the rostrum and the haustellum. The chitin of the anterior arch occupies a much larger proportion of the anterior surface of the rostrum than is the case in the other forms.

The *buccal cavity* approaches more to the type seen in *Musca* than to that of the *Stomoxys* group. It consists of a small chamber with chitinous posterior and lateral walls, formed from a small transverse plate, the up-turned sides of which are united anteriorly by a membrane. I am not able to say whether it has a dilator muscle or not. It is connected with the epipharynx in the same way as in *Musca*. The membrane which unites the buccal cavity with the pharynx is a very short one, and from the structure of this part of the proboscis it is evident that there is a little movement at the joint.

The briefest examination of the haustellum shows that the whole of it has become transformed into a piercing organ, and that the separation of the labella from the labium, though clearly marked, has not the same significance as it has in the *Stomoxys* group. All the structures have become most profoundly modified, the armature has become a most complex one, and the nature of the joints has altered so completely that it is difficult to say in some cases exactly what they represent or at which point the movement takes place. The fundamental changes on which the appearance of the proboscis depends are the predominence of the labial gutter over the mentum in the narrow part of the proboscis; the fusion of the discal sclerite with the end of the labial gutter, resulting in the total disappearance of the anterior joint; and the conversion of a part of the outer surface of the labella, and a part of the surface of the labium itself, into a cutting apparatus. All this is but an extreme stage of what one sees going on in the evolution of the other flies.

To take these changes in detail: The bulb of the proboscis is evidently the same as that of *Stomoxys*, and may at once be termed a part of the mentum. But at the distal end of the bulb the thick and pigmented chitin of which it is composed gives place to a very much thinner sheet which is flexible and membraneous, and which cannot contribute to the rigidity of the organ. In the middle line it is provided with a bilateral row of peculiar spines, which extend right to the commencement of the bulb. (S. & N., figure 2, i, ii) Sections at any point between the labella and the bulb show that the wall of the mentum is a very thin one; on the other hand, the labial gutter is very well developed, and it undoubtedly constitutes the main support of the proboscis, thus reversing the conditions found in *Musca*. The membrane which unites the two is short, but in the sections figured it is shown as thrown into irregular folds, which are very noticeable in my preparations. They run obliquely upwards and inwards, not in the same way in all the preparations but varying in different positions of the labella, in such a way as to indicate that the labial gutter and the mentum do not always occupy the same position in relation to one another. The only trace of the keel of the gutter that is to be found is a thin slip of chitin extending less than half the distance between the gutter and the mentum in the bulb. In the middle line between the two lateral halves of the gutter there is a deep pocket-like indentation in which the hypopharynx lies.

The posterior joint, between the labium and the labella, has undergone most profound changes, and it is no longer possible to recognise the constituent parts as seen in *Stomoxys*. But by reverting to the appearance in *Musca*, and to the essential nature of the parts, one is able to trace the homology fairly closely. The furca in *Musca* is nothing more than a thickening of the external wall of the labella on each side; in the biting flies allied closely to *Musca* it becomes transformed into a strong bar because the important muscles of the bulb are inserted into its lateral arms. In *Glossina* we find a reversion to the more primitive type. The muscles of the bulb are apparently not inserted by one thick tendon, but are spread out over a considerable area of the external wall, and the necessity for a thick rod therefore does not exist. There is instead a transverse plate, which is united with a longitudinal one.* The latter may, without any great stretch of the imagination, be recognised as formed by the fusion of the two rods which form the fork of the mentum, the ventral sclerites of Stephens and Newstead. These authors have pointed out that the lateral arms of this T-shaped piece are variable in position according to the degree of eversion of the labella, exactly as one would expect if they represent the arms of the furca. A considerable amount of the muscle of the bulb is probably inserted into the region referred to as the "dark ventral chitinous area."

The anterior joint has disappeared, and if the sections are traced downwards it will be seen that the walls of the labial gutter become directly continuous with the inner walls of the labella, just as the outer walls of the mentum are continuous with their outer walls. There is, however, a thicker portion shown in their figures 15 to 19, which corresponds to the position of the discal sclerite; the hypopharynx lies at the upper end of this thickening in the position of rest. The situation of the thickening of the internal walls corresponds in position to that of the "dark area" on the outer walls.

The interpretation of the mechanism of the cutting apparatus offers no difficulties. The teeth resemble in shape, though not in arrangement, those of the preceding examples, and the "fans" distal to them are evidently the homologues of the petiolated blades of *Stomoxys*, and therefore of the pseudotracheal rings of *Musca*. The teeth are united at their bases by the three pieces of chitin which bear the rasps, in a manner corresponding generally with that in which the teeth of *Stomoxys* are attached to the tooth plate; whether the rasps really represent the united bases of the teeth or are a detached part of the discal sclerite it is not possible to say. The "jointed chitinous rods" appear to be the rod-like hairs, which, in order to maintain their position in advance of the teeth during the act of cutting, have passed through the wall of the labellum in the manner described.

The mechanism of the proboscis is evidently the same as that of the *Stomoxys* group. But here there is an important point which should be noted in the interpretation of the drawings. I pointed out in connection with *Lyperosia* that the appearance of the labella in the everted position in cleared preparations is not the same as that in fresh dissections, for, when the muscles are dissolved by the action of the potash, the parts relax; it is impossible to get cleared preparations which show the true position of the teeth during the

* An examination of more material has convinced me that the longitudinal and transverse portions of this T-shaped rod are not continuous with one another, but are united by a narrow strip of membrane. This serves to hinge them together, while permitting of free movement.

act of cutting. The same applies to *Glossina*, and I have not the least doubt that the lateral arms of the " fork " are turned much further backwards, and the teeth much more fully everted, than is shown in figure 8 (S. and N.). The chitin between the " dark area " and the bases of the rasps is evidently thin and membraneous, and it is here that the eversion takes place when the teeth are brought into action.

There is a membraneous area between the end of the labial gutter and the fork, as is found in the other flies. But in the case of *Glossina*, the entire mentum, with the exception of the bulb, is drawn upwards when the teeth are everted, and the membrane between it and the labial gutter is thrown into the folds already mentioned. The posterior surface of the mentum is armed with spines which would appear to have some cutting action, and it is probable that many of the spine and tubercles so minutely described are really cutting organs accessory to the teeth and rasps, and that not only the inner wall of the labellum, but its outer wall and the outer wall of the labium also are a part of the cutting apparatus. The whole is actuated in the same way as in *Stomoxys*, by the contraction of the muscles of the bulb, the long tendons of which are so conspicuous in the sections. But instead of a simple eversion of the teeth the whole of the inner wall of the labellum, its outer wall, and part of the mentum are drawn up, until the thickened part which represents the discal sclerite is at the tip of the proboscis. When this has occurred the labrum-epipharynx and the hypopharynx are at the point of puncture, and are able to draw in the blood. The disproportion between the length of these two organs and the total length of the labium and the labella is less than that seen in *Stomoxys*, and this corresponds with the shorter space between the tip and the softer portion of the inner wall at which the eversion takes place. The short excursion of the cutting surface is more than compensated for by its greater lateral extent, for the armature extends from the rasps to the bulb, and includes portions of the inner and outer walls of the labella and also of the posterior surface of the mentum.

The labrum-epipharynx and the hypopharyx are altered in such a manner as one would expect. On account of the more pronounced stylet-shape of the haustellum as a whole, they are reduced in diameter and fit much more closely into the groove in the labial gutter. They are more firmly united to one another, so as to constitute almost a closed tube, and the labrum is closely fitted to the labium by means of an elaborate arrangement of interlocking teeth. Between the labrum and the epipharynx a small comma-shaped interval can be seen in the region of the bulb, in the situation in which the fan-shaped muscle is found in *Musca*. Stephens and Newstead state that the labrum, by which term they designate the combined organ, fuses at the upper end with the bulb, but they do not describe how the separation between the labral and epipharyngeal portions of the organ occurs, and I have been unable to determine this point for want of series of sections. It is a little unlikely that labrum and labium would unite directly. From the fact that the section shown in their figure 25 includes the attachment of the palp, one would suppose that the section is an oblique one, through the lower end of the rostrum, in which case the anterior membraneous portion is really the anterior wall of the rostrum. It is, as a matter of fact, extremely difficult to get the rostrum and haustellum sufficiently into line with one another to get a series of transverse section of both, as I found in the case of *Lyperosia*. It would be still more difficult to do it with *Glossina*, in which the angle is a much more permanent one.

I have never myself seen *Glossina* in the act of feeding, nor is the opportunity likely to occur. I have selected from the numerous descriptions of its mode of feeding one by an observer who presumably had no expert knowledge of the subject, and merely recorded what he saw. It accords so well with what I believe to be the mechanism of the proboscis that I cannot forbear from quoting.

Captain Crawshaw writes as follows in 1896: "When a 'Tse-tse' settles "with the intention of feeding............he inserts his proboscis, lowers his head, "and raises his abdomen till it is almost vertical; when doing this and for some "time after he has commenced sucking, he works his wings, buzzing in a minor "key, rather like a bee when held forcibly, though not so powerfully; when the "keenness of his appetite has been somewhat appeased, he stops working his "wings and sucks in silence. If left to himself he will suck until.................." The raising of the abdomen is rendered necessary in *Glossina* by the fixation of the joint between the rostrum and the head. It does not occur in *Stomoxys*. The period during which the fly produces the buzzing sound is that in which the wound is being made and the proboscis thrust into the skin, and while this is going on the fly is not absorbing food. The motion of the wings and the buzzing sound are produced by the excessively rapid respiratory movements which distend the hæmatocœle with blood; this must occur after each contraction of the muscles of the bulb, in order that the teeth may be replaced in position for the next cut, as explained in connection with *Lyperosia*. I have never distinguished any sound produced by *Stomoxys* while inserting its proboscis, but a faint vibration of the wings can be seen. The eversion and replacement of the cutting teeth in *Glossina* must of course occur with very great rapidity. As I have noted elsewhere, the cutting apparatus of the Diptera is a good example of the extraordinary rapidity of action of which insect muscle is capable. It is possible that by ascertaining the exact pitch of the ncte one could fix definitely the number of contractions made per second by the muscles of the bulb, for there will of course be one contraction for each respiratory movement, and it is these respiratory movements which produce the vibration in the wing.

When the wound has been made to a convenient depth the buzzing ceases, the labella are held in a permanently everted position, and in a very short time the fly sucks up enough blood to distend the abdomen. The motion of the wings does not cease, as Captain Crawshaw supposed, when the appetite is appeased, but at the moment the fly commences to suck, and is no longer occupied in making the wound. The length of the narrow part of the proboscis, the extremely efficient nature of the biting parts, and the rapidity with which the abdomen distends with blood, make it probable that the fly gets well below the epidermis and into a vascular layer before commencing to suck.

In several other accounts it is stated that the bite of *Glossina* causes pain, not at the moment the fly settles down, but after a short interval. One interprets this, as in the case of the mosquito bite, as due to the fact that it is the saliva injected into the wound which causes the pain, and not the actual making of the wound. The cutting parts of *Glossina* are so small and so sharp that one would not expect them to cause pain.

Summary and Conclusions.

1. The blood-sucking Muscidæ are descended from a Musca-like ancestor. The entomological facts make it improbable that the flagellates found in the alimentary tract of blood-sucking flies, and of non-blood suckers which are allied to them, are derived from the parasites in vertebrate blood. They are probably the descendants of parasites which entered the alimentary tract at the time the ancestors of the flies were mandibulate and omnivorous.

2. The first steps in the evolution of the blood-sucking habit can be seen at the present day in those flies which are blood-suckers but have no biting mouth parts. These depend on true biting flies for the making of the wound.

3. In the genus *Philæmatomyia* there are three species which show separate steps in the modification of the Musca-like proboscis to a biting apparatus. The changes all depend on the increase in size and functional importance of the prestomal teeth. They are :—Increase in the strength of the discal sclerite ; separation of the axial apophysis and labellar rods, and displacement upwards of the former ; approximation of the bases of the teeth and the separation of their bases from the discal sclerite, to allow of greater freedom of movement ; displacement of the teeth to the distal end of the labellar rods ; consolidation of the anterior joint between the labial gutter and the discal sclerite ; great increase in the strength of the labial gutter and the development of a " keel " to provide additional attachment for the muscles ; some consolidation of the posterior joint with a thickening of the furca ; increase in all the muscles ; some diminution in extent of the pseudotracheal membrane and the development of the interdental armature from the rings of the pseudotracheæ.

4. Between the genus *Philæmatomyia* and the *Stomoxydinæ* there is a wide gap. Future research will probably reveal other forms intermediate between these.

5. In the *Stomoxydinæ* the proboscis is a piercing one in the true sense of the word. Its spindle shape is due to the increase in extent and alteration in shape of the mentum as seen in *Musca,* and to the diminution in the size of the labella. The biting apparatus is altered upon the following lines :—The teeth are reduced in number and in size ; the interdental armature, which takes on the filtering function of its homologue, is highly developed ; the discal sclerite is altered to a funnel-shaped piece ; the articulation between the discal sclerite and the labellar rods is more or less fixed in the position of extension ; the posterior joint becomes of great importance, and the furca and the arms of the fork of the mentum are both greatly increased in thickness and reduced in size ; notwithstanding the chitinisation of the rest of the wall of the haustellum, there is

a membraneous interval left in the region of the joint which permits the furca to be rotated freely backwards.

6. In all the flies dealt with, in the order given, there is an increase in the relative length of the haustellum, and a diminution in that of the rostrum, together with some diminution in the amount of movement between the latter and the head capsule.

7. *Glossina* represents an extreme case, and there is a wide interval between it and the *Stomoxydinæ*. The alterations in the shape and the diminution in the amount of movement are the same in kind as in *Stomoxys*, but in greater degree. The teeth are more complex, and the interdental armatures are represented by the "fans." The cutting apparatus is not limited to the inner wall of the labellum, but extends on to the outer wall as well, and when the muscles of the bulb contract the outer wall is pulled bodily upward as the inner wall is everted. The discal sclerite is fused with the end of the labial gutter and cannot be recognised as a separate sclerite. The furca and the two arms of the fork of the mentum are closely approximated to one another. The main support of the narrow piercing part of the proboscis is the labial gutter, which is very strong, while the mentum in this region is semi-membraneous. The rostrum is capable of so little movement on the head that the fly has to raise itself on its hind legs to bring the proboscis into position for piercing.

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PLATE I.

Figure 1.—The proboscis of *Philaematomyia insignis*, Austen, from a cleared preparation p., the palp. ap., the apodeme. fu,, the fulcrm. m., the membrane of the wall of the rostrum. L.ep., the labrum-epipharynx. Hy., the hypopharynx, L.g., the labial gutter. Th., the memtum (theca). L.K., keel of the labial gutter. L.R., the labellar rod. T., the teeth. Pt. M., the pseudotracheal membrane. T.f., fork of the mentum, Fr., the furca. D.S., chitinous plates in the outer wall of the labella, reflexed × 33.

Figure 2.—The proboscis of *Lyperosia minua*, Bezzi, from a cleared preparation. f., the posterior cornu of the fulcrum. f'., the anterior arch of the fulcrum. f''., the funnelshaped distal end of the fulcrum. s.d., the salivary duct. ap., the apodeme. b.c., the buccal cavity. tr., trachea. l.g., the labial gutter. mt., the mentum. b., the bulb, l.g., the labial gutter. m. a., the membraneous area which allows of rotation backwards of the furca. v.sc., ventral sclerites (the proximal portion of the fork of the mentum). fu., furca. lb., the labella × 160.

PLATE I.

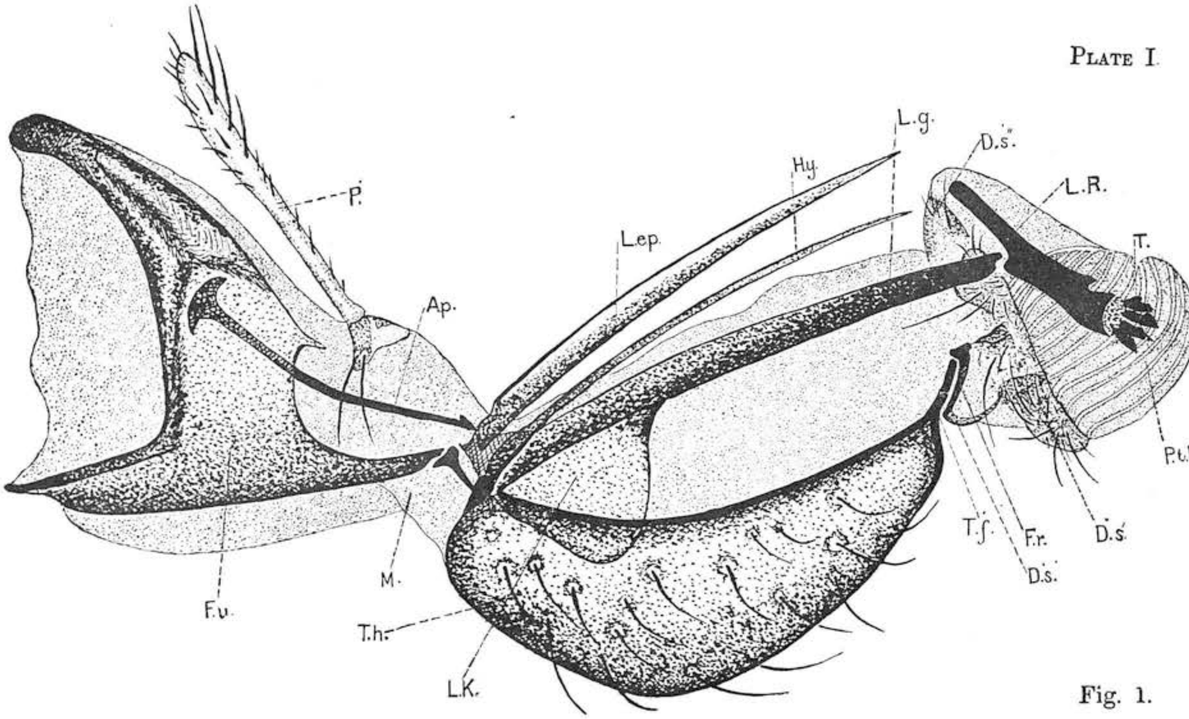


Fig. 1.

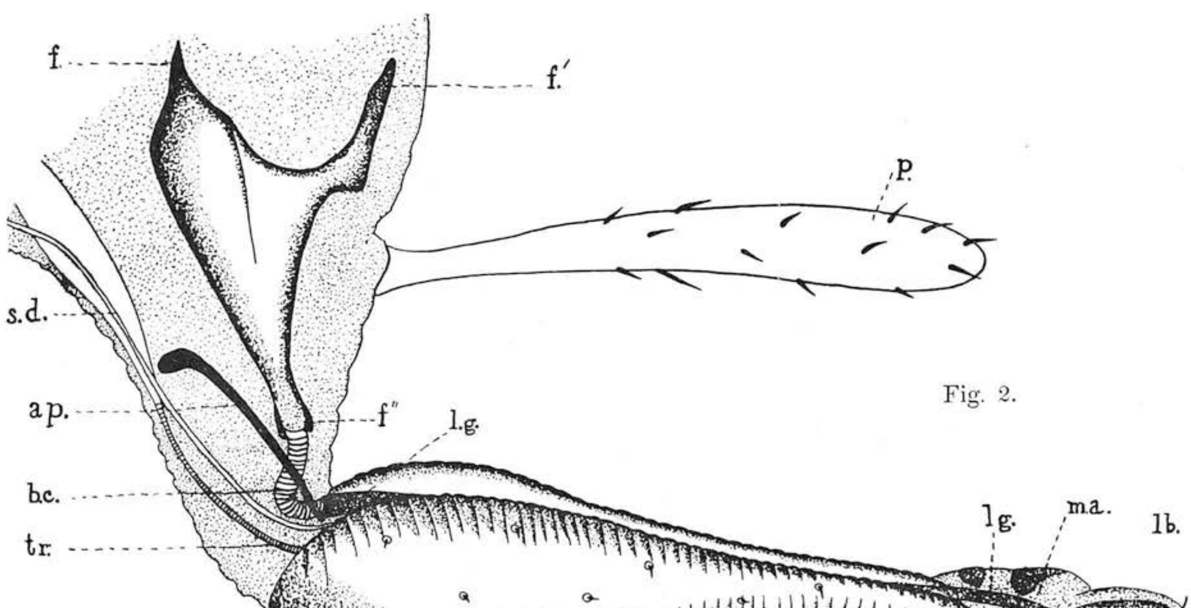


Fig. 2.

Photo.-Engraved & printed at the Offices of the Survey of India, Calcutta, 1913.

PLATE II.

Figure 3.—The mentum and furca of *Musca nebulo*. m., mentum. i., the incision in its distal border. f., the proximal joint of the arm of the fork. f'., the distal joint, in apposition with the furca. fu., the furca. p. s., the posterior plate of thin chitin continuous with the membraneous part of the wall of the labella.

Figure 4.—The anterior wall of the haustellum of *Musca nebulo*, with the discal sclerite attached. hy., the hypopharynx partially fused with the membraneous anterior wall of the labium. m., the membrane which connects the mentum and the labial gutter. l.g., the labial gutter. l.r., the lateral rods. d.s., the discal sclerite, articulated with the lateral rods of the labial gutter.

Figure 5.—The labrum-epipharynx of *Musca nebulo*. l., labrum. ep., the epipharynx. ap., the labral apodemes.

Figure 6.—Two of the prestomal teeth of *Musca pattoni*, with the terminal rings of one of the pseudotracheæ between them. t., tooth. ch. r., the chitinous filaments supporting the end of the channel. r., pseudo-tracheal ring. d.s., the discal sclerite.

Figure 7.—The prestomal teeth and terminations of the pseudotracheal channels of *Musca domestica*, after Kraepelin. t'., t''. t''' teeth of the first, second and third rows. p. s., the pseudotracheal channels. d.s., the discal sclerite.

Figure 8.—The teeth and terminations of the pseudotracheal channels of *Musca convexi frons*. t., prestomal teeth. p.s., the pseudotracheal channels. ch. r., the chitinous rods surrounding the terminations of the channels. d.s., the discal sclerite.

Figure 9.—The termination of a pseudotracheal channel in *Philæmatomyia gurnei*. p.b. the petiolated blades. p.s., the pseudotracheal channel. Note how the rings split at the proximal end; just distal to this they are much elongated. × 500.

Figure 10.—Some of the pseudotracheal rings of *Philæmatomyia gurnei* at a point distal to those of the last figure. × 500.

Plate II.

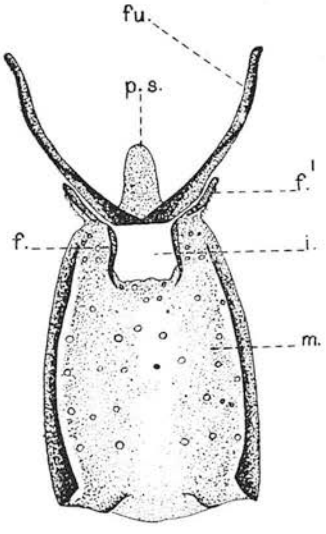


Fig.3.

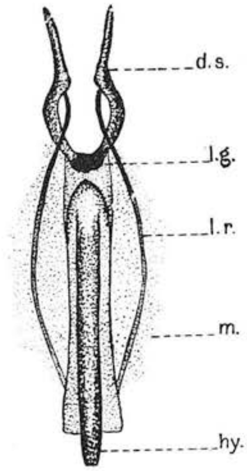


Fig. 4.

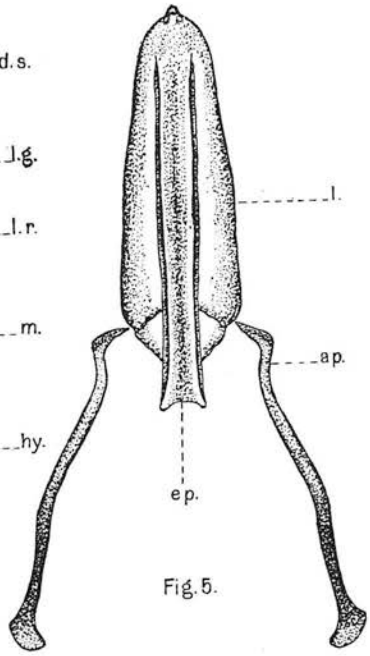


Fig.5.

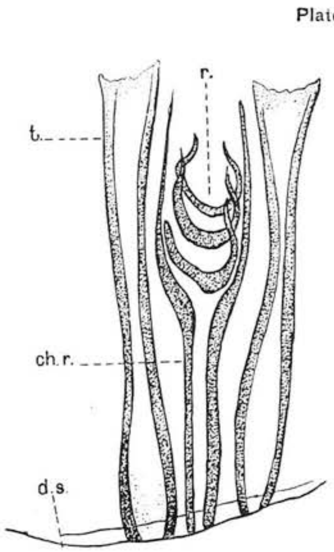


Fig.6.

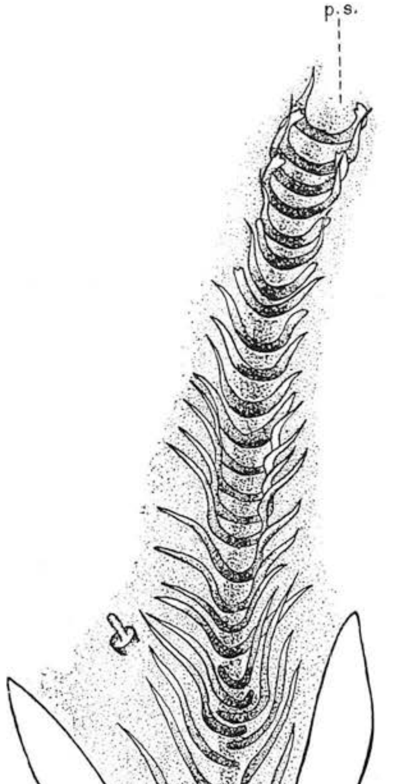


Fig.9.

Fig.10.

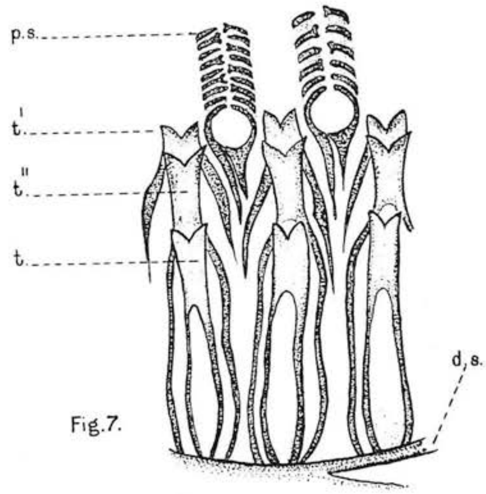


Fig.7.

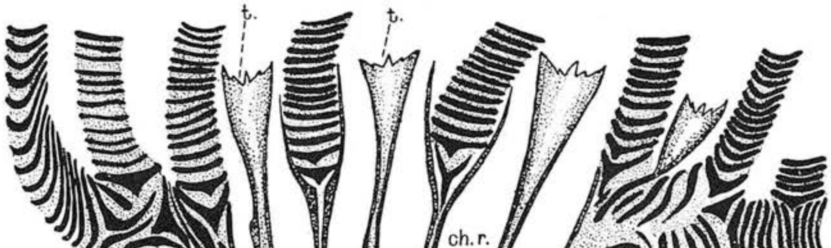


Fig.8.

Photo.-Engraved & printed at the Offices of the Survey of India, Calcutta, 1913

PLATE III.

Figure 11.—The proboscis of *Hæmatobia irritans*. b., the bulb. lb., the labella. ap., the labral apodeme of one side. fa., the fulcrum. b.c., the buccal cavity. p, the palps. × 80

Figure 12.—The labellum of one side, seen in profile. The position of the teeth is indicated by the dotted lines. f.l., the flaps at the distal end of the proboscis. p.s., the position of the channels on the inner wall of the flaps. p.b., the position of the petiolated blades. t., the position of the teeth. l.g., the labial gutter. fu., the furca. m.f., the proximal arm of the fork of the mentum. m.f′., the distal arm, detached and displaced forward. m., the mentum. × 180

Figure 13.—The external wall of one of the flaps, to show the shape and disposition of the squamæ, and the area over which they are deficient. × 1100.

Figure 14.—The internal wall of one of the flaps, to show the pseudotracheal channel and the sense hair at its termination. × 1100

Figure 15.—The upper end of the labial gutter, as seen in profile in a detached cleared preparation. This is the same preparation as the next figure, but as seen at a higher focus. The shaded portion represents the lateral expansion of the gutter, the dotted lines indicate the outline as seen in the next figure.

Figure 16.—As above, at the lower focus.

Figure 17.—The upper end of the buccal cavity, to show the method of junction with the pharynx. r., chitinous rings like those found in the salivary duct. ph., the lower end of the pharynx. × 310

Figure 18.—The first tooth in outline, to show the secondary teeth. × 700

Figure 19.—The fourth tooth. × 700

Figure 20.—One of the rod-like hairs, showing the central canal.

Figure 21.—Some of the rings of the pseudotrachea, showing the transition between the flattened plates as seen in the flaps and the typical rings as seen near the petiolated blades. × 1100

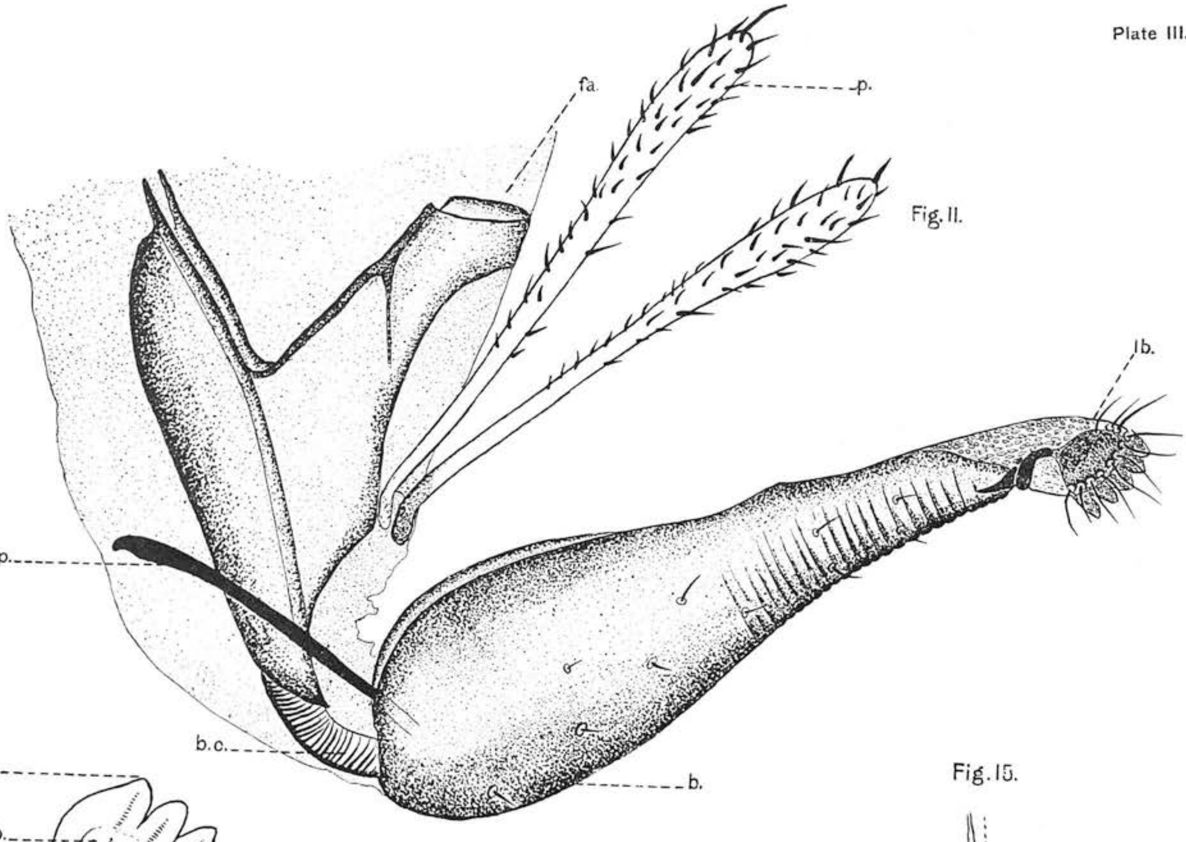


Fig. 11.

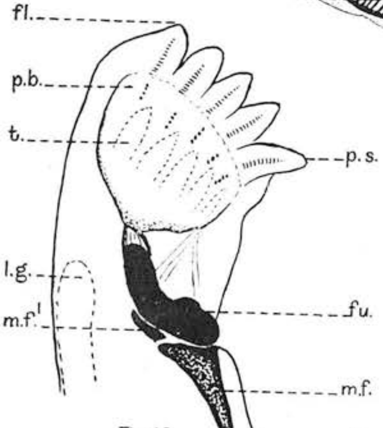
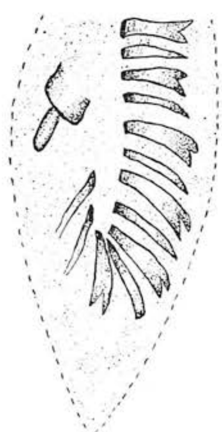


Fig. 12.

Fig. 13.

Fig. 14.



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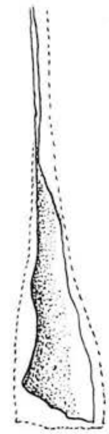

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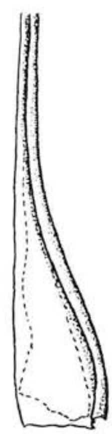

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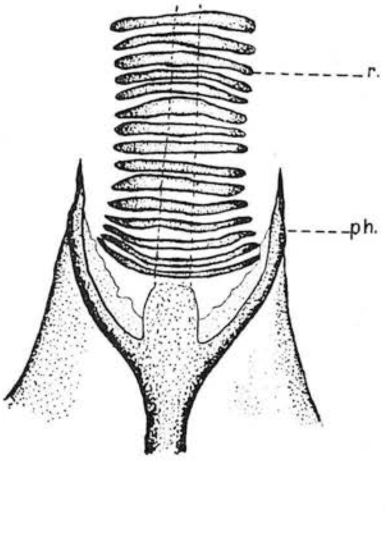

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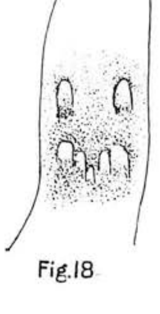

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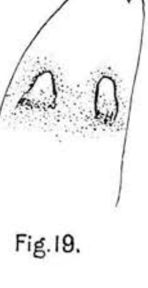

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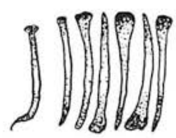


Fig. 21.

Photo.-Engraved & printed at the Offices of the Survey of India Calcutta, 1913

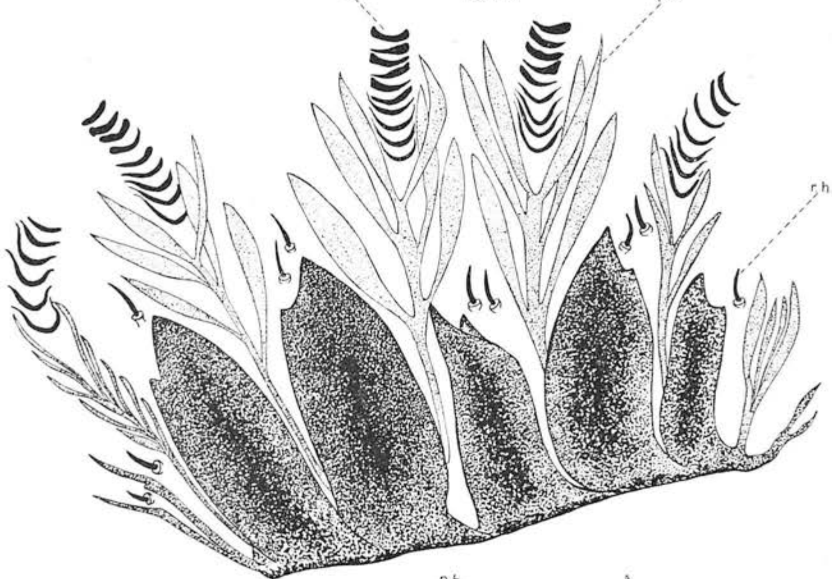
PLATE IV.

Figure 22.—The teeth and connected structures of *Hæmatobia.* The first tooth is on the left of the drawing. r.h., rod-like hairs. p.b., petiolated blades. p.s., pseudotracheal channels. Note the attachment of the teeth to one another at their bases. They are attached to the edge of the discal sclerite by a band of fibres, not shown. × 700

Figure 23.—The teeth and connected structures of *Philæmatomyia gurnei.* The anterior and internal angle is on the right. t.p., the tooth plate. p.b., the petiolated blades, between which lie the pseudotracheæ, as shown in Plate II, figure 9. × 475

Figure 24.—The discal sclerite and the teeth of *Philæmatomyia lineata,* seen from the side. t., the prestomal teeth. p.s., the pseudo-tracheal channels. i.a., the chitinous rods embracing the terminations of the channels, and constituting the interdental armature. r.t., the rudimentary tooth. c.c., the anterior collecting channel. c.c′., the posterior do. t.p., the tooth plate, a flange of the discal sclerite, d.s. l.r., lateral rod of the labial gutter. lb.r., labellar rod. × 600

Fig. 22.



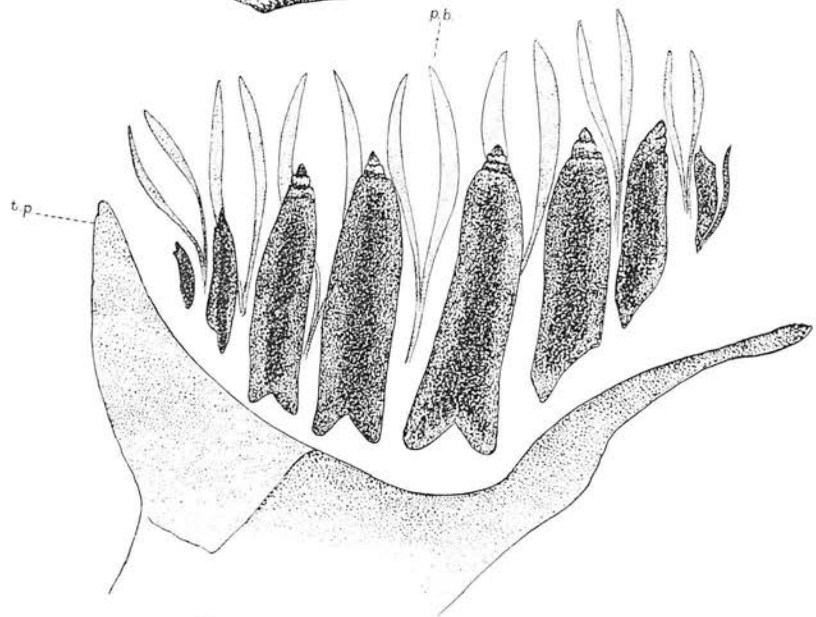


Fig. 23.

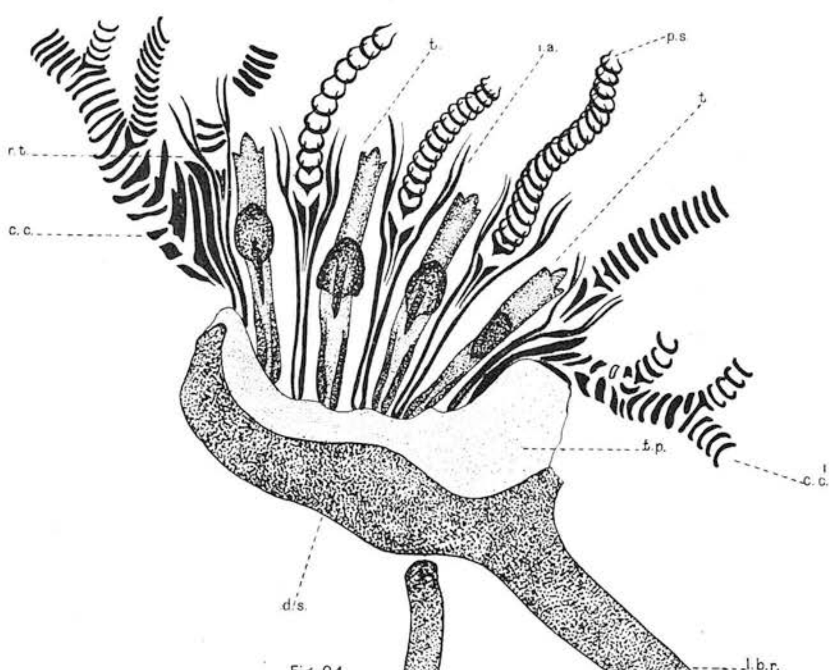


Fig. 24.

Photo.-Engraved & printed at the Offices of the Survey of India, Calcutta, 1913

PLATE V.

Figure 25.—The discal sclerite and the distal end of the labial gutter of *Hæmatobia.* × 400

Figure 26.—The same of *Stomoxys.* × 400

Figure 27.—The discal sclerite of *Musca nebulo,* seen from the front. × 340

Figure 28.—The same, seen from the side. × 340

Figure 29.—The discal sclerite of *Philæmatomyia insignis,* seen from the side. × 130

Figure 30.—The discal sclerite of *Philæmatomyia gurnei,* flattened out and seen from the front. Camera lucida drawing. The faintly shaded area on each side of the axial apophysis is the fractured portion. × 224, *vide* page 24.

Figure 31.—The discal sclerite and the terminations of the labial gutter of *Philæmatomyia lineata.* × 300

Figure 32.—A photograph of the specimen of *Philæmatomyia gurnei* referred to in the text. I am indebted to Major Kirkpatrick, I.M.S., for this photograph. × 30

Reference letters :—ax. p., axial apophysis. lb.r., labellar rod. l.r., lateral rod of the labial gutter. m.g., the medium portion of the gutter. t.p., the tooth plate.

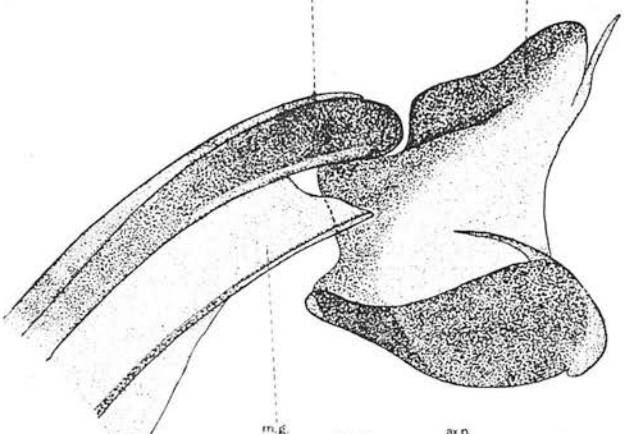


Fig.25.

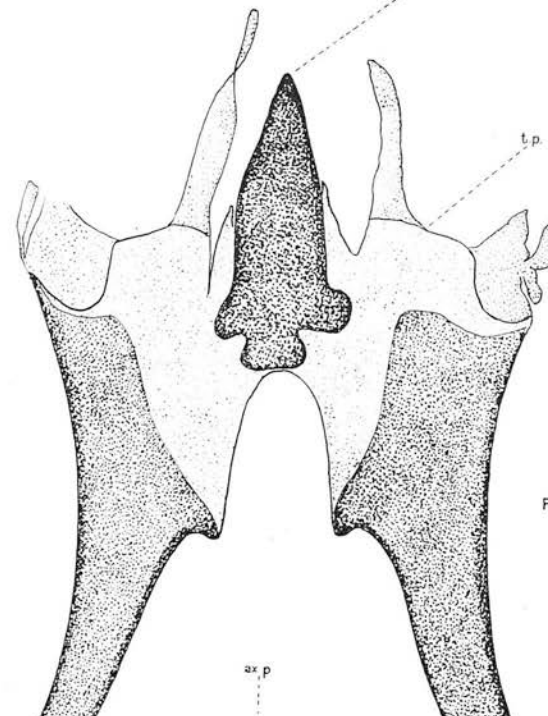


Fig.30.

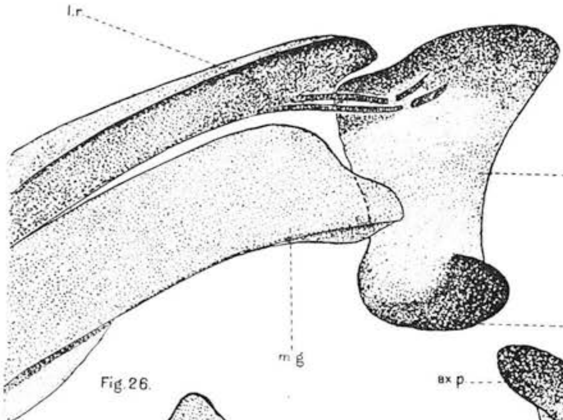


Fig.26.

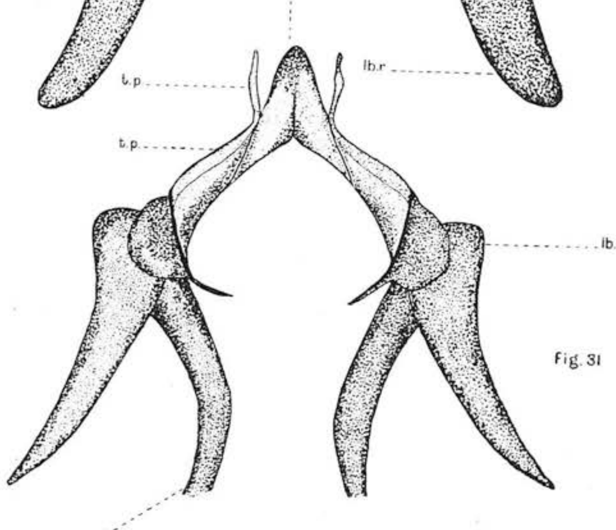


Fig. 31

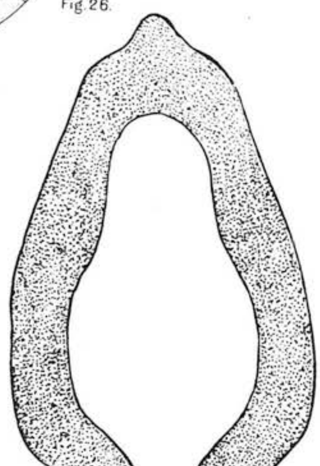


Fig.27.

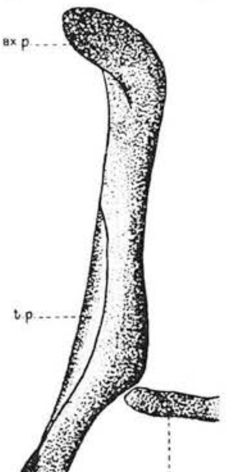


Fig. 28.


Fig. 32

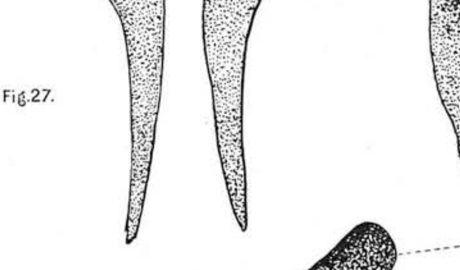


Fig.29.

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