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THE ANATOMY, HABITS AND PSYCHOLOGY

OF

Chironomus pusio, Meigen,
(the early stages)

WITH NOTES ON VARIOUS OTHER INVERTEBRATES,
CHIEFLY CHIRONOMIDÆ.

BY

ARTHUR TERRY MUNDY.

(1880-1908.)

LEICESTER :

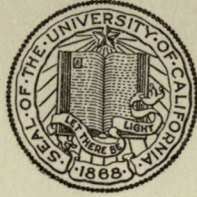
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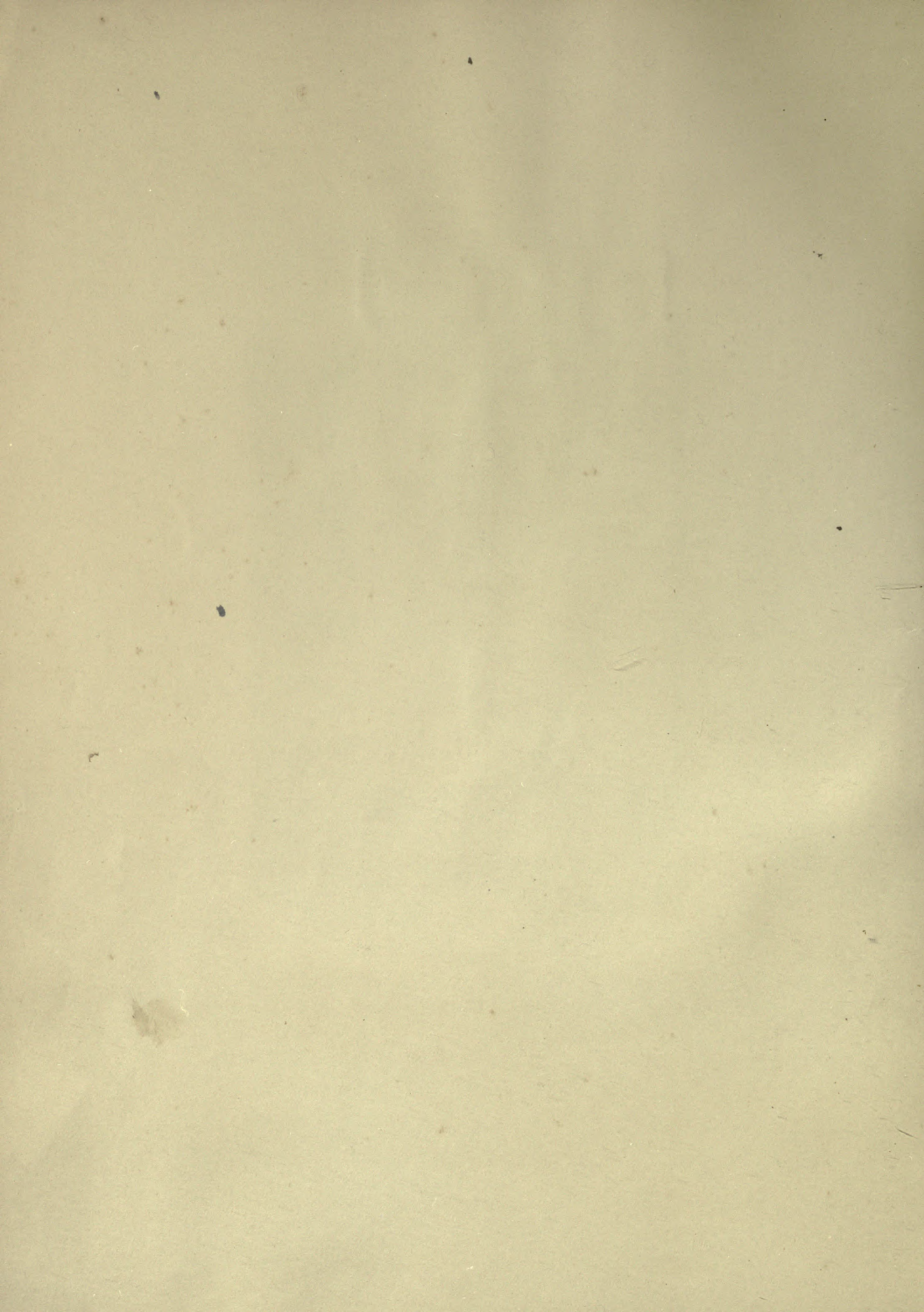
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PREFACE.

ARTHUR TERRY MUNDY, of Cornwood, near Plymouth, was an inspiring example of what may be accomplished under the most adverse circumstances. Prevented from indulging in active scientific intercourse by the heart trouble which has now, at the early age of 27, removed him from our midst, he yet contrived to maintain a cheerful spirit and to exhibit unlimited enthusiasm for the acquisition and increase of natural knowledge.

Even when fully conscious of his near approach towards the Great Unknown, he strove, heroically, to complete the following notes and drawings, the publication of which has been rendered possible by the generous assistance of SIR WILLIAM and LADY PARKER.

Professor MIALL, F.R.S., greatly encouraged him; and to see the work through the press has been the privilege of one who knew and valued the sterling qualities and friendship of the author.

E. E. LOWE.

LEICESTER MUSEUM—January, 1909.

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THE ANATOMY, HABITS AND PSYCHOLOGY

OF

Chironomus pusio, Meigen.

INTRODUCTORY NOTE.

IN the river Yealm, a rocky moorland stream passing through the village of Cornwood, South Devon, are found during the summer months curious brown objects encrusting the stones and moss of the bed of the river. They have superficially a striking resemblance to the common brown Hydra of our ponds in colour, size and form. On closer scrutiny they are found to be the mud tubes of a small aquatic insect-larva. For many years I have known of these tubes; but it was not until the spring of 1905 that I examined them with the microscope and found they were inhabited by a small *Chironomus* larva. PROFESSOR L. C. MIALL, F.R.S., kindly identified the fly for me as *Chironomus pusio*, Meig., and at the same time informed me that they were common in the neighbourhood of Southbeck, Windermere, where he and MR. T. H. TAYLOR found them the summer before (1904). Since then I have kept the larvæ under constant observation, and watched their wonderful habits, and also obtained the insect in all its stages.

In 1907 I wrote a short outline of the habits of the insect, which appeared in the *Naturalist*. In the present paper will be found a more complete account of the life-history, with full anatomical descriptions of the earlier stages, and also remarks on various other species of this genus.

My thanks are chiefly due to PROFESSOR MIALL for help and encouragement, and especially for drawing my attention to DR. LAUTERBORN'S valuable paper on certain new species. MR. R. J. BAKER has also kindly examined the sensory bulbs of the antennæ for me.

**C. pusio and
where found.**

The small larva of *Chironomus pusio* has a greenish appearance, lives in a Hydra-like case, and is found in great abundance during the summer months in the Yealm and Erme, two streams flowing off the southern borders of Dartmoor.

In North Devon I examined the Lynn at Water's Meet in June, 1907, but found no larvæ in either stream; possibly they may be found further up the stream. They first appear about the end of March. In 1906 I noted them first on the 27th and in 1907 on the 23rd. By the middle of the summer if the weather is hot the cases are present in such quantities that many of the large moss covered boulders appear quite brown as if with a sediment of mud. Towards the autumn they get scarce again, and by the end of October there are none to be found. Heavy rains causing the river to become swollen seem fatal; a few days of this treatment, and they are entirely swept away. Whether the flies survive the winter and lay their eggs in the coming spring, I cannot say; but the fact that flies hatched late in the year do occasionally have the ovaries in a very immature condition is suggestive. But this is not absolutely necessary for the propagation of the species, for the larvæ in secluded spots are capable of resisting very severe weather.

Larvæ resist frost.

Out of about 20 larvæ I put in a dish of circulating water in the autumn of 1906, two at least survived until February 18th, 1907, and during this time a layer of ice formed on the surface more than once. These winter larvæ are very inactive, scarcely ever moving far out of their tubes to feed, nor do they grow or develop. I may also mention in order to show the hardihood of Chironomid larvæ, that the water in a small vessel containing some large bloodworms was frozen into a solid block of ice, yet on melting the ice the larvæ appeared at first none the worse for the severe treatment they had undergone, though they died some days later.

Winter dwellings.

If some of the larger pebbles be taken up from the bottom of the river during the winter months, a few decrepit cases of the larvæ may occasionally be found on the under protected surfaces, and some of these contain larvæ which may survive to complete their metamorphoses in the spring.

The larvæ of this *Chironomus* are lovers of swift rushing water, and from the very nature of their habits it is impossible for them to thrive, unless the water, passing swiftly by the nets they spread out on the arms surrounding their tubes, conveys thither suspended matter for them to feed upon. In consequence of this, larvæ that are kept in vessels of still water soon languish and die, without performing their characteristic actions. It is therefore absolutely necessary that the water be kept in constant motion by some mechanical means.

The somewhat crude, though effectual, method that I have used to overcome this difficulty is as follows:—Across the top of an enamel dish, containing larvæ, water and mud, I placed a strip of wood a few inches wide on which was fixed a clock-work paddle. This was made from a cheap day-clock with second hand. The escapement wheel was removed and in its place was put the second hand wheel. To the projecting part of the axle was attached a glass paddle. The clock when wound up was found to keep the paddle in motion for about ten hours, and I found it sufficient to wind up the clock morning and evening, as an hour or two in still water did not seem to injure the larvæ (fig. 40).

THE EGG.

The female fly lays about ninety eggs enclosed in a spherical gelatinous envelope. These egg-masses are attached to the moss covering the boulders and stones of the streams which the flies frequent. They are generally found just below the surface of the water, sometimes a few centimeters down; but this must be because the river has risen since they were deposited, for it seems almost incredible that a fly so small and fragile could climb down so far in such turbulent water. A fly reared in captivity deposited its eggs at the surface of the water, and this no doubt is the usual proceeding. The egg-masses are not easy to find, and it was not until the second year that I obtained any for examination. Fine hot weather in June is the best time, for then the river is full of the cases of full grown larvæ and pupæ, and the flies are coming out daily.

The Egg-mass.

The egg-mass when first laid is 1 mm. in diameter, and in the case of an unfertilized female they remained this size, but the fertile egg-masses found in the water are 1.5 mm. across.

The egg.

Each mass contains from 80-90 eggs arranged apparently without any order. The egg-shell is quite transparent and the developing embryo is clearly seen enclosed within the vitelline membrane, which is not in contact with the shell at the two ends of the egg. The characteristic antennæ of the larva can be easily seen in the egg ready to hatch, and by this means the eggs can be distinguished from those of other Chironomids. The egg is very slightly kidney-shaped, strongly convex on the dorsal surface, and very slightly concave on the ventral; viewed dorsally it is oval. In size it is .16 mm. long by .06 mm. broad. It differs from the egg of *C. dorsalis* in being smaller, relatively broader and more convex.

The development of the embryo within the egg takes about six days. If we now examine one of these eggs just ready to hatch, we can make out the more important features of the larva. In the transparent head we can recognise the antennæ, eye spots, mandibles and labium; while the prothoracic appendages are very conspicuous. The body is very much coiled up, as it has to be compressed into nearly half the space it will occupy on emerging from the egg; however, many of the segments can be counted and sometimes the anal setæ are visible. It may be worth while to mention here, that on the fourth day of incubation the double eye spots are sufficiently visible to enable the eggs of a *Chironomus* to be distinguished from those of a *Tanypus*, the eyes of the latter being single and kidney- or cornet-shaped. However, there are one or two species of *Chironomus* (Nos. 13 and 14 Appendix) in which the double eye-spots are completely fused into single masses, so this test is not absolutely final, but it is of great use in examining miscellaneous egg masses.

Hatching Larvæ.

The embryos about to hatch become very active within the eggs, and may be seen to revolve on their longitudinal axis two or three times a minute, until at last the egg shells burst and the larvæ are set free. They take about a minute to extricate themselves from the shell,

and extend their bodies to their full length ; they then measure .32 mm. The young larvæ remain for some time within the gelatinous envelope of the egg-mass, and seem to feed upon its substance and upon organic particles which are generally found attached to its outer surface, but by the end of the second day they have for the most part dispersed, and henceforth live independent and solitary lives each within its mud-built tube.

THE ANATOMY OF THE LARVA.

The full grown larva is about 4.2 mm. long. The colour of the body is pale green tinged with orange, with the exception of the first three segments which are violet. The head is almost an opaque brown, but the body is transparent, though not equalling in this respect some other species I have met with. One larva specially must be mentioned ; this species (No. 18 of Appendix) is also common in the Yealm, and vies with the "Phantom Larva" (*Corethra*) as regards transparency, so that, in elucidating the more obscure details in the anatomy of *C. pusio*, such for instance as the distribution of the nerves, I have found comparison with this species of great help. I have not come across any larva nearly as suitable for microscopical examination as this one ; and although found in a swift river it thrives very well in the ordinary still-water aquarium.

The larva of *C. pusio* is composed of a head and twelve segments, and most probably, as we shall see later, a rudimentary thirteenth. The first three segments, which go to form the thorax of the fly, are easily distinguished from the rest by their violet colour and rectangular shape, segment 3 being the shortest in the body. Segments 4-10 are barrel-shaped, while the remaining segments bulge very little if at all. Segment 1 bears a pair of prothoracic appendages each of which is thickly covered with fine curved claws capable of being completely withdrawn into the appendage. The last segment bears a similar pair of appendages, the anal feet, which are longer, and bear fewer but much stouter hooks ; the hooks in both cases are amber-coloured. Among the different species I have found very little variation in the

Segments of
the body.

Bifurcating Hairs.

anterior appendages, but the anal appendages vary considerably; for instance in No. 17 (Appendix) there are twelve large almost black hooks slightly separated into two groups; these can be completely retracted into the rather long foot, which is in like manner almost folded into the body. Segments 5-9 bear each a pair of fringed bifurcating hairs (Figs. 4*e* and 10*d*) attached laterally, one on each side, near the posterior border of its segment. I have not been able to detect any nerve terminating in these hairs, yet, as will be shown later, they have probably a very important function to perform, and must be delicate sensory organs. They are also important for classificatory purposes. I have found five different species bearing these organs, DR. LAUTERBORN mentions two, and PROF. MIALI informs me that he has had one, hence we may safely conclude that these larvæ form a distinct group. I have called this the "Pusio" group, and given a list of the known species in the Appendix.

Distribution of hairs.

The head bears numerous stiff hairs arising from the centre of circular pits surrounded by chitinous rings. Similar hairs are found on the thoracic segments, about sixteen dorsal and ten smaller ventral on the first, and a diminishing number on the other two. The abdominal segments have only occasional, very minute, non-pitted hairs.

Anal Setæ.

On the dorsal surface of segment 12 are two bunches of long stiff setæ—the anal setæ. Each bunch is composed of 8 setæ which are chitinous at the base, becoming transparent towards the free ends. The bunch takes its origin in a short transparent prominence, bearing two small hairs at the base. In some species this prominence is of considerable length and in others the cuticle is deeply chitinous, while the setæ may vary in number from one to about ten.

Anal bristles.

Between the setæ and the anus there is a small area characterized by the presence of two small hairs, the anal bristles; this area possibly represents the dorsal part of a now rudimentary 13th segment. I have found three species of *Chironomus* in which a 13th segment is quite obvious, Nos. 8, 10 and 11 (Appendix). In one of these (No. 11) the segment is quite perfect. MIALI and TAYLOR* have also found a *Chironomus* larva "with faint indications of a sub-division of the

* MIALI and TAYLOR. "The Holly Fly" p. 260.

12th larval segment, the part behind the bunches of setæ being constricted off." Figure 9 shows a dorsal view of the last few segments of larva No. 11 (Appendix) with the more important muscles; one can see clearly how the reduction has taken place in *C. fusio* (fig. 8) and the same would apply to *C. dorsalis*, and the great majority of other known species. The letters in figures 8 and 9 refer to what are supposed to be homologous muscles in the two species. The anal bristles are clearly seen, but are not very large; in No. 13 (Appendix) they are quite four times this length and very conspicuous, and enable us to identify the position of the rudimentary segment with facility. It might be said we have here to deal with a false segment, or a modern variation from the type; but when we remember that other Diptera may have thirteen segments, as for instance *Dicranota*,* and that all Lepidopterous caterpillars when carefully examined are found to possess this number, and that the typical number of abdominal and thoracic segments in imaginal insects is thirteen, we must I think conclude that thirteen is the true number, and regard the apparent twelve segments of most *Chironomus* larvæ as due to fusion of the last two segments.

Surrounding the anus are two pairs of blood-gills, in which ramify a dense network of fine tracheal tubes; hence we may call them tracheal gills. They differ from those of *C. dorsalis* in this and in the absence of red blood. These organs vary a good deal in the different species I have examined. For instance, in one very small species (No. 16 of Appendix) they were nearly three times the usual length and deeply constricted in the middle. In another species (No. 11) the gills were capable of almost complete retraction into the rectum.

Anal blood-gills.

There are no ventral blood-gills on the eleventh segment, and from my own observation I should consider this form of gill of rare occurrence. I have only come across one species (No. 9 of Appendix) bearing ventral gills; this larva resembles *C. dorsalis* very closely in most respects, but as may be seen from fig. 19 the ventral gills are much longer than usual, and much coiled. But more remarkable still, on segment ten are found a pair of small gill-like organs laterally placed and projecting

**Ventral
blood-gills.**

* MIALL. Aquatic Insects, p. 165, fig. 50.

posteriorly. These rudimentary gills are especially interesting because DR. LAUTERBORN* has also found a larva possessing gills (only in his case fully developed) arising from the tenth segment.

In LAUTERBORN'S Larva I. they resemble mine very closely, in his Larva II. they are much larger. So here we have a species combining in one larva both types of ventral blood gills. These facts I think show that the ventral gills are morphologically of very little constancy compared with the anal gills, and I may also mention that the presence of red blood is no indication of their presence, for one larva of the "Pusio" group, resembling the blood-worm superficially, is quite devoid of them, as is also *C. niveipennis*.† So it is hardly possible to use the two characters, red blood and ventral gills, as indicative of a distinct group of larvæ, as was suggested by MEINERT.

THE HEAD.

The head of *C. pusio* is a wonderful object, when viewed through the microscope with a fair magnification, and I should think it would be hard to find a Chironomid more suitable for examination than this species. The chitin is sufficiently dense to enable all the parts to be clearly contrasted and defined, and at the same time transparent enough to let them be seen by transmitted light.

The following details can all be made out in the living larva. A good plan is to place the larva in a Ross or other accurately adjustable compressorium, and retain it under slight pressure in such a position that the various appendages are spread out to their full extent.

The head including the extended labrum, is .26 mm. long by .2 mm. broad and may be described as dark amber in colour. It is composed of a medium dorsal clypeus, and the two lateral epicranial plates which curve round the head to meet each other on the ventral surface in their anterior part, while behind a large open space or bay remains. This allows the head to be easily flexed on the ventral surface of the thorax. The clypeus is a narrow oval plate of somewhat irregular outline. Near the anterior edge arise a pair of chitinous

* LAUTERBORN. Zoologischen Anzeiger Bd. XXIX., No. 7.

† MIALl—The Harlequin Fly, pp. 11 and 13.

hairs, and a similar pair halfway down, and the rings of a third pair at the base but no hairs. Each epicranial plate bears a pair of pigment eye-spots placed antero-laterally; they are surrounded by a few hairs of medium length. Two long hairs arise on each side of the head and some short ones near the eye-spots, and on the ventral surface of the epicranial plate. Some species of the "Pusio" group can withdraw their heads partly into segment I. and then the posterior hairs are not present or are very small, but the pits and chitinous rings can generally be seen.

The position of the eyes varies in different species, and in two species (Nos. 13 and 14 of Appendix) the eyes are fused into one.

On the ventral surface great variations are found in the shape of the bay, and the density of the chitin, in some species portions being quite black. The free edge of the bay is slightly thickened, otherwise the epicranial plates and also the clypeus are of a uniform density. This is true of all the larvæ I have examined belonging to the "Pusio" group, but not so in other species. In larva No. 7 a large area surrounding the bay and reaching to the striated flaps is black with chitin; and in larva No. 14 half the ventral surface is thus chitinized, while in larva No. 15 the bay is divided into an anterior and posterior part united by a narrow isthmus. A slight groove separates off a small anterior portion of the epicranial plate, which rises upwards and projects slightly beyond the rest of the plate as a kind of boss from which the antenna arises. A similar boss is seen in *Anopheles*,* but the most remarkable extension of this prominence is seen in LAUTERBORN'S Larva III., belonging to the "Pusio" group, while in my larva No. 5 the prominence is of considerable size, extending as far forward as the extended labrum.

The antennæ are very highly developed. Each is composed of a long basal segment, curving outwards and downwards; this bears near the proximal end a small chitinous ring (sensory spot) without a hair, and a third of the way up the segment there is another smaller ring with a long chitinous hair attached. This segment is moved by strong muscles and is capable of slight retraction beneath the boss. Other

The Antennæ.

* *Anopheles*, by NUTTALL & SHIPLEY, *Journal of Hygiene*, vol. I., No. 1.

species have this power somewhat more developed, and this is interesting as it shows how the completely retractile antennæ of *Tanyptus* (a closely related genus) may have originated from small beginnings. From the distal end arises a second segment, broad at the free end but narrow at the base; beside this on the ventral side arises a double transparent hair the longer branch equalling the second segment in length. At the distal end of the second segment, arising from a transparent enlargement, are three processes, a median process consisting of three minute segments, and two transparent processes of the same length swelling out into minute transparent bulbs. There is also a small papilla between the outer and central processes.

There seems at first sight a great difference between this specialized antenna of *C. pusio* and the rudimentary antennæ of the blood-worms, but the homologous parts are easily identified. In the blood-worm there is a stout basal segment with sensory spot, equivalent to that of *C. pusio*; beyond this are two terminal pieces, the one simple and the other composed of three or four joints, the simple piece is equivalent to the double hair of *C. pusio*, while the proximal piece of the four-jointed member represents its second segment; finally the three last joints are easily identified with the three-jointed median process, which is comparable in size.

The lateral processes with their transparent bulbs have no representatives in the blood-worm, but among the smaller free-swimming species they can generally be detected. This fact points to the conclusion that the now rare and specialized form of antennæ was probably possessed by the ancestral form from which most existing species have diverged in a degenerative manner, and this ancestral form would also have probably possessed the 13th segment already referred to.

Bow-net.

This form of antennæ was first described by DR. LAUTERBORN and figures were given of various species showing the curious form of sense organ borne by the lateral processes. This organ (see fig. 15) he calls a "bow-net" (Reuse). In *C. pusio* larvæ the "bow-net" is exceedingly small if it exists at all; it appears rather to be a minute transparent "bulb" surrounding a small sensitive "pin," and sometimes even the

bulb is absent, only the pin remaining. MR. R. J. BAKER kindly examined these organs for me with a twelfth-inch oil-immersion lens, but was unable to discover any signs of curved bristles surrounding the pin. The measurements of the sensitive organ are: length, 8μ ., breadth, 5μ . and length of pin 3μ .

In the beautiful transparent larva No. 18 already mentioned, the sensory organs (see fig. 14), which are highly developed, are undoubtedly of the "bulb" and not the "bow-net" type. The bulbs are not placed opposite each other but alternate on very short stalks, and a new segment seems to have been introduced between them. Each consists of a perfectly transparent smooth bulb enclosing a small basal pin which only extends a short distance into the bulb; the bulb is four times as large, but the pin is only the same size as in *C. pusio*. I have only found the bow-net in larvæ belonging to the "Pusio" group, in species resembling very closely those drawn by DR. LAUTERBORN in his Fig. 11 (closed bow-net), in Fig. 13 (open bow-net) and in one which is probably the same as my Larva No. 5. Possibly the curved bristles originated as longitudinal thickenings in a bulb-like organ, while the intermediate spaces became thinner and finally disappeared setting the ribs free. DR. LAUTERBORN has suggested that they may serve the purpose of giving information to the creature of some change in the chemical or physical quality of the water outside the tube, but I am more inclined to give them a tactile function, at any rate in the two species whose habits I have studied, No. 4 and No. 5. I do not think that in either of these species the organ is of much functional importance to the insect, and we have yet to find the larva whose mode of life brings them into full activity. Other examples of perfect though apparently functionless organs will be mentioned further on. The sensory bulbs in *C. pusio*, in the stalk-cased larva (No. 1), and in the transparent larva (No. 18), are tactile I should think, and in the arm-builders they take the place of eyes in looking for particles on their webs.

Beyond the clypeus and between the bosses of the antennæ lies the labrum. This organ in the living larva hangs down as a flap or upper lid in front of the mouth. When the larva is placed under a

compressorium the labrum gets pushed forward and takes a horizontal position, so that all the parts can easily be seen, and it is in this somewhat unnatural position that it is shown in my figures of the head.

For convenience of description we may divide the labrum into three portions, (1) the dorsal surface, (2) the anterior free extremity or "lip," and (3) the ventral surface or "epipharynx." The dorsal surface is chiefly made up of two sclerites or thickenings of the cuticle. The posterior sclerite is an elliptical chitinous plate abutting on the anterior edge of the clypeus; from its foci arise long chitinous hairs. In some species this plate is absent, *e.g.*, in No. 13; in others it is fused to the clypeus; and in one species (No. 15) it is found in a partially evolved condition.

In figure 6 we can clearly see that the complete sclerite must have arisen from the growth of two separate sclerites forming around the chitinous hairs, and which, gradually approaching each other, finally coalesced into a single plate.

The anterior sclerite is much larger and of more complex outline; in front it extends right across the labrum, and curving round the sides is seen to give attachment to appendages on the ventral surface, while behind it narrows and, after giving rise to "lateral inlets," extends backwards until close to the posterior sclerite. Near each inlet a chitinous hair is found; these may be the starting points of separate sclerites which afterwards fused together, but we have no proof in this case. In the clear space on each side of the anterior sclerite is a long chitinous hair with two short hairs arising from the same base, *i.e.* a triple chitinous hair, surrounded by an exceptionally large chitinous ring, the largest in the body.

The Lip.

The lip is non-chitinous and bears a number of sensory organs. At the base are a pair of median short hairs, and outside them a pair of broad-based prominences bearing minute papillæ. Above these and somewhat more central is another pair of prominences, stalk-like and bearing on their free ends long toothed feelers. At the anterior extremity of the lip, from a kidney-shaped bulb, arise a pair of

short-toothed feelers. On each side of these is a row of four long slender transparent "tentacles" minutely toothed at their free ends, and arising from the free edge of the lip. Still further round on each side are a pair of chitinous spines arising from the very base of the lip, or possibly from the anterior sclerite. On the under surface of the lip, below the tentacles, are on each side a group of about five small papillæ, and between them is seen the ventral surface of the kidney-shaped bulb, which now appears round. Within this bulb can be seen a transverse and slightly V-shaped chitinous rod finely pectinated on its posterior surface: this I shall refer to as the anterior comb.

With the exception of the comb all these appendages of the lip appear to be sensory in function; on the other hand the armature of the epipharynx now to be described is undoubtedly motor in function.

The epipharynx is bounded in front and at the sides by narrow chitinous flanges, the ventral extensions of the anterior sclerites. The central portion of each flange is somewhat enlarged and serves as a point of attachment for a remarkable appendage, which may turn out to be of some morphological importance. This organ consists of three parts, a broad basal portion notched at the extremity for articulation with the sclerite, and two terminal parts (an inner curved palp enlarged at the free end, and covered with spines, and an outer smooth chelate limb). All the parts are chitinous. This organ I have found present in many larvæ, and there is little doubt but that all species possess it in some form or other. MIALL gives a figure of the labrum of *C. dorsalis*, in which a very similar organ is drawn.* A somewhat similar organ may be seen in *Anopheles maculipennis*.† This organ has a striking resemblance to the generalized appendage of the Arthropoda, the base being equivalent to the protopodite, while the distal members are suggestive of the exopodite and endopodite. It is possible that this organ may be the remnant of a true insect appendage. According to PARKER and HASWELL‡ the

The Epipharynx.

* MIALL & HAMMOND, *The Harlequin Fly*, fig. 16, p. 27.

† NUTTALL & SHIPLEY, *Journal of Hygiene*, vol. I., No. 1, plate 2, fig. 8.

‡ *Text-book of Zoology*, vol. I., p. 607.

insect appendages are homologised with the crustacean according to the following scheme :—

CRAYFISH.	COCKROACH.
Antennules.	Antennæ.
Antennæ.	Absent.
Mandibles.	Mandibles.
First Maxillæ.	First Maxillæ.
Second Maxillæ.	Second Maxillæ.

Since the "Pusio appendage" is placed far forward on the labrum, it probably represents the most anterior appendage of the crayfish, viz., the antennules; then the antennæ and other appendages would all be brought into line with those of the crayfish. Under this arrangement we homologize the appendages in the two classes as follows :—

CRUSTACEA.	INSECTA.
Antennules.	Generalized appendage (absent in imagines, present in Dipterous larvæ).
Antennæ.	Antennæ.
Mandibles.	Mandibles.
1st Maxillæ.	Maxillæ.
2nd Maxillæ.	Labium.
1st Maxillipedes.	1st Legs.
2nd Maxillipedes.	2nd Legs.
3rd Maxillipedes.	3rd Legs.

Speaking of insect appendages, MIALL & DENNY* write, "The mandibles and maxillæ exist to the same number in both groups, and are homologous organs, so far as is known; the numerical difference relates therefore to the antennæ, of which the Crustacean possesses two pairs, the Insect only one. Whether the pair deficient in the Insect is altogether undeveloped, or represented by the pair of prominences which give rise to the labrum, is a question of much theoretical interest and of not a little difficulty." That the labrum does represent a pair of appendages has been held by certain writers (KOWALEVSKY, CARRIERE, PATTEN and CHATIN),† and the presence of

* The Cockroach, p. 56.

† PACKARD Text book Entomology, p. 43 and p. 547.

such organs as have been just described, lend considerable support to the view that the half-labrum and its appendages are the equivalent of of the Crustacean antennule.

The central portion of the epipharynx is occupied by a U-shaped rod, closed-in in front by a second pectinated rod, the posterior comb. Within this enclosed region are two bunches of slender chitinous hooks, the grappling hooks. Each bunch contains about eight hooks, which pass forwards and outwards and then curve downwards outside the U-shaped rod. Below the U is a small slightly chitinous plate. The two bunches of hooks can be entirely withdrawn within the U, or protuded so as to form a rake-like organ. The claws are moved by powerful muscles, and when these are set in action the various parts of the epipharynx change their positions and appear so different, that it is difficult to discover what has taken place, and quite impossible to explain the changes.

Grappling hooks.

If we compare the toothed feelers, the tentacles and the combs, we find that they can be all reduced to one pattern, a rod-like process with irregular outline towards the free end; the tentacles are in fact feelers very minutely toothed. In the combs the change is somewhat greater. Each comb is really composed of two chitinized feelers bent over on their sides until they just meet in the middle line, while the toothed surface, here entirely confined to one side, takes the form of a stiff fringe of spikes, the two together having a most comb-like appearance. This can only be made out under the most favourable conditions. The labrum may truly be described as a sensory-motor equipment of remarkable complexity.

**Similarity of
feelers, tentacles
and combs.**

The mandibles are the most densely chitinous portion of the head, quite black and opaque at the tip. Each shades off into translucent brown at the base, where it articulates with the epicranial plate behind the antennal boss. The distal half of the mandible is toothed on the inner side and fringed with stiff curved hairs. The proximal portion is broader especially on the ventral side (compare fig. 7 with fig. 6) and the inner surface is somewhat concave; from the dorsal side of the cavity a curious arborescent hair arises with three main branches and

The Mandibles.

many smaller divisions; it is quite transparent and therefore easily overlooked. Two chitinous hairs of the ordinary kind arise from the outer proximal surface, and a little farther up another hair of quite a different character is found. It is quite transparent, gracefully curving outwards towards the end, which is rounded and not pointed as is usual with hairs. Possibly this is the rudiment of the mandibular palp as seen in Crustacea.

Mandibular palp.

Maxillæ.

Next to the mandibles come the first pair of maxillæ. These are very transparent and consequently difficult to see. Each maxilla (fig. 7) is seen to consist of a large rounded base and two short segments, the last being covered with minute papillæ. The base bears three minute hairs externally, and internally a long somewhat chitinous chelate claw. The two claws lie horizontally and are partly hidden by the deeply chitinous submentum. They almost meet in the middle line, and as they are capable of slight movement it seems probable that they are concerned with the guidance of the silk threads as they pass out of the mouth.

2nd Maxillæ.

The second pair of maxillæ unite to form the labium. This is composed, as is usual in these insects, of two parts, a slightly chitinized mentum and an intensely chitinized submentum (fig. 7*l*). The submentum forms the floor of the mouth and is fused with the ventral portion of the epicranial plates. The anterior edge is armed with a row of strong teeth, five lateral on each side, and a large five-pointed tooth in the middle. The fusion of the two maxillæ is incomplete behind, and it is not difficult to separate them entirely by pressure. Beneath the submentum and entirely hidden by it in front lies the mentum; the posterior handle-like portion projects backward beyond the submentum and can be easily seen. It is capable of considerable movement. Two portions may be distinguished, an anterior transparent part dotted with minute papillæ, and fringed with very fine hairs; and a posterior part, partly chitinous and looking like a handle (fig. 7*n* and fig. 16).

Labial palps.

The labial palps lie on each side of the submentum, and are fused to the epicranial plates. They are known in *Chironomus* as the striated

flaps on account of the fine lines that run transversely across them, and have been found present in all species examined. What then is the meaning and function of these flaps? Without a doubt they strengthen the labium, but why the striæ? Fortunately in this case we need not speculate on the structure of the organ from which they have come down as rudimentary survivals; for among the larvæ collected during the progress of this study, I have found two specimens possessing the original organs of which these striæ are the remnants. The striated flap of one of these larvæ (No. 7) is shewn in fig. 18*a* and *b*, in which it can be seen that the striæ are prolonged into about twenty-four long bristles or vibrissæ projecting from the side of the head in a similar manner to a cat's whiskers. In fig. 17 we have a highly magnified drawing of the striated flap of *C. pusio*, in which it is evident that the striæ are equivalent to the roots of these vibrissæ. In the second larva (No. 8) the two forms are united in the same insect, that is to say the proximal half of the flap is simply striated, while the distal half bears a number of fully developed vibrissæ.

The larva No. 7 with a complete set of vibrissæ is found in still and running water, in mud or rotting twigs, and does not seem to have any definite instincts that can be in any way correlated with this remarkable structure. Popular science has bestowed upon the cat's whiskers the function of restraining the animal from attempting to pass through too small apertures. MIVART in "The Cat" makes no mention of this when speaking of the vibrissæ, but it may be true nevertheless, and if so we should expect the vibrissæ of this curious Chironomus larva to possess a similar function, but its habits as far as I have observed them do not give any encouragement to this supposition.

Vibrissæ.

When we come to discuss the habits of *C. pusio* and its nearest relatives, I shall endeavour to show that it is not necessary to suppose that every fully developed organ is functional in all species which possess it; rather we must count ourselves fortunate if we find one or two perfect examples. Of these latter I am persuaded that the bifurcating hairs in *C. pusio* are an illustration, while the vibrissæ of Larva No. 7 belong to the former; that is to say they have lost their

physiological importance while still remaining anatomically perfect as far as externals go, though probably the nerve centres or fibres have degenerated.

Many insects have been described which possess organs fully developed, and yet without any function to perform; thus PACKARD writes: "In *Platysamia* (Lepidoptera), the cocoon-cutters of the pupa though well developed, do not appear to be used at all, and the pupa like that of the silk-worm and other moths protected by a cocoon, moistens the silk threads by a fluid issuing from the mouth."* And SHARP mentions that according to certain observers the eggs of some kinds of Saw-flies, are laid not in but on the leaves, so that we may conclude that in these cases the saws are not used by their possessors.† Perhaps the most remarkable example of a fully developed organ capable of performing its function, and yet never doing so is that of *Didelphys azarae*, one of the opossums. Concerning this marsupial MR. W. P. HUDSON writes:§ "In every way it is adapted to an arboreal life, yet it is everywhere found on the level country far removed from the conditions which one would imagine to be necessary to its existence. For how many thousand of years has this marsupial been a dweller on the plain, all its best faculties unexercised, its beautiful *grasping hands pressed to the ground, and its prehensile tail dragged like an idle rope behind it!* Yet if one is brought to a tree, it will take to it as readily as a duck to the water, or an armadillo to the earth, climbing up the trunk and about the branches with a monkey-like agility." If this is true of Vertebrates why not of Invertebrates also? In the case of *D. azarae* it was easy enough to put the animal back into its original environment, but we have no means of ascertaining what were the original conditions under which the vibrissae were used by larva No. 7.

THE ALIMENTARY CANAL.

Œsophagus.

The mouth leads into a narrow longitudinally folded œsophagus with thin and transparent walls. On each side lie the convoluted lobes of the salivary glands in which the enormous nuclei of the cells

* PACKARD'S Text Book of Entomology, p. 635.

† Cambridge Nat. Hist., Vol. V., p. 513.

§ The Naturalist in La Plata, p. 18.

composing its walls are easily seen. Very fine salivary ducts pass forward from them and unite into a single tube beneath the labium, which presumably opens on the floor of the mouth (Fig. 4c). The œsophagus leads into the cardiac chamber occupying segment 4. It originates at the posterior broad end of the œsophagus, and projecting forwards surrounds it like a cuff; it is composed of a single layer of very large cells which bulge externally, but no true caecal processes, such as are found in *C. dorsalis*, exist in the cardiac chamber of this larva. The anterior edge of the cuff is supported by a pair of lateral muscles. The space between the inner surface of the the cuff and the œsophagus seems to be in free communication with the body-cavity. Peristaltic contractions starting from the anterior end can be seen from time to time to pass like a wave along the œsophagus and within the cardiac chamber to its base; and this movement besides forcing the food down the œsophagus, will cause blood to circulate within the cuff and so nourish its cells.

Cardiac chamber

The œsophageal valve is a transparent funnel-shaped organ projecting from the base of the œsophagus some way into the stomach. It has the effect of entirely preventing any food passing backwards from the stomach into the mouth, while food still in the œsophagus is frequently regurgitated into the mouth by larvæ under the compressorium. At the base of the pericardial chamber is a distinct constriction, and immediately behind it the alimentary canal enlarges to form the stomach, a wide tube lying in the central segments of the body. Within the stomach and protecting it from direct contact with the food is the peritrophic membrane, a clear chitinous tube attached to the stomach at its anterior end only. Both the cardiac chamber and stomach are coloured brownish yellow. At the junction of the stomach and the small intestine are four short malpighian tubules. The small intestine is a short slightly waved transparent tube and abruptly enlarges to form the large intestine or colon, a large transparent thin-walled tube opening to the exterior by the anus.

Œsophageal valve.

From this short description it will be seen that the chief differences between this larva and that of *C. dorsalis* are the simple form of

cardiac chamber and œsophageal valve, the absence of any distinct enlargement at the anterior end of the small intestine, the large thin-walled colon, and the very short malpighian tubules.

RESPIRATION AND CIRCULATION.

Tracheæ.

Before describing the tracheal system of *C. pusio* we must glance at the general arrangement found in most of these larvæ. Nearly all the different species that I have examined (the *C. Pusio* group excepted) possess fully developed longitudinal trunks beginning in or near the head, and passing down one on each side of the body to the last segment. Lateral branches pass off in each segment, ramify on the body-wall, or penetrate into the brain or other internal organ. The trunks vary in thickness, in the amount of pigmented epithelial cells surrounding them, and in the number of branches given off, but the general plan is always the same.

Now in *C. Pusio* and the rest of this group the main trunks are only represented in the thorax and in the last three abdominal segments.

The thoracic tracheæ consist of a pair of main trunks in the first segment; these pass forwards into the head and end in fine ramifications, and push backwards into segment 2, where they end in a similar manner. About the middle of segment 1 a stout branch is given off, which soon ends abruptly in a mass of radiating twigs spread over the dorsal surface. When we remember that this segment is the only part of the body that is exposed to the full force of the water (the rest of the body being protected by the larval tube) we see a reason for this distribution. It is probable then that this cutaneous network of tracheal branches is functional and acts as a tracheal gill, absorbing oxygen from the water and conveying it to the internal organs. The main internal branch passes to the brain, which is exceptionally large, and may require a special supply of oxygen. If this is the case we have here a case of a degenerating organ once more regenerating itself. The posterior trunks begin in the middle of segment 10, and pass down to the anal gills where they end in fine twig-like ramifications. A few

branches are given off laterally; these chiefly end in the walls of the colon. One would naturally suppose that this system was the chief respiratory one, but as the posterior end of the body is very rarely exposed outside the case (chiefly to evacuate) this can hardly be so.

The heart lies in segments 10 and 11. It is a long hour-glass shaped organ, almost divided into two chambers by the central narrowing (fig. 10*f* and *i*). There are posterior and anterior pairs of lateral inlets or ostia, and alary muscles pass off laterally from each chamber. From the anterior end, guarded by a pair of valves, arises the aorta; it is a transparent tube, without valves, non-contractile, and passes forward along the dorsal wall of the alimentary canal towards the head. The dorsal vessel thus resembles the type except for the median constriction of the heart. A second form of dorsal vessel is also known in which the aorta is contractile and valved, but it does not seem very common, only two of my species (No. 11 and No. 12) possessing this form of blood-vessel.

Heart and Aorta.

The blood in the young larva is quite transparent, in the older ones it becomes greenish or even slightly reddish. In larva No. 5, a very closely related species, though much larger, the blood goes through an additional phase. When the larva is about the size of *C. pusio* the blood is greenish, but by the time of full growth (2 cm. long) it has become a deep blood-red.

THE FAT SACS.

In segment 10 are found a pair of oval bodies which have not as far as I am aware been hitherto described. They are very variable in size, and not always easy to see on account of their transparency, and the fact that they are often hidden by the fatty tissue generally very plentiful in this region of the body. Having found them in one larva, I examined many other species for the same organ, and found that they were by no means rare, and I have also noticed the same organ in a small undescribed species of *Tanyptus*. All the larvæ of the "Pusio" group possess them. In No. 18 they are rather small but

more detail can be made out in them than in most larvæ, on account of the perfect transparency of this insect. I have seen them in many of the unspecialized species, and probably they exist in all but are too small to be recognized amid the other tissues; but they reach their largest development in a small larva (No. 17), which is interesting in more than one respect. I will briefly describe the habits of this larva, as they possibly have some connection with the development of its "fat-sacs." The larva is found on smooth slabs of rock near waterfalls and splashing streams, not in the water but in such positions that the spray from the fall continually keeps the slab moist. Such stones may be found covered with larvæ wriggling about in all directions and feeding on the thin layer of slime-like confervæ always present on these stones. When full grown (5mm.) they form small mud shells adhering to the rock surface, and change into short thick-set pupæ, dark-brown in colour. Figs. 21 and 23 give highly magnified drawings of the fat-sacs dissected out from one of these larvæ. On the outside was found a thick brown layer of tissue; this was easily removed, and within was seen a clear transparent membrane forming a sac. The contents of the sac were of two kinds (1) a fine granular substance, (2) a mass of large transparent spherical bodies, no nuclei being visible. Fig. 22 shows the same organ as seen in the transparent larva (No. 18). Here we see that two transparent threads are given off from the base, and a single one from the anterior end. In *C. pusio* the following details have been made out concerning its attachment within the body. At the lateral anterior edge of segment 5 is attached a long strand of tissue, which, passing down the side of the body ends abruptly in segment 10. Adhering to the free end, or connected to it by a transparent nerve-like thread, is the fat-sac, from the posterior end of which one or more threads pass down for further attachment and keep the sac suspended freely in the body cavity. The strand, composed of an elastic sheath without and a mass of small spherules or fat-drops within, is green in colour, and capable of considerable longitudinal contraction whereby the sac is drawn up as far as segment 9. At the junction of the segment the strand is reduced almost to a thread, is transparent, and devoid of spherules.

The fatty tissue of *Chironomus*-larvæ is divided into an inner and an outer layer, and I think that the longitudinal strand and the fat-sac must be classed as a special development of the former, but what special function they perform I have not been able to find out.

From the point of view of comparative anatomy the fat-sacs are, I think, of some importance for they probably show us how *Corethra* (Phantom Larva) has come to possess those remarkable organs, the air-sacs, whose hydrostatic function is well-known.* These organs consist of a pair of large sacs in the thorax, connected by long transparent tubes containing fluid to a similar pair near the end of the abdomen. In order to convert one system into the other, we have only to suppose a second enlargement in the dorsal region of *C. pusio* and replace the fat-drops by an air space.

The air-sacs of
Corethra compared
with the fat-sacs.

We have already seen that *Chironomus pusio* possesses a rudimentary tracheal system in the neighbourhood of the fat sacs, though quite independent of them; larva No. 12 possesses, in addition to its large sacs, a complete tracheal system extending without interruption from head to anal gills, and also in one species of *Corethra* I found rudimentary tracheæ in head and anal region. These facts suggest that the air-sacs of *Corethra* are not, as generally supposed, a modification of the tracheal system, but of the internal layer of the fatty tissues.

THE NERVOUS SYSTEM.

The nervous system of *C. pusio*, as in *C. dorsalis*, consists of a brain, a subœsophageal ganglion, three thoracic and eight abdominal ganglia, the last two being partly fused together (fig. 5). The brain is bi-lobed and much larger than is usual in *Chironomus* larvæ, and in dorsal view completely hides the subœsophageal ganglion; tracheal branches penetrate into its substance. Paired connectives unite the thoracic ganglia, but in the abdomen the connectives become fused into single strands along the greater part of their course. The distribution of the nerves as far as I have been able to trace them may be seen in fig. 5. No. 18 is another large-brained larva; in this species, as

* MIALL.—Aquatic Insects, p. 118.

in *C. Pusio*, the supra- and sub-œsophageal ganglia occupy the greater part of the first segment. The large brain is naturally associated with the high psychical life of the insect. Only one larva among those described in the appendix was found to have the brain situated within the head, and in this case the brain was very small, and the head exceptionally large.

THE FIRST INSTAR.

The larva in its first instar or before its first moult is exceedingly transparent, save for a mass of greenish-yellow yolk cells, which still occupy the body cavity. The head is at first transparent but by the third or fourth day is quite dark. The blood is quite transparent and remains so for many weeks. The nervous system is very large in comparison with the size of the insect, especially the brain, which occupies the whole of segment 1, a large part of segment 2, and also projects some way into the head cavity. The fusion of the last two abdominal ganglia is incomplete. The tracheæ are not visible, and if present contain no air. The processes of the labrum seem to form a less complete apparatus, fewer parts being visible. The hairs distributed over the body are slightly different, but the chief point is that the bifurcators are entirely absent, and in their place are found very minute simple hairs. Each anal sense organ contains only four setæ; the fat-sacs are present but very small.

Length of larva—·32 mm.

Diameter of head—·04 mm.

Diameter of sensory bulb—·003 mm.

THE PREPUPAL LARVA.

When the larva is full grown and about to change into a pupa certain changes take place in its appearance. The thoracic segments become very distended, the body becomes more opaque and redder in colour, but not nearly so red as in the blood-worm. The fatty tissue gets very dense and massive, hiding the internal organs from

view, and the fat sacs often increase in size. The Malpighian tubules become swollen to twice their original diameter but remain the same length as before. Rudimentary sexual organs become more or less visible in the last two segments of the body. The rudiments of the imaginal organs are also clearly seen in the thorax, where the greatest changes are taking place, and they account for the swollen appearance of the anterior segments.

I may mention here that many larvæ are infested by parasites (nematoid-worms?) which coil themselves up in the body cavity. They are often between two and three times the length of the larva they are feeding upon, and one-third the diameter. Between 5 and 10% are thus infected. The only other parasite I have noticed is an Alga-like plant found in the rectum; it consists of strings of minute oblong green cells, and some single ones attached to the walls. Similar Algæ are mentioned as being found in the cockroach.*

TUBE BUILDING AND OTHER HABITS.

Chironomus pusio makes a dark-brown mud tube composed of rough particles carefully plastered together by saliva, but there is no internal lining of silk such as is often found in the cases of Trichoptera. The tube is attached for a variable length to rock or moss stem in the bed of a river, but it gradually curves away from its support, so that the anterior end projects freely in the water; this end is the widest, from which it gradually tapers towards the base. From the circumference of the wider free extremity curve out at right angles to the tube a number of slender arms, in the full sized specimens generally from four to seven, but in the small ones often only two or three, though some cases, even those belonging to the first instar, may have as many as five. The arms spread outwards and forwards, and when covered with a net-work of threads, form a kind of shallow cup in which floating particles are entrapped to become the food of the sagacious larva. The diameter of a fair-sized net is 8 mm. and the tube .615 mm. The larva lives inside the tube, only coming out from time to time to collect food or mend the net, and it is important to

Tube of *C. pusio*.

* MIALl & DENNY, Appendix p. 221.

note that even to reach the furthest extremity of an arm, the last four segments of the body need not be exposed outside the case, nor are there any other actions which require further extension of the body.

Larva No. 18 is slightly smaller than *C. pusio*. It builds a still more elaborate case, composed of a long stalk to which is attached a short tube with three long arms given off at the free end; the case is not quite so opaque as that of *C. pusio*, and is of a lighter brown colour.

Larva No. 19 I found in a fixed tube attached along part of its length to the stems of moss. The tube was composed of fibres and very small sticks placed transversely in the same fashion as is done by *Limnophilus rombicus* (Trichoptera) in making its free case. Another larva, No. 10, feeding on Starwort (*Callitriche verna*) and living in ponds, builds a fixed case composed of short lengths of the starwort leaves placed longitudinally round the body. All the abdominal segments except the last two bear 8-10 branched hairs in a similiar position to the bifurcators of *C. pusio*. Possibly they have the same function as in *C. pusio*. The cephalic-brained larva No. 17 is interesting; it is found in swift running brooks, buried in little tangles of *Spirogyra* which it apparently works into oblong masses in which two or three larvæ are generally found together. The green masses are found moored to the water-worn pebbles, and swaying freely in the stream. Larva No. 5 builds perpendicular tubes rising up from the bottom of deep muddy pools to a length of 10 cm. In order to accomplish this feat two or three larvæ generally build their tubes side by side in order to gain mutual support, but when the tubes are finished they appear as one, and are then about 3 or 4 mm. in diameter. It still remains to be found out by what method this larva procures materials for its long tube, as there is no net formed at the free end and generally there is no flow of water to bring particles; possibly it brings up mud from the bottom of its tube, but of this I have no evidence.

If a larva of *C. Pusio* be taken out of its tube, and placed in a dish containing water with a little mud suspended in it, and also a little sediment lying on the bottom, the whole process of case-

building can be watched; but in order to see it to perfection the water must be kept in rapid circulation by means of a paddle-wheel, as described in the introduction, or some other mechanical means. After floating along for some minutes in the current the larva manages to get a foot-hold on the side or bottom of the dish, usually in that part where the motion of the water is most violent, and sets to work at once to build itself a new protecting home. That they greatly appreciate a strong current is shown by the fact that quite a number of the larvæ in my permanent dishes always take up their position on the edge of the paddle itself, where the motion is so strong that their nets are often broken.

The first thing the larva does is to gather a number of particles of mud together and form them into a short strap or band passing across the middle of the body and fixed to the dish on each side. Using this band as a starting point the larva sets about building a simple straight tube closely applied to the dish and open at both ends; at first the band is merely broadened so as to cover more of the body, but soon it is shortened as well until length and breadth change places and a real tube is formed. It is interesting to watch the methodical way in which material is collected. Anchored, as it were, to the strap by its anal feet, it rapidly sweeps through an angle of about 60° , touching the surface here and there with its mouth as it passes; then firmly grasping a particle by means of the labral armature and the anterior appendages, it powerfully contracts its body, thus drawing the particle towards the centre of operations; but not only does the above mentioned particle move, but all those touched during the sweeping movement follow in its wake, having been united together by silk threads or mucus during the first action. In this way abundance of material is collected and the building of the case proceeds rapidly. When all the larger grains have been removed in the neighbourhood of one end of the growing tube, the larva turns round in its case and repeats the same action at the other end. After having removed all the larger objects it is curious to watch how carefully it gathers up every speck, using the epipharynx like a rake, until a perfectly clear space is left for some distance all round the primitive tube.

These labours often come to an untimely end ; a sudden swirl in the water and the insect, losing its foot-hold, is swept away and has to begin all over again in another place. It is not the habit of the larva to work with the whole body exposed, and this instinct would save a larva from a catastrophe of this kind, but here having no case to speak of it is compelled to act otherwise and take the risks.

So far this description will apply either to *C. pusio* or the stalk-cased larva (No. 1), but now differences begin to appear ; *C. pusio* has only to build its arms, but the stalk-cased larva has a more elaborate work to perform. This latter larva having built a straight tube about 3 mm. long on the surface of the dish, continues the tube at almost a right angle to its former direction so that it projects freely into the water ; this, the anterior end, is made more and more compact, while from the posterior end the larva now continually tears away particles to apply in front, and goes on in this way, robbing one end to add to the other, until the whole of the horizontal tube has been destroyed. Meanwhile by the transposition of these materials a stiff upright tube has been formed only attached to the dish at its base ; but now the larva has to alter its tactics for if it continued to remove material from the base the whole case would be dislodged and swept away. In order to avoid this the larva is very careful in taking away materials from behind, to leave a narrow strip uninjured on one side ; and as further particles are taken away all round, this strip gradually grows longer and longer until it appears as a stalk supporting the short case at its free end. In order to strengthen this stalk the larva turns round in its tube and, appearing at the posterior end, plasters it vigorously with its labrum, paying special attention to the point of attachment that all may be safe. When removing material to build on in front, the larva comes out of the anterior end and, bending over, stretches down outside the tube as far as it can reach, without breaking its habit of keeping three or four segments within, and tears off the most distant particle it can reach (see fig. 35) ; this distance will of course be less than the length of its body, so the case, although continually growing in front, never becomes as long as the insect and is in fact always

The Stalk.

much shorter, never reaching the head and first nine segments in length: the psychological reason for this will be made plain later on.

On the other hand the length of the stalk is very variable, depending simply upon the time that the larva chooses to continue robbing the bottom to add to the top; such wide differences in length as from 1 to 4 mm. may be met with. There now remains only the construction of the three arms; at first they are made at the expense of the lower end of the tube, but as soon as they are a millimeter or so in length, webs are stretched across, and soon a supply of building material is at hand to finish the work without having recourse any longer to the parsimonious habit I have just described. **Length of stalk.**

To build the arms the larva collects a mass of particles into a small lump and applies it to the rim of its case and continues placing nodule upon nodule to the free end until the arm is the required length. During the construction of the arms, as well of the case and stalk, after putting a nodule in position, the larva makes a number of rapid movements whereby the material is smoothed and plastered down, and saliva poured into the crevices between the particles. In strengthening an arm the larva will twist its head right round it describing thereby a complete circle, completing the forward and return movement with the greatest rapidity. In fact all its movements are performed in what appears to be a feverish state of excitement, in which the antennæ partake, with their perpetual interrogation by rapid vibratory movements of every object within reach, and it seems certain that these organs must be highly sensitive, in spite of the small size of the sensory bulbs they bear. Only when retired within its case, so that the head alone appears, does the larva become at all quiet; and in this position it is well protected from danger.

The arms as before mentioned are connected by webs so as to form a net to retain all passing objects, but even with a high power lens I have been unable to detect single threads, the net-work seems only to be made up of irregular bands of slime or mucus passing between the neighbouring arms, so probably it issues from the creature's mouth in this form. **The net.**

Net making.

To build its net the larva proceeds as follows: running up one of the arms for some distance, it swings across to the next arm carrying with it a thread of silk, then quickly back again, at the same time retreating somewhat into its case; this zigzag movement is repeated two or three times until the base of the arms is reached, when the whole process may be repeated over again, until a sufficient number of threads have been stretched across to make a rude net-work which, whatever its workmanship compared with that of a spider, is at any rate good enough for its purpose, and effectually stops all objects floating by. In the case of larva No. 1 this has only to be done twice, but in *C. pusio* from four to seven times according to the number of arms present.

Drawing in nets.

From time to time the larva pulls down the net between two arms, using the labrum and thoracic feet to collect the particles together into a compact mass, which may then be used for further building operations, or may be pressed into the mouth to be devoured.

Both these larvæ seem never to extend the full length of their bodies from their tubes, but always retain at least one of the segments bearing the bifurcating hairs, that is to say not less than the four posterior segments.

Advantages of the net.

That the net is useful to *C. pusio* and to larva No. 1 is obvious from what has been already said, but it is interesting to discover what are the advantages gained by these larvæ over the net-less species, of which there are at least three, all about the same size, inhabiting cases without arms and nets, and living together in the same situations. If these can procure all they require without a net to catch it, what can it benefit the net-builders to go to so much pains? Two reasons, I think, may be given. In the first place the food eaten by the net-builders must be of a much finer quality than that of the others, for the nets would catch all the light flocculent matter, mostly organic, which remains suspended in the water, while the other larvæ would have to feed on a much coarser pabulum containing much sand and grit. In the second place, the net-builders occupy a more superficial stratum of water containing fewer creatures; being thus elevated from the stones, and suspended freely from the moss, they would escape many

of the enemies, which their neighbours living in the mud and sand so frequently fall a prey to, such as for instance the carnivorous and ubiquitous *Tanytus* larva.

When the larva is full grown, and the thoracic segments are beginning to get swollen on account of the imaginal organs which are forming beneath the skin, it seems to find the end of the tube too narrow for the enlarged part of the body, so it starts again building on to the end of the tube, gradually widening the entrance as it proceeds. The enlarged part when completed is about 1.5 mm. long, and rather less in width. In one larva that I kept under observation the work took four days to accomplish. The ultimate object of the enlarged tube is to make room for the large thorax of the coming pupa.

Enlarging the tube.

The larva is now ready to pupate and starts building a cover or operculum to close in the free end of the tube. This is done by building inwards on to the edge of the case, the larva working round and round in an ever diminishing spiral. Earthy particles are collected from the arms, and the arms may themselves be utilized; sometimes however they are bitten off and at other times twisted round outside the case so as to form a rim surrounding the operculum. The operculum is gradually built in from the circumference towards the centre, the larva always stretching through the central open part for fresh material until the opening becomes too small for it to pass through, after which it finishes the process from within until only a very small hole is left, just large enough to allow the pupal respiratory cones to pass through. This operation takes about one day to finish.

Operculum.

In one case I removed the operculum as soon as it was finished; the larva immediately set about building a second, which it completed in the short space of six hours; this I again removed, but now the larva's energies were exhausted, and it made no further attempt to close the opening; by the next morning it had passed into the pupal stage.

In the ordinary course of events the larva remains quiescent for about twenty hours after completing the cover, before casting the larval skin. If after this time the case be opened, and the pupa extracted

the larval skin will be found still enveloping most of the abdominal segments, the head having slipped round to the ventral surface. But when the pupa finally leaves the case the skin is left behind.

THE PUPAL LIFE OF *C. PUSIO*.

The pupal stage in warm weather lasts four days, but towards winter it may become much longer. The activities of the pupa chiefly consist of continuous movements of the abdomen which no doubt aid in respiration. In larva No. 1 the movement causes a strong current to pass in at the posterior end of the case and out through the central opening of the operculum; but in *C. pusio* very little current can be detected and what there is seems to be in the opposite direction; the weakness of the current is due to the very small size of the central hole of the operculum. During the four days of the pupal stage considerable change takes place in the abdominal spines and hairs; at first quite transparent and very difficult to see, they gradually become stiffer and more chitinous. This fact may help to explain how it is that when development is complete the pupa is able to leave its case. If a one-day old pupa be partially extracted from its case by gently pressing the tube, it will when left alone withdraw again into its original concealed position by means of the undulatory movements of its abdomen. It seems probable that at that time the backwardly projecting spines are not sufficiently strong to grip the walls of the case. If the spines harden when the imago is ready to emerge, then during the movement of the abdomen the spines will grip the walls, and prevent any backward movement, while forward movements will be facilitated. This will cause the head and thorax to press against the operculum until it finally gives way, allowing the exit of the pupa into the stream. Thus the hardening of the spines may with some truth be said to compel the pupa to leave its case.

Emergence of the fly.

And now the pupa, lashing the water vigorously by means of its powerful tail-fin, swims to the surface, where the back of the thorax immediately bursts the surface-film, and the thorax itself splitting along the back allows the fly, when the right moment has arrived, to liberate

itself from the pupal skin. Then after a few unsuccessful attempts at aërial navigation (in one observed case three attempts) it flies away to join the insect world.

The rapidity of insect emergence has often been remarked upon and this species is no exception to the rule. I have, while watching a pupa with thorax exposed above the water, allowed my eyes to wander for a moment, only to find the perfect insect flown, and the hyaline pupal skin floating like a raft upon the water, the thorax spread out on the surface like a boat and the abdomen submerged like a rudder.

The rapidity of the last metamorphosis is in this case very important for the welfare of the insect, for the emerging fly is liable at any moment to be swamped by the rushing, tumbling stream, splashing in and out among the boulders, bearing on its surface the floating pupa skin.

The time taken to complete the early stages of this *Chironomus* probably varies very considerably with the temperature. On July the 19th, 1907, I placed some freshly hatched larvæ in one of my dishes of moving water, and on November 14th, 1907, some of the flies appeared. This gives 118 days—rather less than four months for the earlier stages; but if I had procured eggs in early June, I feel sure they would have completed their metamorphoses in half this time.

N. B.—THIENEMANN has recently divided *Chironomus pusio*, Meigen, into several species, but in the absence of specimens it has been impossible to determine which form MR. MUNDY studied. This does not, however, affect the value of his observations.—E.E.L.

PSYCHOLOGY.

**The function of
the bifurcators.**

The larva of *Chironomus pusio* has already been shown to possess a pair of bifurcating fringed hairs on segments 5 to 9. The problem now to be considered is what function do they normally perform in those larvæ which possess them; and are they functionally active in this species, or only persistent, though useless, organs like the vibrissæ on the striated flaps of larva No. 7.

I think I shall be able to show that in this larva, and also in the stalk-cased larva No. 1, they have a very important part to play in the economy of the insect.

From the position of the bifurcators it is obvious that they must be continually coming in contact with the sides of the tube as the larva moves about, but if the larva begins to come out of its case some of the bifurcators will no longer be touched, and by the time the larva has extended the first nine segments no hairs will be left within the tube at all. Supposing the stimulation of these hairs gave rise to a painful sensation, we should expect the larva to remain extended as far as possible from its case so that nothing might be in contact with the hairs; but if on the other hand the feeling-tone of the hairs was one of pleasure, then we should expect the larva to retain as many pairs of bifurcators as possible in contact with the tube so as to enjoy to the full the agreeable sensation set up by the stimulation of these hairs. The facts which I have seen seem to argue in favour of the latter supposition. When at rest all the segments bearing bifurcators are kept within the tube and the head alone appears outside, with perhaps one or two of the anterior segments bearing no bifurcators. When actively employed it comes far out of its tube, but only for a moment at a time, and even then never exposes all the segments bearing these sensory organs, the ninth segment at least remaining within, so that it may enjoy an occasional stimulus from at least the last pair of bifurcators. If it occasionally oversteps the mark the absence of a pleasant stimulus will immediately cause it to retreat until a pleasurable feeling-tone is once more started. In this way the bifurcators will act as a continual check upon the over-activity of the larva, and prevent it from advancing

beyond the region of safety; so that we may say, speaking generally, the further the larva comes out of its case the more uncomfortable it feels, and the more certainly it will quickly retire.

These actions, which I have ventured to interpret on psychological grounds, may be easily observed with a magnifying glass by watching the insects at their work. It is not well to rely upon general observations such as these which may easily have a too great significance put upon them, seeing how small the insect is, and how quickly all its actions are carried out. To prove that the bifurcating hairs are responsible for a series of actions so complicated and have such a high psychological significance, it is but natural that more tangible evidence should be demanded. Fortunately the arms which this insect builds enable the truth of these observations to be tested in a very definite way by measurement which cannot well be disputed.

In order to build the arms the larva must come out as far as the arms extend; hence the length of the arms is a sure indication of the amount of the body that is willingly extended outside the case. The actual measurements in four different instances are as follows:—

Proof by measurement.

	Measurements.				Average.
	mm.	mm.	mm.	mm.	mm.
Length of larva	4·6	4·2	4·5	4·1	4·35
Length of head and nine segments	3·7	2·6	3·8	3·1	3·3
Length of arm	2·9	2·4	2·5	2·5	2·57
Difference between length of head and nine segments and length of arm	·8	·2	1·3	·7	·7

These figures show that not only is the arm much shorter than the length of the animal but that it is also decidedly shorter than the head and first nine segments, the average difference being ·7 mm. In other words the larva can reach the extremity of its arms without exposing all the first nine segments, that is without the last pair of bifurcators losing contact with the case.

Here we have positive proof that the distinguishing habit of this larva can be performed without violating the principle of bifurcator control. Until some more simple explanation of the fact that the arms are thus definitely correlated to the length of the first nine segments can be brought forward, we may, I think, accept as true in those larvæ possessing functionally active bifurcators the following hypotheses:—(1) The bifurcating hairs are sensory organs. (2) The feeling-tone set up in the brain of the insect when they are stimulated is pleasurable. (3) In consequence of this feeling-tone the larva avoids doing anything that would put an end to this sensation, and so never exposes more than the first nine segments. In other words the bifurcators generate a new instinct.

Effects of bifurcator control.

The bifurcator instinct as we have seen controls the movements of the larva in and out of its case. It regulates the length of each arm of the net, and consequently the diameter of the net as a whole. This is a very important point, for if it was not for the bifurcator instinct the net might be 3 or 4 mms. wider than it actually is and so be able to bring to the larva a larger supply of food. But if the larva not having this instinct, came right out of its case as far as possible, and so built full length arms, its whole body would be exposed to the full force of the current; but by slightly restricting the size of the net comparative safety is ensured to the animal.

The remarks apply to both *Chironomus pusio* and the stalk-cased larva, but in the latter not only is the length of the arm controlled by the bifurcator instinct, but the length of the case is also affected in the same way. For this larva stretches out over the edge of its case and reaching backwards tears away material from the posterior end to add to the anterior end. The bifurcator instinct will not allow it to expose the last four segments, consequently it cannot reach very far down the outside of the case to begin its destructive and constructive work, so that the actual case existing at any moment cannot be longer than the head and the first eight segments, if we assume the ninth segment to occupy the bend and the last four to be within the tube.

The bifurcators are therefore responsible for (1) the stay-at-home habit, (2) the habit of never exposing the last four segments, (3) the length of the arms of the case, (4) the length of the case (in *Chironomus* No. 1).

If the above mentioned characteristics are the result of the presence of the bifurcators, then a larva similar in all other respects to the full-grown *C. pusio*, but lacking these organs, would be expected to manifest none of these characteristic habits. The nearest approach to this desired similarity is to be found in the newly-hatched larvæ of *C. pusio*, which have no bifurcating hairs until after their first moult.

Negative evidence.

These minute larvæ are very restless in their habits, continually leaving their tubes before they are completed, so that few remained long enough to complete a five-armed case, and whenever I examined the aquarium in which they were kept some were always to be seen swimming about freely in the water. Concerning one that made a well-finished case, I have made a note to the effect that the arms were about as long as the case and the case about as long as the body; hence in the absence of bifurcators these larvæ must venture to expose the whole length of their bodies during arm construction (I regret that I can give no measurements, but I have been unable to procure eggs or young larvæ since I have realized the importance of this point).

I must now say a few words about the other larvæ which bear bifurcating hairs. What has been said about *C. pusio* applies equally well to the Stalk-cased Larva No. 1. Larva 4 and Larva 6 I have not observed, while Larva 3 appears to act in the same way as *C. pusio*, but as it has no arms measurements cannot be taken. The Pipe-larva No. 5 possesses the hairs but they are much smaller in proportion to the large size of this species and very often much broken, so that I doubt if they are functionally active, at any rate in the full-sized larva. I have observed that at night they extend far out of their tubes exposing almost the whole body, often (I should say) overstepping the ninth segment. A small smooth and transparent prominence arises in the mid-dorsal region of the eleventh segment, and this and the two adjacent segments are very much flattened out. I conclude that this

**Bifurcator control
in other larvæ.**

“boss” has usurped the function of the bifurcators and checks the larva from going out too far. Similar but larger bosses are described by LAUTERBORN in two out of his three case-builders, and they may be the means by which these larvæ are retained in their cases. Lastly there is LAUTERBORN’s Larva 3, which makes a truncated case, in which it moves about. It resembles *C. pusio* closely in its anatomy and possesses bifurcating hairs. A function, such as I am arguing for the bifurcators, would be of considerable use to this larva in crawling about as it has no sensitive boss to check its movements. I have not found the species and DR. LAUTERBORN does not mention this point in his paper, so I cannot say whether or not the habits of this larva are favourable to the bifurcator control theory.

Many other animals besides the Chironomids make cases in which they dwell and in which they often crawl about, as, for instance, the Trichoptera. Many of these larvæ have fleshy prominences on the first abdominal segment and a fringe of black hairs running along each side of the body. It has been suggested that the prominences steady the larva during the undulatory movements kept up by the abdomen for respiratory purposes.* Possibly they also help the larva to hold on to the case when crawling about.

More important for us are the lateral fringes of hairs. These may on the principles already indicated be sensitive hairs with a pleasurable feeling-tone, and thus act in the same way as the bifurcators of *C. pusio*, and check the larva from passing too far out of its case. It is to be noted that they are much larger in young larvæ than in those that are full grown (I have noticed the same comparative difference in size between the bifurcators of the second and fourth instars of *C. pusio*). This is quite in accordance with psychological principles, for until the habit has been formed the stimulus must be strong, but after the habit has become deeply ingrained in the organisation, secondary associations have sprung up and the primary stimulus need not be so great, and is often entirely absent.

Prof. A. JAMES shows that the habit of walking originates in this way, for he writes†:—“Until the impulse to walk awakens by the natural ripening of the nerve centres and sensory nerve termini, it seems

* MIALl—Aquatic Insects, p. 247.

† Principles of Psychology, vol. II., p. 405.

to make no difference how often the child's feet may be placed in contact with the ground, the legs remain limp and do not respond to the sensation of contact in the soles by muscular contractions pressing downwards. No sooner however is the standing impulse born than the child stiffens his legs and presses downwards as soon as he feels the floor."

When the child has acquired the habit of walking, the feeling tone in the feet gradually diminishes until it becomes unconscious of it altogether. So also with the case-dwellers, when they have acquired the habit, the primary sensation becomes less important and consequently the sense organ may degenerate without loss of the corresponding action.

Some of the case-building Trichoptera have neither fleshy prominences nor sensitive fringes to generate a retiring habit; how then are we to account for the instinct in these species? I think it will be found generally that where it is impossible to explain on sensational grounds, mechanical reasons can be shown to exist to prevent the larva from escaping from its case. (If not, we must be content to leave it for a time among the pure instincts due to the innate mental constitution of the animal, or better still confess our ignorance and own that we do not know the cause.)

Many species of *Setodes* and Hydrophilidæ, of which two species are found in the Yealm among the Chironomids, have no sensitive fringes, but these larvæ make cases of hardened silk with very narrow necks so that the head and thorax can just pass out, but the abdomen, which in these species is very large and fleshy, is quite unable to pass through so small an opening however much the larva might desire it.

Many of the Polychæte worms inhabit beautifully constructed tubes, and some even make movable cases after the manner of the Trichoptera. I shall therefore give two examples, one to illustrate the psychological and the other the mechanical means by which the animal may be kept from extending too far from its case.

Hyalinoecia tubicola builds a nearly transparent horn-like case 8 cm. long by 5 mm. wide, quite open at both ends, tapering and somewhat curved. The worm carries on each segment a pair of parapodia; each

**The retiring habit
in the Polychæta.**

**Psychological
control.**

parapodium bears a motor organ (the bunch of setæ) and a number of sensory organs (the soft filamentous cirri). No definite function has, I believe, hitherto been assigned to these organs; possibly they generate the retiring habit, just as the bifurcators do in *C. pusio*. *Amphicora sabella* would be another good example.

Mechanical control.

The Ammocharidæ are a family of the Polychæta which build flexible sand-covered tubes lined with a transparent gelatinous substance and are capable of burrowing slowly through the sandy sea-bottom. The habits of *Ammochares filiformis* have been described minutely by WATSON.* The thoracic segments, and the abdominal, except the last three, bear each a pair of bundles of setæ; in the abdominal region each bunch is followed by a torus bearing a large number of minute uncini. We might be led to think that either the setæ or the uncini acted as the controlling organs of this animal, but this cannot be, for WATSON has shown that the function of the bunches of setæ is to spread the cement from the thread glands when the animal is building the internal gelatinous sheath, and that the function of the uncini is to grasp the tube when the animal is boring through the sand. As there are no other external organs that can have a psychological function, there must be a mechanical means for retaining the larva within its tube. This is accomplished by the transparent conical tip of the elastic sheath, which has a small pore at the end, through which the branchial tentacles can be passed and spread out, so that the conical tip slips to the base of the tentacles and forms a close fitting sphincter, which acts as a mechanical means of preventing further egress of the tenant from its case.

Psychological functions of the other sensory organs.

Anal setæ.

If the bifurcators of *C. pusio* have such an important function to perform, it is possible that the less remarkable hairs and setæ may contribute something towards building up the character of the larva. The anal setæ are found in all Chironomus larvæ and are evidently a characteristic of great antiquity. They are generally supposed to be tactile organs to warn the larva of danger from the rear. In this larva I doubt whether they are of any use whatever, in fact the larvæ in turning round in their tubes must find them a considerable inconvenience; while from the rear no danger is to be expected. They

* Structure and Habits of the Polychæta, Linn. Soc. Journal Zool., vol. XXVIII., pp. 230-260.

are, I think, persistent organs whose higher psychical function has been lost, like that of the labial vibrissæ, though they probably have a warning function in a few species.

The apparently insignificant hairs on the head and first two segments have really far more claim on our attention than the anal setæ. STANLEY* in his work on the Emotions, postulates undifferentiated pain as the primitive and simplest form of consciousness, and I think that we may take it as a general rule that sensory hairs, which do not suggest by their position and structure any highly differentiated sense, have this function, and not—as is generally assumed by physiologists—the neutral sense of tact or touch.

Thoracic hairs.

If the feeling tone produced by stimulation of these hairs was painful it would generate the following habit. When any object touched the head or anterior segments the larva would shrink away and retire down its tube; but when safe within its tube it would be liable to knock the hairs against the sides and consequently as soon as the danger was over it would come out a little way again. Thus would gradually be evolved the habit of resting with at least the head exposed. This is to some extent the case with *C. pusio* and more so with the stalk-cased larva, which has indeed scarcely room for its whole body within its tube as this is very short. It is to be noticed that the hairs of this larva are larger and more numerous than those of *C. pusio*.

We shall find more convincing evidence among larvæ such as *Culex* (Gnat), *Anopheles* (Mosquito) and *Corethra*. In these larvæ we find large single or multiple hairs projecting from all parts of the body and in many instances nerve connections can be traced, and the habit that we find common to these and other like aquatic insects is that they all avoid contact with solid objects. This avoidance of objects leads to the habit of living in the open water rather than among weeds. Simple tactual sense scarcely seems likely to cause this habit, while a disagreeable feeling-tone, a kind of undifferentiated pain, might produce it. On the other hand *Ceratopogon*, *Tanytus* and many of the smaller Chironomus-larvæ, or "Motitators" as MEINERT called them, whose bodies are quite free from long hairs, are found creeping and swimming about among water-plants.

* Evolutionary Psychology of the Emotions, ch. II.

Granting that many habits may arise from external causes, let us be careful how we speak of them in relation to the insect producing them. We are often in the habit of speaking of such and such an *organ as being wonderfully adapted to the habits* of the insect possessing it; but do not these considerations rather suggest that it would be more correct to say that *the habit was wonderfully adapted to the organ?* Instead of saying that a certain organ *enables* an insect to perform a certain action, would it not be more accurate to use such words as *compels, constrains, or urges?* Let me give a few examples to make my meaning clear. The bifurcators of *C. pusio* compel it to remain within its case; the anal feet force it to grasp the wall of its dwelling, and the pain-hairs compel it to shrink when touched: the stiffening spines urge the pupa forward until the operculum is burst off the pupal-case: the particular articulation of the limbs of the Cockroach and other Blattidæ constrain them to live in cracks and crevices: the palmate hairs on the abdomen compel Anopheles to maintain a fixed position during respiration. The function of the palmate hairs has only lately been pointed out by NUTTALL AND SHIPLEY, who write "The whole [bundle of hairs] forms a most delicate little cup, and it is by means of these five pairs of palmate hairs, which cling to the surface film, that the larva maintains its position close under the surface of the water."

To speak of optic, auditory or olfactory stimuli compelling an insect to act in a certain way is no new thing. We are accustomed to speak of a bright light drawing, attracting or fascinating a moth, or an odour alluring one sex to the other; so that to claim that cutaneous sensations should govern an insect's actions is really only an extension of a well-known principle. This principle, with its enlarged meaning, is that the insect is driven to its actions by direct sensations arising from the stimulus of all sensory nerve terminations whether they belong to the special or the general senses, or by tendencies that are themselves the product of direct sensations.

It will be advisable to state shortly the three ways in which we can account for insect actions. First we have those actions which are the result of innate tendencies, born in the animal, and resulting from

the constitution of the central nervous system. The great majority of insect actions can only be accounted for in this way, and once all these actions were thus explained under the term instinctive.

Secondly, we have those actions which are the result of sensational principles, either the product of direct stimulus or of habits generated from direct stimulus.

On account of these latter principles and possibly others yet to be discovered the mass of insect actions that can be truly called instinctive, that is originating entirely within the brain, is ever decreasing and may one day cease to exist.

The third way in which insect actions can often be explained is by reference to mechanical laws. Many attempts to give mechanical explanations of biological phenomena have been made from time to time; as the contact-pressure theory of SCHWENDENER to explain the arrangement and origin of the lateral members of a plant shoot; the mechanical embryology of HIS & ROUX; and in particular the explanation of the segmentation of the ovum by HAECKEL, in which the various forms are shown to result mechanically from the larger or smaller quantity of yelk within the ovum. In the insect world perhaps the most interesting example of the application of mechanical principles is the explanation of the formation of hexagonal cells by the Bee. It has been shown that not only is this form best under the given conditions but that mechanical necessity compels the bees to construct six-sided cells, no other alternative being possible.

APPENDIX.

List of larvæ and pupæ mentioned in the text.

I.—INSECTS WHICH, IN THE LARVAL STAGE, HAVE BIFURCATING HAIRS
ON SEGMENTS 5-9, *i.e.*, THE "PUSIO" GROUP.

CHIRONOMUS PUSIO, THE TYPE.

LARVA : length=4 mm. ; antennæ long, with minute bulbs ; tracheæ in segments 1 and 2 and 10-12 ; fat-sacs in segment 10.

LARVAL DWELLING ; 5- to 7-armed mud tube.

PUPA : length 3 mm. ; respiratory cones usually projecting forward, converging, spinous ; large tail fin.

PUPAL DWELLING : mud tube, circular operculum of mud with central pore.

HABITAT : moorland streams.

CHIRONOMUS 1 (stalk-cased larva, LAUTERBORN'S FIG. 14).

LARVA : differs from the type in being slightly smaller and more hairy.

LARVAL HABITAT : a 3-armed stalked case of mud.

PUPA : respiratory cones bent at right angles (elbowed).

PUPAL DWELLING : stalked case covered in by transparent operculum with large central pore.

HABITAT : moorland streams and brooks.

CHIRONOMUS 2 (LAUTERBORN'S Larva 3).

LARVA : antennæ arising from projecting bosses.

LARVAL DWELLING : a reed-like case, smaller behind, truncated at both ends, covered with rhizopod scales, length 3-5 mm.

CHIRONOMUS 3.

LARVA : antennæ longer than in type ; hairs on first four segments.

LARVAL DWELLING : similar to type but without arms.

HABITAT : similar to type.

CHIRONOMUS 4.

LARVA : antennæ very large, closed bow-nets ; head partly retractile ; anal hairs as long as the anal setæ.

LARVAL DWELLING : indefinitely long, winding, mud tube.

HABITAT : clear ponds.

CHIRONOMUS 5 [LAUTERBORN'S fig. 10 and fig. 13(?)].

LARVA: length 2 cm.; red blood; antennæ very long with open bow-nets on long arms; dorsal hump on segment 11; last three segments flattened; head partly retractile.

LARVAL DWELLING: perpendicular mud tubes, 10 cm. long.

PUPA: 1 cm. long, dark brown; respiratory cones covered with long transparent hairs.

PUPAL DWELLING: same as larva.

HABITAT: marshes and slow streams.

CHIRONOMUS 6.

LARVA: length 2 cm., red blood; antennæ very long, spear-shaped.

LARVAL DWELLING: tough mud case 5 cm. long.

II.—LARVÆ WITH BRISTLES ON THE STRIATED FLAP.

CHIRONOMUS 7.

LARVA: length 2 cm.; colour dirty white; head chitinous; about 23 bristles on the striated flap; tracheæ from head to anal gills.

LARVAL DWELLING: loose earthy tube among mud and sticks.

PUPA: length 1.1 cm.; respiratory cones broad, blunt-pointed, spinous; last segment very small; anal swimming plates united; large tail fin.

HABITAT: ponds and streams, on sticks or in mud.

CHIRONOMUS 8.

LARVA: length 1 cm. (?); a few bristles on the exterior part of the striated flap; tracheæ from head to last segment imbedded in pink tissue; claws of anal feet completely retractile; anal sense organ three setæ.

HABITAT: peaty bogs and pools.

III.—OTHER LARVÆ.

CHIRONOMUS 9.

LARVA: length 2 cm.: red blood: long coiled ventral blood gills on segment 11; small backwardly projecting gills on segment 10; tracheæ on segments 1 and 2,

LARVAL DWELLING: oval mud case in muddy streams.

C. NIVEIPENNIS.

LARVA: red blood; no ventral blood gills.

LARVAL DWELLING: mud tube.

PUPA: tracheal gills with only a few secondary branches; tail-fin 30-40 long setæ; second abdominal segment with paired postero-lateral transparent appendages; pair of long setæ on conical prominence on vertex of head.

C. ORTHOCLADIUS (LYONET AND MIALL).

LARVA : length 10-12 mm. ; pale green ; anal sense organs, 6 setæ ; well developed tracheæ ; epithelium with purple colouration.

LARVAL DWELLING : a free jelly-like case among filaments of Spirogyra, on which it feeds.

PUPA : respiratory cones tapering and spinous ; second abdominal segment with dorsal spinous prominence ; tail plates with 100 minute setæ to each.

HABITAT : ditches and streams.

C. MINUTUS.

LARVA : length 7 mm., pale green ; prothoracic claws toothed ; well developed tracheæ.

LARVAL DWELLING : irregular gelatinous tube fixed to a stone, covered with particles.

PUPA : respiratory trumpets minute ; no tail fin.

PUPAL DWELLING : structureless transparent gelatinous case with spout-like aperture at each end.

HABITAT : streams.

LAUTERBORN'S CHIRONOMUS 1.

LARVA : length 3-4 mm. ; reddish yellow ; prominent dorsal boss on segment 11 ; from segment 10 lateral pipe-like processes, hooked.

LARVAL DWELLING : like a spectacle case, compressed, opening by a slit at each end, brown, opaque, free, resembling *Agraylia pallidula* (Trichoptera).

HABITAT : meadow bogs and alder marshes.

LAUTERBORN'S CHIRONOMUS 2 (REAUMUR).

LARVA : length 4-5 mm. ; triangular boss on segment 11 dorsal ; a pair of very long pipe-like ventral blood-gills on segment 10 (none on segment 11).

LARVAL DWELLING : a spindle-shaped free case, translucent.

HABITAT : meadow bogs and alder marshes.

CHIRONOMUS 10.

LARVA : length 7 mm., green becoming yellow before pupating ; eight branched hairs postero-laterally on segments 4-11 ; small 13th segment ; tracheæ complete, fine ; anal tracheal gills.

LARVAL DWELLING : fixed case composed of green leaves of *Callitriche verna* (Starwort).

PUPA : small respiratory cones ; no tail-fin ; spinous projections on abdominal segments 2-5.

PUPAL DWELLING : silken cocoon within larval case.

HABITAT : ponds.

CHIRONOMUS 11.

LARVA : length 8 mm. ; pale green ; well developed 13th segment, with two pairs of small bristles ; anal gills partly retractile ; fat-sacs present in segment 9 ; aorta valved and contractile ; anal sense organs each five setæ ; anal claws completely retractile ; tracheæ complete.

LARVAL DWELLING : transparent silk tube, frequently renewed.

PUPA : length 6 mm.; small spinous respiratory cones; large tail-fin; anterior and posterior spinous bosses on abdominal segments 3-6, and anterior one also on segment 2.

PUPAL DWELLING : double walled transparent silk cocoon open at both ends.

HABITAT : ponds.

CHIRONOMUS 12.

LARVA : length 5 mm.; brown; small 13th segment; very large brown or transparent fat-sacs in segment 9; anal gills constricted and tracheal; tracheæ complete; aorta contractile and valved.

LARVAL DWELLING : free.

PUPA : dark brown; large thorax; small respiratory cones; no tail-fin.

PUPAL DWELLING : brown mud shell covering pupa, and attached to smooth wet stone.

HABITAT : smooth stones receiving spray from waterfalls.

CHIRONOMUS 13.

LARVA : length 8 mm.; nearly transparent; single pair of lunate eyes; antennæ moderately developed; ventral surface of epicranial plate deeply chitinous; no posterior sclerite on labrum; complete tracheæ; anal gills constricted; anal sense organs six chitinous setæ from chitinous prominence, and below them pair of simple hairs.

LARVAL DWELLING : free.

HABITAT : swift clear brooks.

CHIRONOMUS 14.

LARVA : length 10 mm.; colour brown; single pair of cornet-shaped eyes; anal tracheal gills; tracheæ complete; anal gills partly retractile.

LARVAL DWELLING : long winding mud tube of loose texture.

HABITAT : rivers.

CHIRONOMUS 15.

LARVA : length 10 mm.; head as wide as body; dark red; antennæ moderately developed; basal sclerite of labrum represented by two separate chitinous spots; anal claws few, large, red; ventral surface of epicranial plates deeply chitinous; tracheæ from head to anal gills; eyes partly fused; long hairs at base of anal sensitive organs.

LARVAL DWELLING : case fixed on one side, of wood, earth, etc.

PUPA : respiratory cones small, tapering, spinous; anal swimming plates fringed with short hairs, posterior two enlarged into strong hooks; abdominal segments with transverse bands of spines dorsal and ventral.

PUPAL DWELLING : the larval case, attached to it only by anal hooks.

HABITAT : streams and ditches.

CHIRONOMUS 16.

LARVA : length 3 mm. ; green ; segments 1, 2 and 3 swollen ; head pointed ; pointed submentum bearing twisted hairs ; tracheæ complete ; tracheal gills double usual length, constricted in the middle ; sides of the body fringed with many single and tufted hairs, all short.

LARVAL DWELLING : free.

HABITAT : rivers and streams.

CHIRONOMUS 17.

LARVA : length 8 mm. ; pale green ; head short, as wide as body ; very small brain within the head ; tracheæ complete ; tracheal gills ; single long hair from segments 5-10 laterally ; anal setæ 6.

LARVAL DWELLING : mass of confervæ moored to stone.

HABITAT : clear running brooks and rivers.

CHIRONOMUS 18.

LARVA : length 10 mm. ; quite transparent ; long antennæ with large transparent bulbs, one on each side of antenna, unsymmetrically placed ; fat-sacs small but easily seen in segment 10 ; body hairless.

LARVAL DWELLING : mud tube, winding, with transparent silk web over it and extending beyond it.

HABITAT : in bed of rivers and streams.

CHIRONOMUS 19.

LARVA : 8 mm. ; brown ; complete stout tracheæ.

LARVAL DWELLING : tube 1-2 cm. long, attached most of its length to stem of moss, composed of transversely placed fibres and sticks, after the manner of the case of *Limnophilus rhombicus* (Trichoptera).

P.S.—All these larvæ possess the usual two pairs of anal gills. The tracheæ of all larvæ possessing them are closed, there are no open spiracles, but initial threads may often be seen.

EXPLANATION OF PLATES.

(N.B.—The figures are of *Chironomus pusio*, Meigen, except where otherwise stated).

PLATE I.

Fig. 1.—Egg-mass on leaf natural size and magnified.

Fig. 2.—Egg just before hatching.

Fig. 3.—Larva just hatched. *a* brain, *b* fatty tissue.

Fig. 4.—Full grown larva. *a* prothoracic appendage, *b* anterior tracheæ, *c* salivary gland, *d* chitinous hair, *e* bifurcating hair, *f* œsophagus, *g* cardiac chamber, *h* stomach, *i* longitudinal section of stomach, *j* peritrophic membrane, *k* malpighian tubule, *l* small intestine, *m* colon, *n* anus, *o* posterior tracheæ, *p* anal foot, *q* tracheal gill.

Fig. 5.—Nervous system and fat-sacs as they appear in a medium sized larva. *a* fat-sac, *b* strand of tissue connecting to the anterior end of segment 5, *c* point of origin of strand, *d* brain, *e* subœsophageal ganglion beneath it, *f* connectives, *g* nerve, *h* abdominal ganglion.

PLATE II.

Fig. 6.—Dorsal view of head and first segment of full-grown larva. *a* lip, *b* short toothed feeler, *c* long toothed feeler, *d* tentacles, *e* broad-based prominence, *f* chitinous spines, *g* anterior sclerite, *h* triple chitinous hair, *i* last three segments of antenna, *j* sensory bulb, *k* double transparent hair, *l* mandibular tentacle, *m* mandible, *n* arborescent hair, *o* boss, *p* posterior sclerite, *q* eyes, *r* epicranium, *s* clypeus, *t* tracheæ, *u* tracheal capillaries ramifying on the dorsal surface of the first segment, *v* chitinous hair, *w* chitinous ring, *x* dorsal surface of the labrum, *y* lateral inlet,

PLATE III.

Fig. 7.—Ventral view of the head of fully-grown larva. *a* bulb, *b* anterior comb, *c* papillæ, *d* posterior comb, *e* epipharynx, *f* ventral portion of the anterior sclerite, *g* grappling hooks, *h* v-shaped rod, *i* generalized appendage, *j* maxilla, *k* chelate claw of maxilla, *l* submentum, *m* striated flap, *n* mentum, *o* epicranial plate, *p* salivary duct, *q* trachea, *r* recurrent trachea to the brain.

Fig. 8.—Dorsal view of the last segments of *C. pusio*.

Fig. 9.—Dorsal view of hind segments of larva No. 11 showing the 13th segment, and the arrangement of some of the muscles.

PLATE IV.

Fig. 10.—Last four segments of mature larva. *a* pericardial cell, *b* strand of fatty tissue, *c* aorta, *d* bifurcator, *e* fat-sac, *f* anterior chamber of heart, *g* longitudinal trachea, *h* alary muscles, *i* posterior chamber of heart, *j* posterior valve of heart, *k* rudimentary sexual organ, *l* prominence bearing anal setæ (setæ not drawn), *m* anal bristle, *n* tracheal gill.

PLATE V.

Fig. 11.—Antenna: segments numbered. *a* bulb.

Fig. 12.—Side view of bulb.

Fig. 13.—End view of bulb.

Fig. 14.—Antenna of larva No. 18. *a* bulb.

Fig. 15.—Antenna of larva No. 4. *a* bow-net.

Fig. 16.—Mentum.

Fig. 17.—Striated flap.

Fig. 18.—Ventral view of one epicranial plate of larva No. 7. *a* striated flap, *b* vibrissæ, *c* anterior bay, *d* posterior bay.

Fig. 19.—Hind segments of larva No. 9. *a* ventral blood-gill on segment 10, *b* anal seta.

PLATE VI.

Fig. 20.—Longitudinal sections of *a* cardiac chamber, *b* œsophageal valve, *c* peritrophic membrane and *d* œsophagus.

Fig. 21.—Fat-sac.

Fig. 22.—Fat-sac of larva No. 18.

Fig. 23.—One half of fat-sac of larva No. 12. *a* fat drop, *b* inner transparent membrane, *c* outer pigmented membrane.

Fig. 24.—Pupa, No. 15, anal plates with hooks.

Fig. 25.—Ventral view of last segment of male pupa showing imaginal genital armature (anal fringe omitted).

Fig. 26.—Pupa No. 1, respiratory cone.

Fig. 27.—Pupa No. 5, respiratory cone.

PLATE VII.

Fig. 28.—Female pupa, dorsal surface.

Fig. 29.—Female pupa, ventral surface. *a* respiratory cone, *b* enlarged second segment of antenna, *c* eye, *d* labial palp, *d'* labrum, *e* antenna, *f* rostrum, *g* 1st leg, *h* 2nd leg, *i* 3rd leg, *j* wing, *k* 3rd abdominal segment, *l* lateral swimming plate, *m* seta, *n* backward projecting hairs, *o* longitudinal area of minute spines, *p* transparent oval body seen through cuticle, *q* chitinous portion of lateral plate, *r* anal swimming plate, *s* anal fin, *t* genital armature seen through pupal sheath.

Fig. 30.—Male pupa in pupal case. *u* vertex, *v* halter, *w* spur of wing, *x* anterior spines, *y* central spines, *d* process of sheath of labrum, * operculum.

PLATE VIII.

Fig. 31.—Larval case, mature, with an immature case attached.

Fig. 32.—Same case as Fig. 31, enlarged for pupa. *a* operculum, *b* respiratory cones of pupa.

Fig. 33.—Pupal case, another form.

Fig. 34.—Operculum.

Fig. 35.—Larval case of *Chironomus* No. 1 (Stalk-cased larva). *c* arm, *d* case, *e* pedicel, *f* net, *g* larva removing material from posterior end of case.

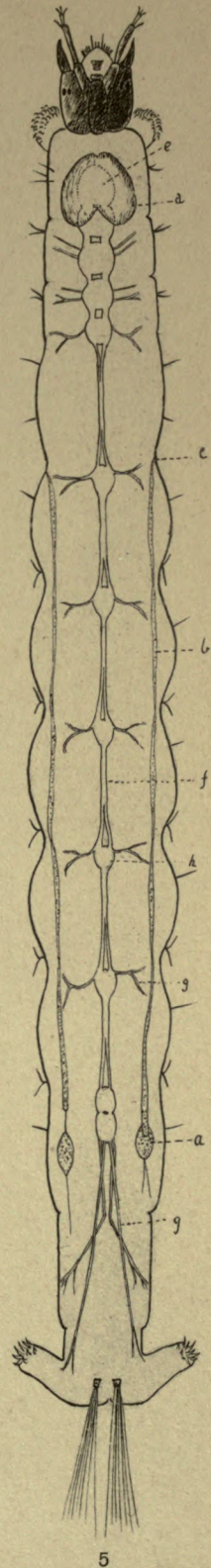
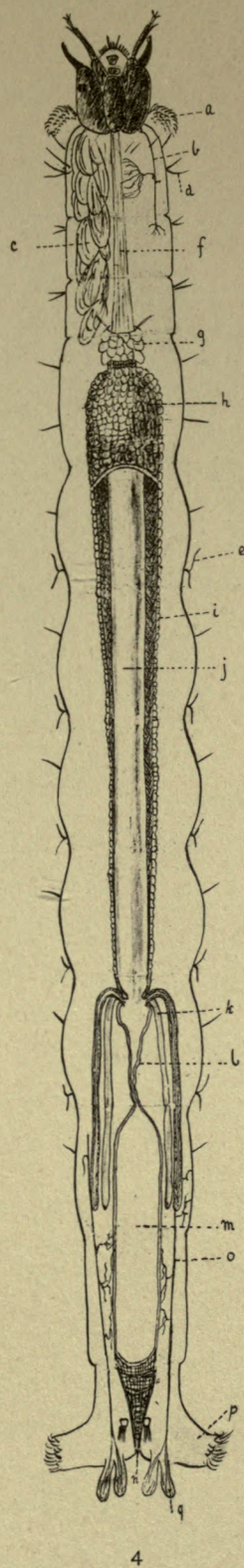
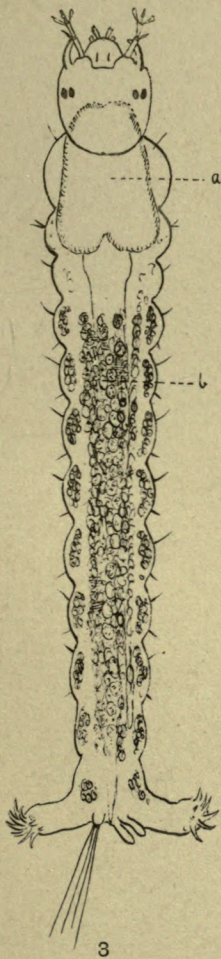
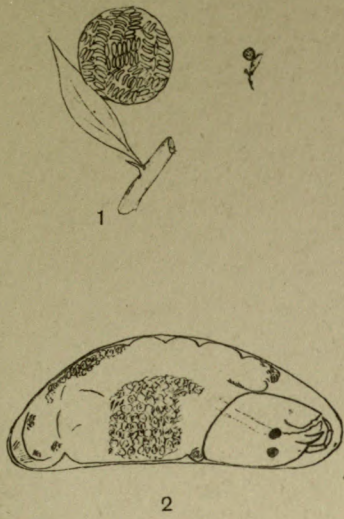
Fig. 36.—Pupal case of *Chironomus* No. 1. *a* operculum; *b* respiratory cone of pupa.

Fig. 37.—*Chironomus* No. 1. Operculum.

Fig. 38.—Group of cases in various stages of *Chironomus pusio* and *Chironomus* No. 1.

Fig. 39.—Six stages in the process of building a stalked case. *a* the start, *b* after twenty minutes, *c* 40 min., *d* 1 hr. 20 min., *e* 2 hrs. 20 min., *f* 4 hrs. 40 min.

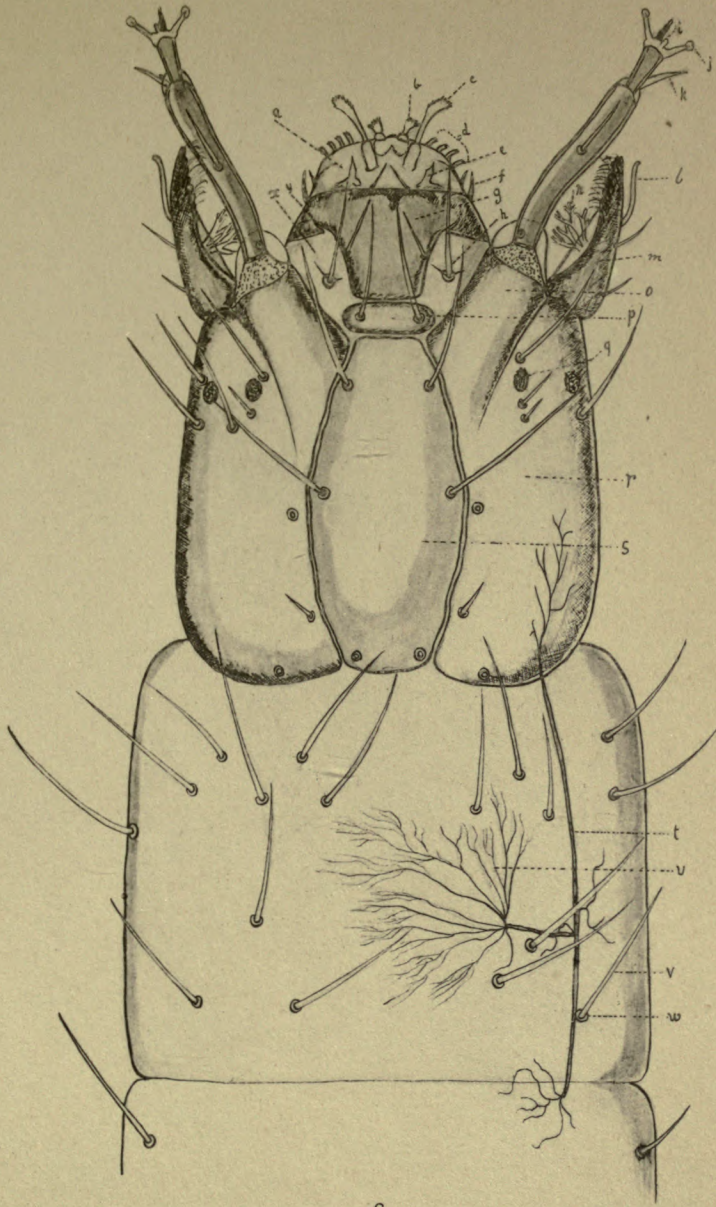
Fig. 40.—Mechanical arrangement used to keep the insects alive. *a* revolving glass paddle, *b* wooden support, *c* clock-work mechanism, *d* dish.



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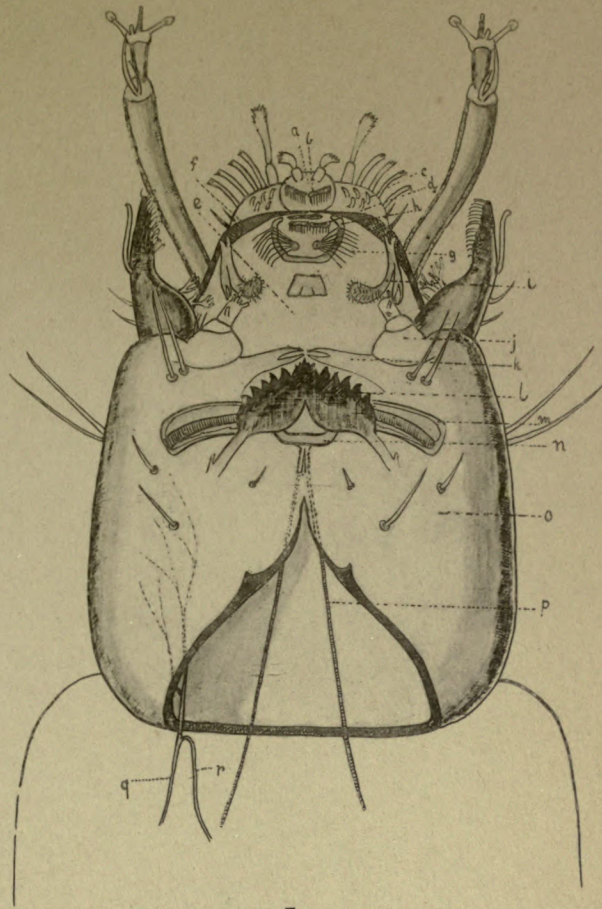


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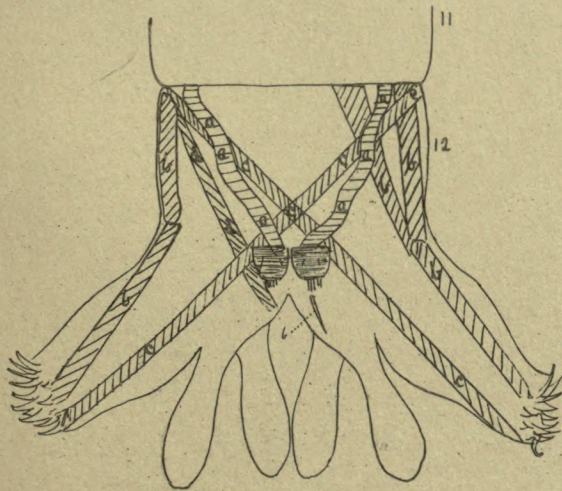
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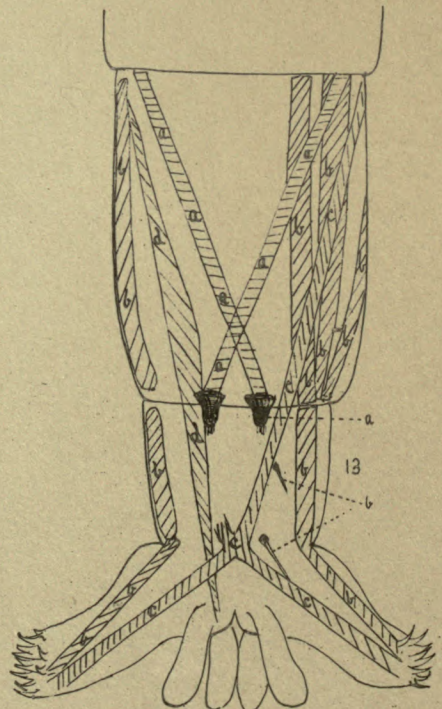
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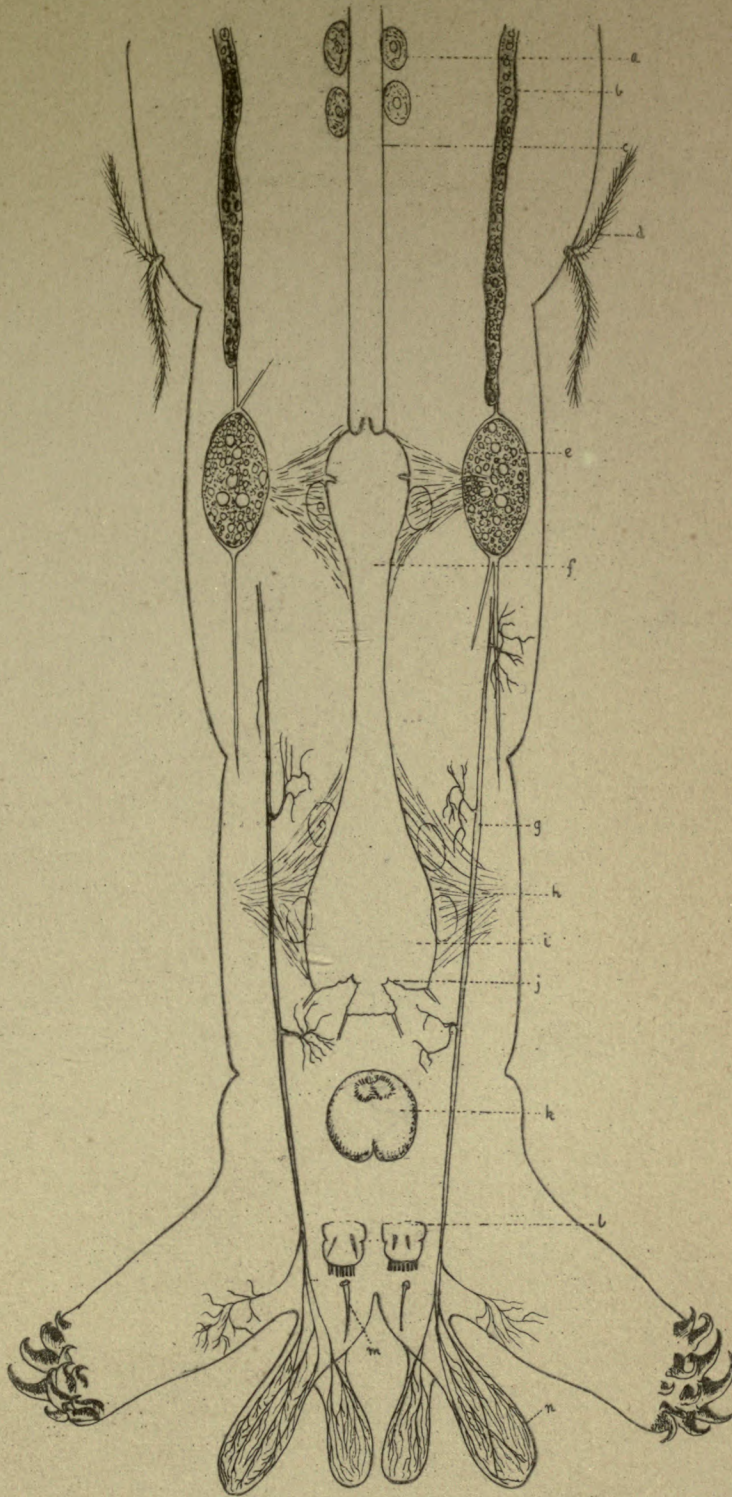


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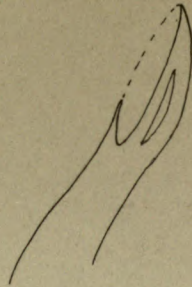


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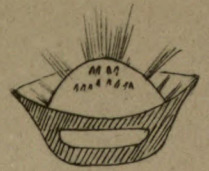
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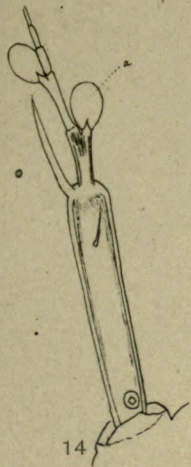
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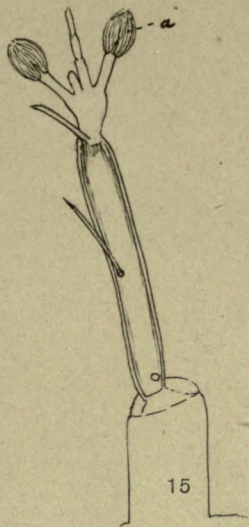
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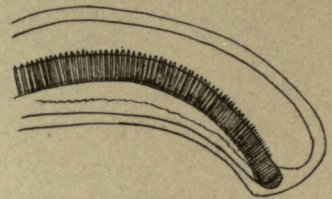
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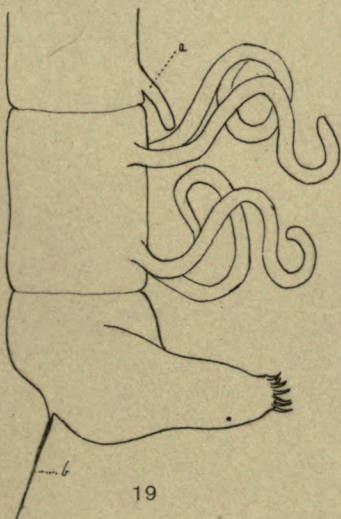
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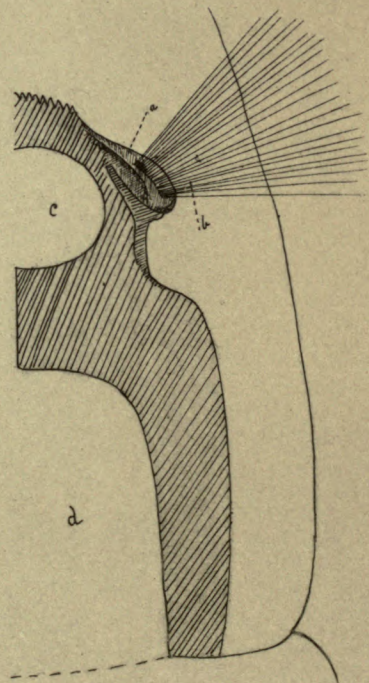
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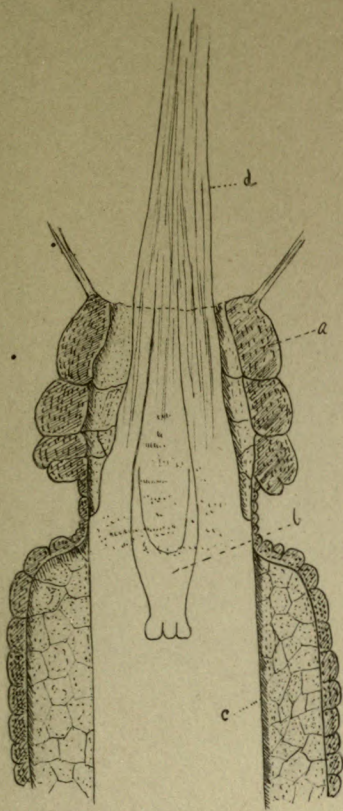
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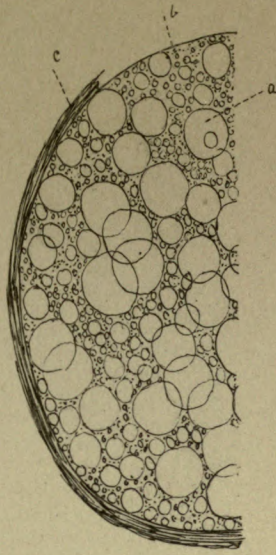
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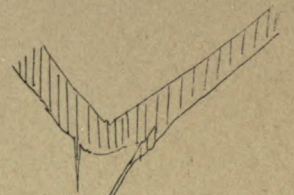
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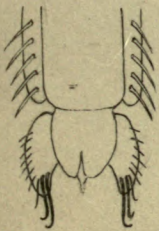
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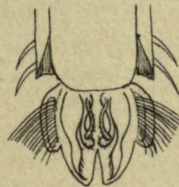
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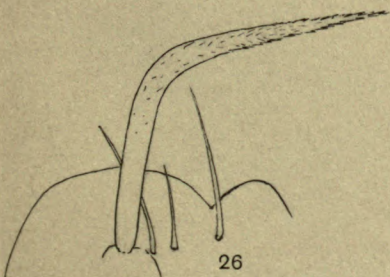
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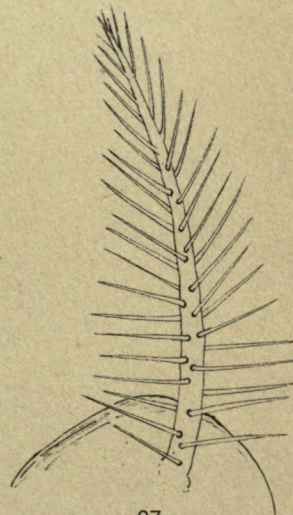
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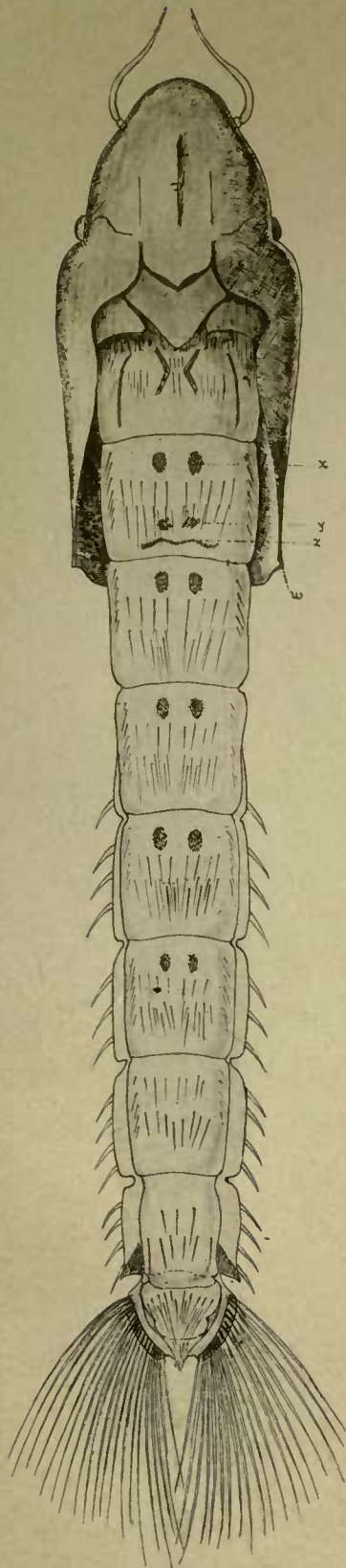
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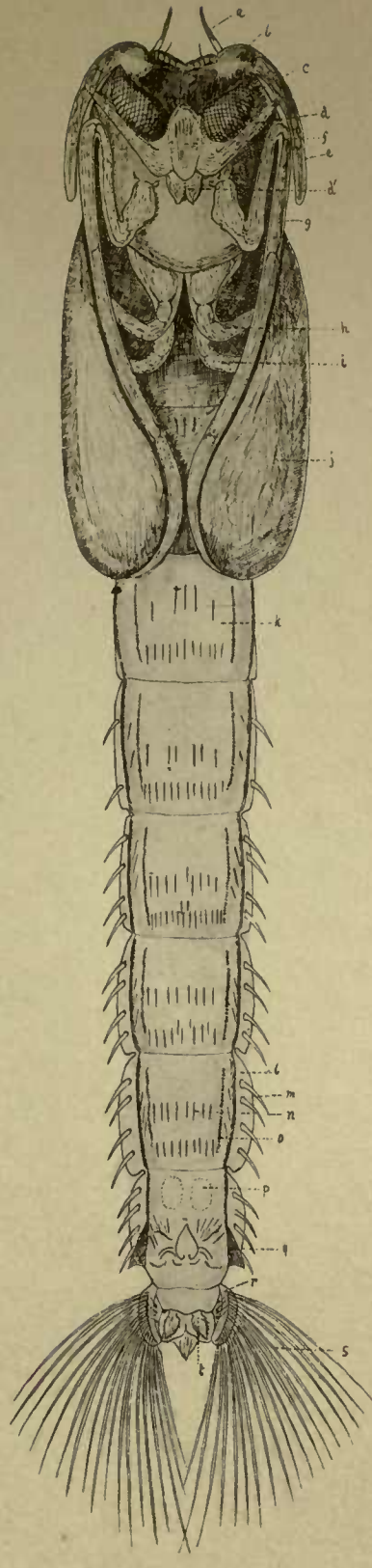
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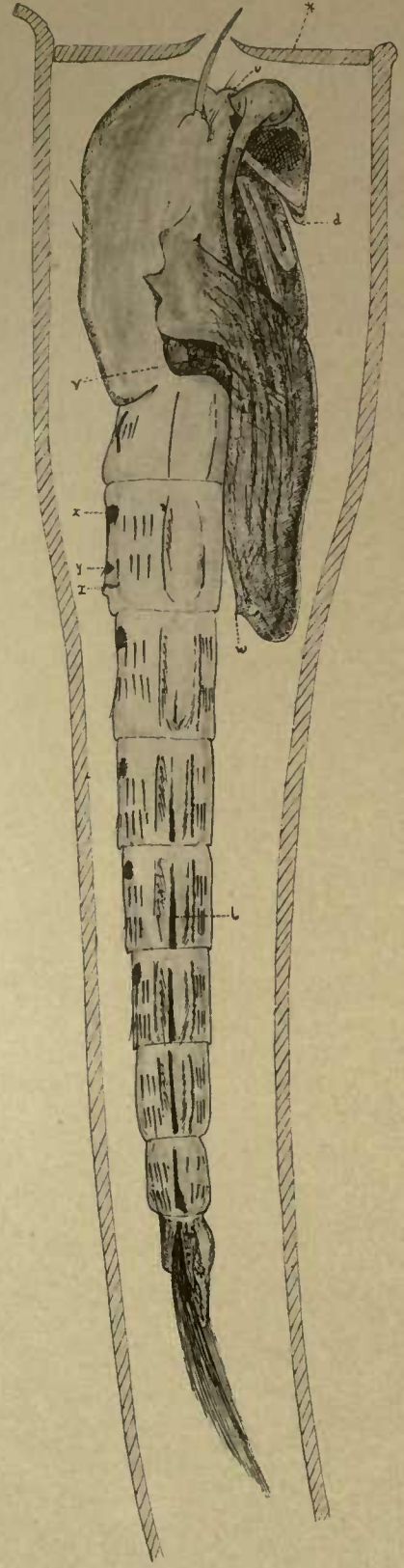
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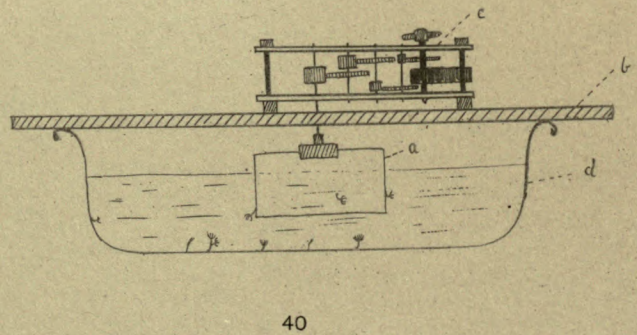
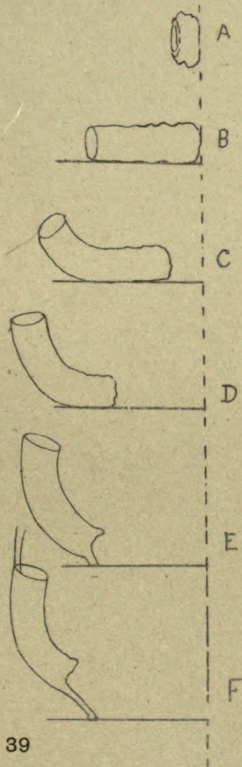
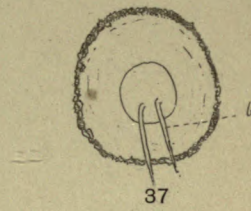
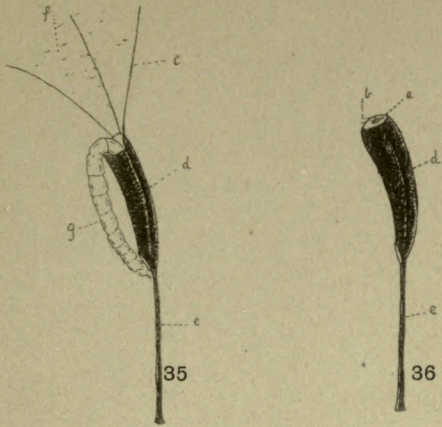
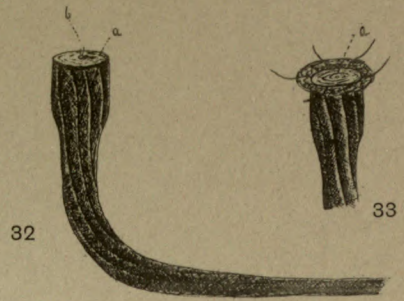
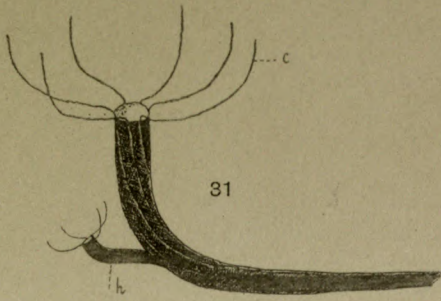


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